

## ABSTRACT

Title of Dissertation: PATTERNS IN DIVERSITY AND DISTRIBUTION OF  
BENTHIC MOLLUSCS ALONG A DEPTH GRADIENT IN THE  
BAHAMAS

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Species richness and abundance of benthic bivalve and gastropod molluscs was determined over a depth gradient of 5 - 244 m at Lee Stocking Island, Bahamas by deploying replicate benthic collectors at five sites at 5 m, 14 m, 46 m, 153 m, and 244 m for six months beginning in December 1993. A total of 773 individual molluscs comprising at least 72 taxa were retrieved from the collectors. Analysis of the molluscan fauna that colonized the collectors showed overwhelmingly higher abundance and diversity at the 5 m, 14 m, and 46 m sites as compared to the deeper sites at 153 m and 244 m. Irradiance, temperature, and habitat heterogeneity all declined with depth, coincident with declines in the abundance and diversity of the molluscs. Herbivorous modes of feeding predominated (52%) and carnivorous modes of feeding were common (44%) over the range of depths studied at Lee Stocking Island, but mode of feeding did not change significantly over depth. One bivalve and one gastropod species showed a

significant decline in body size with increasing depth. Analysis of data for 960 species of gastropod molluscs from the Western Atlantic Gastropod Database of the Academy of Natural Sciences (ANS) that have ranges including the Bahamas showed a positive correlation between body size of species of gastropods and their geographic ranges. There was also a positive correlation between depth range and the size of the geographic range. Nearly 80% of the species of gastropods in the ANS data set are less than 30 mm in body size, indicating that most gastropods in the Bahamas are small. A relatively high number of species of gastropods in the ANS data set that occur in the Bahamas had geographic ranges that extended into the Eastern Pacific (37%) and into the Brazilian (50%) provinces, though ranges of species tended to show highest densities centered in and near the Caribbean province. One of the more obvious faunal boundaries for the gastropods in the ANS data set was their northernmost limit, around Cape Hatteras, where colder northern water masses converge with the warmer waters of the Gulf Stream.

PATTERNS IN DIVERSITY AND DISTRIBUTION OF BENTHIC MOLLUSCS  
ALONG A DEPTH GRADIENT IN THE BAHAMAS

by

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This effort is dedicated to my daughters

Karin, Jackie, and Annie

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## CHAPTER 1

### ABUNDANCE AND DISTRIBUTION OF BENTHIC MOLLUSCS OVER A 244 M DEPTH GRADIENT IN THE EXUMAS, BAHAMAS

#### ABSTRACT

A total of 773 individual molluscs comprising at least 72 taxa were collected from benthic collectors deployed at 5 m, 14 m, 46 m, 153 m, and 244 m depths off Lee Stocking Island in the Exumas, Bahamas, from December 1993 to June 1994. Results of this study focus on the “coastal curve” that occurs from shore to around 300 m. Mean numbers of species and individuals collected in the three shallower depths (5 m, 14 m, 46 m) were significantly higher than those at the two deeper depths (153 m and 244 m). Although it is possible that some environmental factor affected collectability of individuals, it is likely that abundances are indeed lower in the deep than shallow sites. Rarefaction also showed that the number of species of bivalves was significantly lower at 46 m than at 5 m. Rarefaction failed to show a significant decline in species number for gastropods or total molluscs at the 5 m, 14 m, or 46 m depths, however, and small sample sizes prevented conclusions about diversity at the two deepest sites. Irradiance, temperature, and habitat heterogeneity all declined with depth. All are likely to exert effects on the abundance and diversity of the benthic biota. Irradiance, followed by habitat heterogeneity, showed the greatest percentage decline over the depths studied. The shapes of the curves for numbers of species and individuals over depth were most similar to those of temperature and habitat heterogeneity. Dissolved oxygen and salinity were also examined, though did not change sufficiently with depth to show a strong

relationship to molluscan abundance or diversity. This study represents the first quantitative characterization of the benthic molluscan fauna over these depths in the Bahamas or elsewhere in tropical waters. This study also identifies a bimodal pattern of diversity over a broad depth gradient from shore to the deep sea, peaking at 10 - 30 m in coastal habitats, declining, and then peaking again at about 1,000 - 1,500 m depths.

## INTRODUCTION

### Gradients in the Diversity and Abundance of Species

Much of the ecological theory for gradients of species diversity in marine systems has focused on climatic or latitudinal differences (Ricklefs, 1973; Lamshead, et al., 2000; Gray, 2001). Well-documented latitudinal patterns in species numbers appear to be related to climatic factors such as temperature and seasonality (Ricklefs, 1973), though it is more difficult to find convincing links between physical parameters and patterns of diversity within local environments (Pianka, 1966). Thorson (1957), Stehli et. al (1967, 1969), and Sanders (1968) all showed that marine diversity followed the terrestrial pattern of increasing diversity from the poles to the tropics. Deep-sea bivalves and gastropods exhibit clear latitudinal gradients of diversity of increasing species richness from north to south in the North Atlantic and strong inter-regional variation has been documented in the South Atlantic (Rex, et. al., 1993), although the explanation for these patterns remains uncertain (Rex et al., 2000). Latitudinal gradients in the deep sea were unexpected because it was believed that environmental gradients of factors such as temperature would not affect the biota at such great depths. However, higher amounts of

phytoplankton at higher latitudes and greater predation, along with higher rates of decomposition, likely produces a latitudinal gradient of lower organic matter falling to the ocean bottom at lower latitudes, which could help explain the observed gradients.

On a more local scale relevant to the present study, Chiappone et al. (1997) reported that they did not find any consistent latitudinal pattern in common species of reef invertebrates in the Exuma Cays in the Bahamas (the Bahamas may include too little latitudinal distance to demonstrate gradients in species diversity). They noted the apparent latitudinal uniformity in environmental conditions throughout the Bahamas, which contrasts with the changes that occur with depth, such as light, temperature, and habitat heterogeneity that were examined in the present study.

Considerable interest has been generated by studies that have examined trends in diversity from the shelf into abyssal depths (Gray, 2001). Much research has been devoted to coastal benthic regions (shore to 200 - 300 m) (e.g., Pearson, 1970; Gage, 1973; Gray et al., 1997) and a number of studies have sampled benthic biota from the “deep sea” (200 - 300 m to around 6,000 m) (Hessler and Sanders, 1967; Sanders, 1968, 1969; Rex, 1973; Hessler and Jumars, 1974; Grassle and Maciolek, 1992; Etter and Grassle 1992; Rex et al., 1993; Poore et al., 1994). Species diversity on global deep sea soft bottom communities is claimed to be in the hundreds of thousands or millions of species because of the huge area involved (Grassle and Maciolek, 1992).

Although there is likely considerable regional variation in patterns, the best set of samples comparably collected and analyzed (the Atlantic Continental Slope and Rise study with samples from Georges Bank and deeper water off Massachusetts and a transect

out into the deep North Atlantic) (Rex, et al., 1997) shows that, when corrected for sample size, deep soft-bottom environments have higher diversity than shallow ones (< 200 m). Across a linear depth gradient from  $\geq 100$  m to 2,250 m, species richness is hump-shaped, with lowest numbers of species on Georges Bank (around 100 m), a peak at approximately 1,250 m, and then a decline to 2,000 - 2,250 m (Etter and Mullineaux, 2001). Species richness of gastropods shows a similar broad-scale pattern (low on the continental shelf, maximal on the continental slope, and lower on the abyssal plain at > 4,000 m) (Rex, 1973; Rex et al., 1997).

Much less is known about broad-scale patterns of diversity over depth on deep sea hard bottoms (Etter and Mullineaux, 2001). Sites of sea-floor spreading, mid-ocean ridges, and sea mounts provide hard substrates with which a considerable biota is associated. Recent discoveries of extensive beds of deep corals, especially in the North Pacific and North Atlantic, have attracted widespread interest and attention (Etnoyer and Morgan, 2003; Roberts and Hirshfield, 2003). The hydrothermal vent fauna and cold seep fauna on hard substrates have riveted the attention of the scientific community for the last several decades (Grassle et al., 1985), but documentation so far suggests that these faunas are not especially diverse, and patterns of diversity across depth gradients have not been quantified. Most hydrothermal vent faunas and some of those from sea mounts, however, are highly endemic (83 percent of 443 species in vent fauna, Tunnicliffe et al., 1998; as many as 28 percent of species on sea mounts, Wilson and Kaufman, 1987; Etter and Mullineaux, 2001). One third of the species found on some sea mounts off

New Caledonia are unique and up to half of the fish and invertebrates on sea mounts off Chile occur only there (Malakoff, 2003).

Because the focus of this chapter is on how aspects of the environment as well as the diversity and abundance of major molluscan taxa change over depth, the next section of the Introduction will examine the main physical and biological factors that historically have been associated with gradients in species diversity and abundance. The last section of the Introduction will address a gaping hole in our knowledge of depth gradients: how do patterns of diversity within the nearshore environment (0 - 300 m), and in particular, coral reefs, relate to the broader paradigm (Figure 1.1) given above for gradients of marine diversity from shallow water to the deep sea?

#### Physical and Biotic Factors Associated with Gradients of Diversity and Abundance

Physical and biotic factors that have been used to explain gradients of species abundance and diversity over the last thirty years include: a) light, b) temperature, c) physical disturbance, d) time-stability, e) spatial complexity, f) predation, g) recruitment, and h) productivity (Ricklefs, 1973).

##### *Light*

Although there are many physical and biotic factors that influence diversity of marine organisms, light appears to be one of the most common variables that shows a consistent relationship with the decline of diversity and abundance with depth, even though light intensity may vary among regions. For example, the extremely clear, oligotrophic waters of Exuma Sound in the southeastern Bahamas enable light to

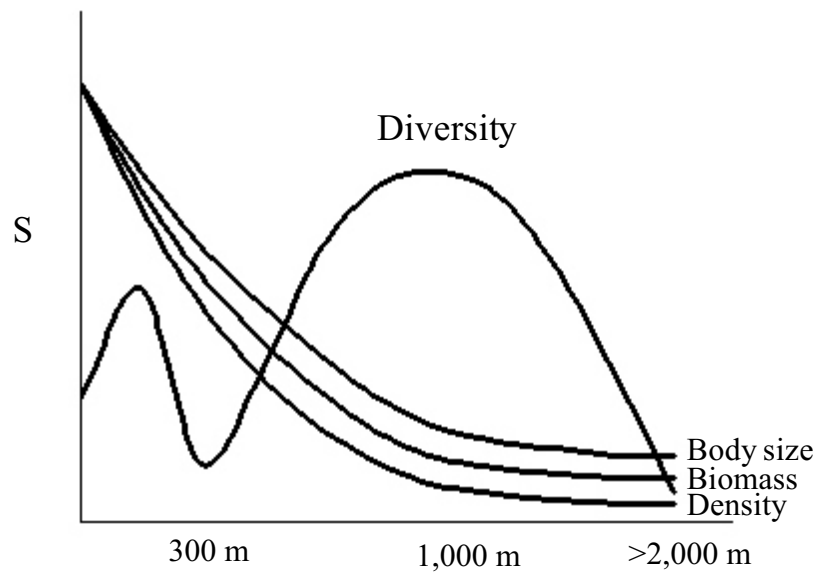


Figure 1.1. Conceptual diagram of bimodal species diversity over depth (S = species), along with concomitant declines in body size (macrofauna), biomass, and density of benthic organisms. The dip in species diversity at 300 m represents the “coastal curve” which rebounds to a peak at around 1,000 m, then declines at around 2,000 m.

penetrate about 15 m further than in Discovery Bay, Jamaica (Liddell, 1997). Light controls primary productivity of local environments, which has been related to diversity and abundance of benthic biota. Along depth gradients in coral reef environments, notably the range of depth between 15 m to around 30 m, the environment is highly productive and relatively stable, carrying capacities are higher, and there tends to be higher species diversity.

### *Temperature*

Temperature also can have important effects upon the biota. Like other physiological functions, photosynthesis has an optimum temperature range, above and below which the rate of primary production decreases rapidly (Ricklefs, 1973). Metabolic processes increase two to five times for each 10°C increase in temperature (or, more relevant to the present study, *decrease* two to five times for each 10°C *decrease* in temperature) at moderate light intensities (although the rate of photosynthesis is less sensitive to temperature in low light conditions (Giese, 1979; Levinton, 2001). Decreases in temperature reduce activity levels and reduce the frequency of biotic interactions (e.g., competition, predation, bioturbation). Low temperatures also slow chemical reactions, such as deposition of calcium carbonate skeletons, affecting morphological traits of organisms that relate to their efficacy in predation, defense against predation, and competition (Vermeij, 1987).

### *Physical Disturbance*

Physical disturbance of the environment also has been shown to influence species diversity of the community. Connell (1978) proposed that community diversity is highest



at intermediate levels of disturbance. He tested this hypothesis by examining the diversity of coral reefs relative to their exposure to hurricanes and other disturbances, and found that coral reef diversity was highest in areas of intermediate disturbance. He reasoned that when disturbance occurs, numbers of species are depressed at the near and far ends of disturbance gradients; i.e., competitive exclusion tends to reduce number of species in undisturbed conditions but severe disturbance also reduces the number of species, since only a few rapidly-growing populations are able to recover from a massive event or only a few species can resist the disturbance. Since disturbance to benthic communities would appear to be highest in shallow water environments of the Bahamas due to wave action, currents, and severe episodic storm or water warming events, number of species may be enhanced in environments such as the insular shelf edge, which is subjected to less extreme physical conditions, yet still is a well-lit environment.

#### *Time-stability*

According to Sanders' (1979) time-stability hypothesis, adaptation by individuals in shallow or polar areas is primarily to the physical environment rather than to other species, contrasting with the deep sea and tropical areas where the environment is relatively "stable" (though this is strongly debated) and organisms adapt evolutionarily to biotic interactions (e.g., competition, predation). Thus, species richness of shallow and polar areas is "physically controlled," compared to the deep sea and tropical areas which can be said to be "biologically controlled" (Gray, 2001). This hypothesis, which is based primarily on changes that occur over evolutionary time, predicts that the shallow assemblages in the Bahamas will be more accommodated to variations in the physical environment and the

deep assemblages to be more diverse and possess more adaptations for biological interactions such as predation. However, greater diversity and especially abundance of species in the shallower than in deeper environments would suggest the opposite.

### *Spatial Complexity*

The more spatially complex the environment, the higher the biotic diversity it can support, other things being equal (Valentine and Jablonski, 1991). Habitat heterogeneity has been shown to have a direct relationship to diversity and abundance of organisms in various types of environments (Kohn, 1967; McKaye and Gray, 1983; Thistle, 1983; Gilinsky, 1984; Minshall et al., 1985; Thormann, 1986; Turner, 1987). The greater the structural heterogeneity, the more difficult it is for predators to drive animals to extinction (Ricklefs, 1973); greater physical complexity (more places for partial or complete sequestration from predators) likely will correspond to more partial (i.e., only a portion of the population) as opposed to complete mortality. Greater structural complexity also provides more different types of microhabitat, allowing greater numbers of species with different specialized requirements to co-occur.

### *Predation*

The basis of the classic “predation hypothesis” is that with increasing predation, diversity increases to a maximum at an intermediate predation intensity, then shows a decline (Menge and Branch, 2001). Low diversity results from competitive exclusion at low predation rates and predation-caused extinctions at higher predation rates. Paine (1966) made substantial contributions to understanding the role of predation in community diversity in his studies of predation on the coast of Washington. His research

demonstrated that predation by the sea star, *Pisaster ochraceus*, maintains a diverse benthic assemblage where no single species predominates. Removal of this “keystone predator,” however, results in competitive monopolization of substrate space by the mussel, *Mytilus californianus*, and reduction of benthic diversity. Predators can also have indirect effects on community structure, where direct effects on one species can in turn affect other species in other trophic levels (Dayton, 1971). This also can ultimately affect diversity and zonation of a community of organisms.

### *Recruitment*

Ricklefs (1973) provided an overview of recruitment and its importance in determining abundance and diversity of organisms. Recruitment is strongly affected by biotic processes such as predation and abiotic environmental factors such as oceanic circulation and settlement patterns. Populations of benthic organisms can recruit from local or other sources, depending on biological and physical conditions. Duration of larvae in the water column, the timing of larval release, stage at development at hatching, swimming and sensory ability are examples of biological features that help determine recruitment success. Physical factors influence the spatial and temporal settlement patterns, including local flow retention mechanisms, depth, and substrate type.

### *Productivity*

Primary production in shallower water is regulated largely by available light and a source of nutrients. Productivity in the deep sea depends on other sources of energy such as organic matter generated by surface phytoplankton production, or other residual material such as zooplankton feces, marine snow, and bacteria (Lenihan and Micheli,

2001). In shallow water generally less than 150 m, soft sediment organisms graze on benthic algae if the photic zone extends down to the substratum. In deeper water, secondary benthic production is closely linked to primary production in surface waters that can result in a plentiful supply of organic carbon to the seafloor. Understanding the processes that regulate primary and secondary production (e.g., light, circulation, upwelling,, etc.) is integral to interpreting diversity and abundance of organisms over a depth gradient such as in the present study.

### *Deep Sea Diversity*

Contemporary views on deep sea diversity (reviewed by Etter and Mullineaux, 2001) emphasize the role of spatio-temporal heterogeneity and meta-population patch dynamics to explain the hump-shaped pattern of species diversity (low in shallow coastal waters [ $< 100$  m] to a peak at approximately 1,250 m, and then a decline in deeper waters [ $\sim 2,250$  m] that is observed in fauna from soft sediments). Spatio-temporal heterogeneity (a mosaic of patches in different stages of succession) is more diverse, and occurs on smaller spatial scales and over longer time scales, in the deep sea than in shallow communities. Particulate organic matter (food) declines exponentially with depth in deep sea soft sedimentary environments, as does biomass and density of populations. Etter and Mullineaux (2001) argue that a greater variety of tiny biogenic structures, disturbance patches, and food patches persist for longer periods (due to low temperatures and low biological activity) in the deep sea than in shallower environments. Longer duration of these micropatches in the deep sea gives subordinant species more time to find new patches and makes local extinction of populations in patches less frequent than in shallow

environments. Species persist regionally if the rate of colonization of new patches is greater than the average rate of extinction of patches. These conditions also provide more opportunities for partitioning the sediments. Further, the low food environment constrains species to small body size. Small organisms are universally more diverse than large species, presumably because they experience the environment on a smaller scale (Hutchinson and MacArthur, 1959; Morse et al. 1985; May, 1986, 1988; Reaka-Kudla, 1997). Small body size in turn places constraints on energy assimilation from detritus, since there is an upper limit to the size and complexity of types of food the organisms can eat and their bodies are too small to handle complex feeding/processing apparatus. Both small body size and food limitation reduce the amount of energy available for reproduction. Low fecundity and low capacity for energy assimilation preclude rapid population increases in response to pulses of food, giving rise to potential recruitment limitation, low species dominance, and reduced rates of competitive exclusion. Recruitment limitation in high diversity systems (Tilman, 1994; Hubbell et al., 1999) can promote co-existence by decreasing the intensity of biotic interactions. Ultimately, competitive exclusion can occur in the deep sea, but the frequency of unoccupied sites and low number of recruits slows the process so much that a large number of species using the same resource can co-exist among patches for long periods of time.

#### Gradients in Diversity and Abundance over Depth in Coastal Environments

While much attention has been devoted to the diversity and ecology of deep sea environments, and hundreds of studies have been conducted on shallow water coastal communities, virtually no attention has been paid to how the shapes of the diversity curves

for shallow to deep sea environments (e.g., 200 - 2000 m) compared to those for coastal environments (e.g., 0 - 300 m), and whether similar kinds of ecological and environmental factors govern the shapes of these curves.

Coral reefs represent critically important tropical coastal habitats that have received considerable study. Most of the work on coral reefs has focused on relatively shallow (< 30 m) environments, and those that are below 60 m that are difficult to sample with conventional techniques are far less common (Liddell et al., 1997). Several studies of coral reef environments have examined changes in diversity over depth in the Red Sea (Loya, 1972), Jamaica (Huston, 1985), and the Indian Ocean (Sheppard, 1981), and all show relatively low diversity in the shallows, highest diversity between 15 - 30 m, and a decrease in diversity beyond 30 m.

Studies of bivalve and gastropod molluscs over depth gradients in various coastal and shelf habitats are not uncommon in the literature, and often (with a few important exceptions) show decreasing species richness from the shore to the shelf edge or beyond. Most of these studies examined molluscan assemblages in soft bottom habitats, however, rather than on hard substrates. For example, species richness of benthic fauna, including molluscs, declined from 10 - 70 m depths in a sedimentary shelf region along the west coast of India (Harkantra et al., 1980). In a study of soft bottom benthic communities dominated by polychaetes, molluscs, and crustaceans in the Norwegian Trench, Rosenberg et al. (1996) found that average diversity along soft bottom transects between 144 - 682 m was significantly higher on the shallow slope compared to the deeper habitat. And, in an

Antarctic study, abundance and biomass of macrobenthos, including molluscs, decreased with depth between 8-1,129 m (Thatje and Mutschke, 1999).

In contrast to the above studies, Allmon et al. (1993) showed that the number of species of gastropod molluscs on the east and west coasts of Florida *increased* from the shore down to around 100 - 200 m, where the increase began to level off and then showed little or no increase from 200 - 1,000 m. Also, although the following studies did not examine diversity over the shelf, Rex (1973) and Rex et al. (1997) found that species richness of gastropods increased from the shelf out to the slope in the North Atlantic, but then declined again in deeper water.

Although in many cases decreasing light penetration and productivity may explain patterns of declining species richness with depth in coastal environments, other characteristics of the habitat also must be considered. In a study of benthic molluscs inhabiting soft bottoms in a coastal lagoon off West Africa, horizontal zonation was affected by salinity, and sediment particle size affected molluscan distribution over depth (Maslin and Levet, 1992). Distribution and abundance of 20 species of gastropods and four species of bivalves in sedimentary habitats were studied over the depth range of 24 - 83 m on the continental shelf off the Pacific coast of Mexico (Rios et al., 2001). Gastropods were most abundant in sandy silt substratum and bivalves were found mainly in sandy silt and medium-sized sand. In one of the few studies that examined the species richness of molluscs on hard substrates over depth, a study of molluscs on coral reefs in the Red Sea from shallow intertidal to 40 m water depths concluded that the dominant influence on molluscan distribution was type of substrate available (Zuschin et al., 2000).

These results, even though from a limited number of studies, suggest a gap in our understanding of the continuity of processes that form diversity gradients over broad depth ranges and diversity gradients in shallower coastal areas over depth. If the general hump-shaped curve for deep sea diversity (soft bottoms) found in the Atlantic Continental Slope and Rise study (Etter and Mullineaux, 2001) and by Rex and colleagues (1973, 1997) is real and not an artifact (i.e., if there is only one hump-shaped curve from the shore to the deep sea overall), one should expect by extrapolation to find greater species richness in deeper coastal regions than in shallow regions. Yet the above studies on both coral reefs and soft bottom coastal habitats suggest that there is *usually* (though not universally) a similar hump-shaped curve or at least a decline in diversity in the deeper regions of the coastal zones. Although low diversity in extremely shallow, physically rigorous coastal environments is easily understood, what accounts for the decline in diversity observed on deeper reefs and in many deeper soft bottom coastal habitats? If declining light, productivity, temperature, or habitat complexity accounts for *declining* diversity and abundance in deep coastal areas, why does diversity *increase* again as one progresses out into the mid-regions of the deep sea as indicated in the review by Etter and Mullineaux (2001)?

#### Description of the Study Area

Lee Stocking Island in the lower Exumas, Bahamas, is a relatively undisturbed coral reef site with a variety of shallow and accessible deep water habitats spanning a depth gradient of 0 - 300 m (Figure 1.2). The Caribbean Marine Research Center's (CMRC) facility on Lee Stocking Island provided the use of a deep-water submersible and



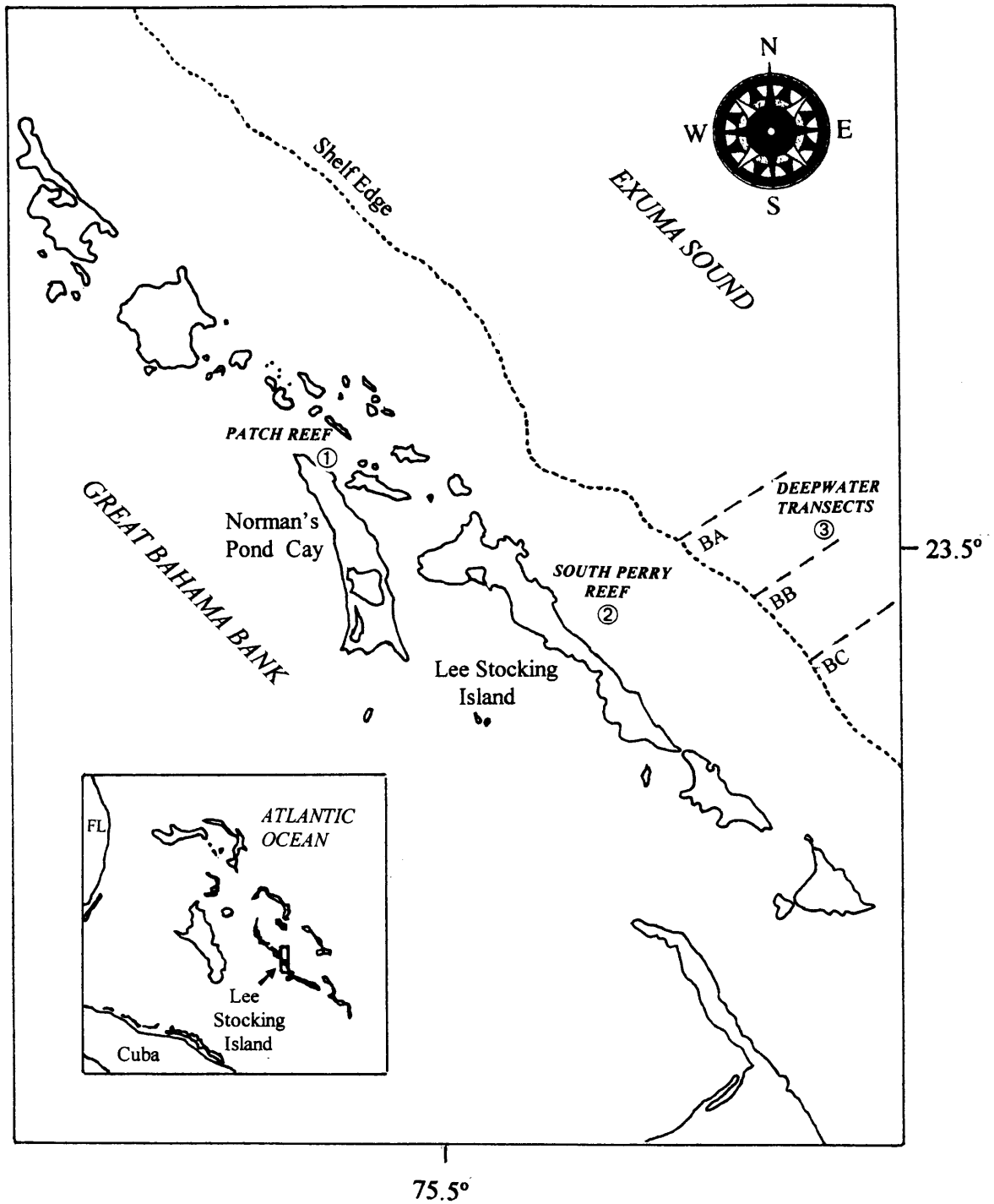


Figure 1.2. Location of study area showing sampling locations near Lee Stocking Island, Bahamas: 1) Norman's Pond Cay 5 m patch reef; 2) South Perry Reef 14 m; and, 3) deepwater transects (BA, BB, and BC), including the shelf edge 46 m; slope "lower wall" 153 m; and, slope "cemented rock slope" 244 m. The shelf Inset: larger context showing the position of Lee Stocking Island in the Bahama Islands.

laboratory space to perform the study. The use of the CMRC submersible NEKTON GAMMA for deep water and SCUBA for shallow water studies allowed for successful deployment and retrieval of benthic collectors and observation of the habitats at each depth. The submersible permitted siting the collectors in deeper habitats, which otherwise could not have been accomplished.

The 5 m site off Norman's Pond Cay, referred to as “North Norman’s Reef,” consists of extensive patch-reefs located between grass beds in the deeper channel and emergent fringing reef inshore. The coral *Acropora cervicornis* is abundant in the area adjacent to the grass beds in the channel, with larger boulder and brain corals intermittently spaced closer to the fringing reef. The bottom is intermittent sand and hard bottom with abundant hard and soft corals, reef fishes and invertebrates. Water clarity is high due to the interchange of water with Exuma Sound. This area is protected by land (cays) on two sides, offering protection from direct wave action from Exuma Sound (depending on wind direction), though the constricted flow in the main channel is influenced by very strong tidal currents.

N. Smith (pers. comm.) summarized shallow-water tidal and wind-driven currents of the Exuma Sound and Great Bahama Bank in the vicinity of Lee Stocking Island. Along-shelf currents on the seaward (Exuma Sound) side of Lee Stocking Island flow is predominantly toward the northwest. Wind-driven surface flow is generally towards land (from the Sound), and channels and areas between cays are influenced by strong tidal flows up to 60 - 70 cm s<sup>-1</sup>. At times of low rainfall and light winds, “spikes” of shallow bank water of high salinity “leave” during ebb tides. These relatively dense salinity

plumes are entrained by gravity currents and transported to the shelf and slope, where they cascade over the steep edge of the shelf into Exuma Sound (B. Hickey, pers. comm.). These studies highlight the complexity of currents in the Lee Stocking Island area and adjacent shelf.

South Perry Reef is a fringing reef that runs roughly parallel to Lee Stocking Island, approximately 1.2 km offshore. The submerged crest of South Perry reef begins near 9 m and has a well-defined fore reef that slopes abruptly to approximately 18 m, where it meets the sandy shelf. Grassbeds are evident several meters seaward of the fore reef at approximately 20 m depth. The submerged reef crest has the appearance of a high-energy, wave-worn environment that has direct exposure to localized wind-driven waves and larger offshore swells. Significant portions of the upper fore reef slope appear somewhat overgrown with algae, with broken and scattered coral chunks indicative of storm damage. The reef slope at 14 m is more structurally intact with prolific soft and hard coral reef growth, and presented a suitable area to secure and properly space the collectors on relatively level surfaces between coral growth. Water clarity is generally high, with little or no significant runoff from adjacent Lee Stocking Island.

The 46 m site is at the edge of the island slope facing the deep water of Exuma Sound. McNeill and Grammar (1993) developed a generalized slope characterization (Figure 1.3) and morphological description based on submersible dive observations along three of six permanent transect lines (AA, AB, and AC) established by the Caribbean Marine Research Center on Lee Stocking Island. Three of the deep-water transect lines to the north of Lee Stocking Island are known as “AA, AB, and AC” transects, and are

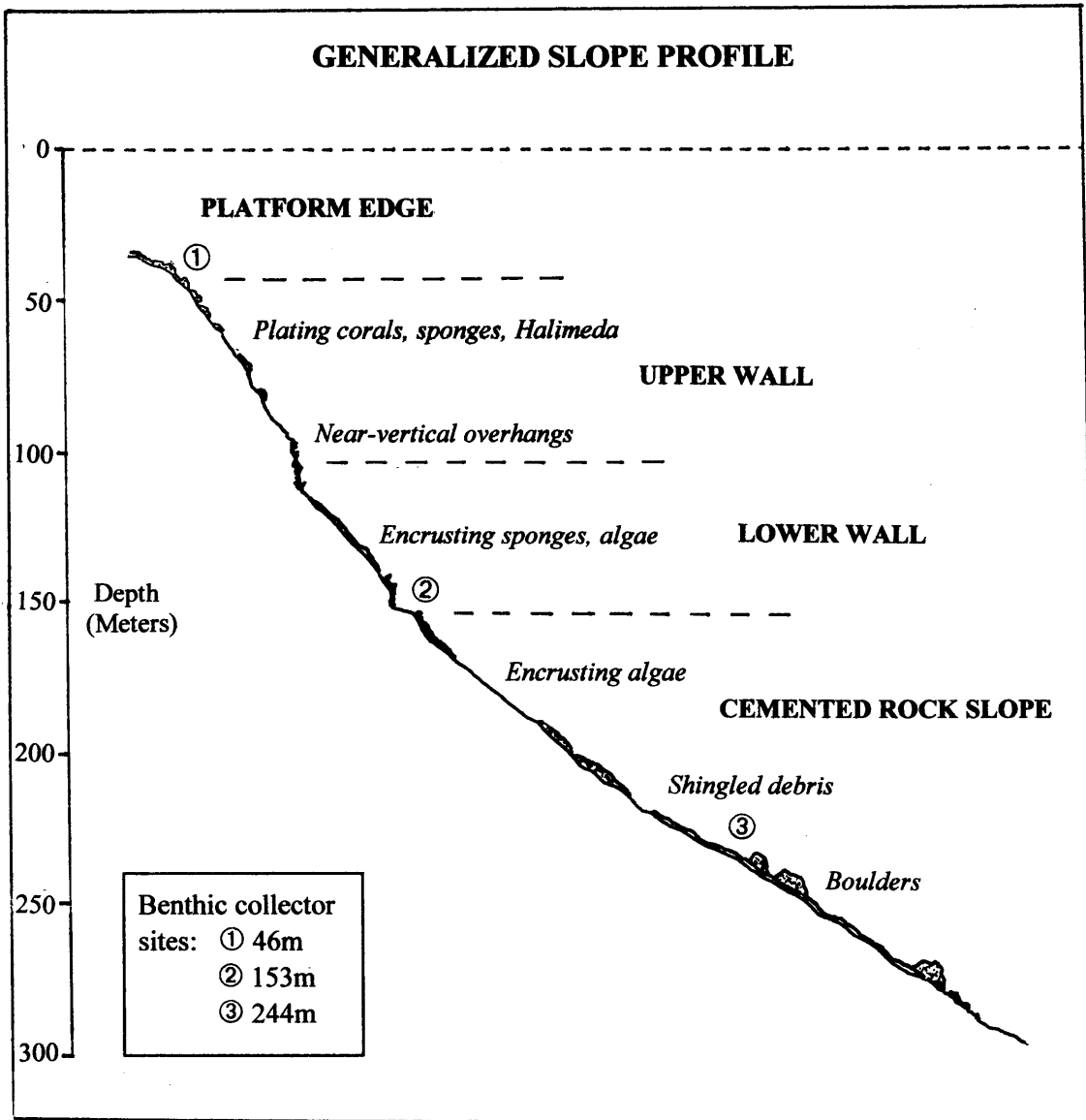


Figure 1.3. Generalized profile of the slope off Lee Stocking Island Bahamas in Exuma Sound, based on observations from the NEKTON GAMMA in January, 1993, by D. F. McNeill and G. M. Grammar, University of Miami. Profile was modified to reflect features observed in the present study along the deep water transects where benthic collectors were deployed.

described by McNeill and Grammar as a “bank-source” locality. Three other transects, used in the present study, “BA, BB, and BC,” lie to the northeast of the island (Figure 1.2), and are considered to be on a “sediment-starved slope” or “low deposition environment,” contrasting with the “A” series of transects that are more directly in the path of density-driven currents that transport shallow bank sediments to the shelf edge and slope in Exuma Sound. The “B” series of transects were chosen because of lower current intensity and sedimentation than at the “A” series (G. Dennis, pers. comm.).

There are the four morphologic zones of the slope to 300 m: the Platform Edge, Upper Wall, Lower Wall, and Cemented Rock Slope (Figure 1.3). The Platform Edge is characterized in its shallowest portion by patchy reef corals and sand downward to intermittently formed spur and groove coral formations, the latter of which function as “sediment shutes.” The Platform Edge environment extends down to around 46 m on the BA, BB, and BC transects where benthic collectors were deployed. The Platform Edge consists of hard and soft corals, sponges, abundant *Lobophora* sp. (brown macroalgae) and encrusting coralline algal growth. Slopes on the Upper Wall range from around 40° to 60° to nearly vertical (70° to 90°). Further down, bottom relief is characterized by coarse sand and intermittent cliffs and occasional large boulders. Plating coral (*Agaricia* spp.) and *Montastrea cavernosa* occur to around 75 m and *Agaricia* spp. to a maximum depth of approximately 90 m (Liddell et al., 1997).

The base of the Lower Wall (153 m) was the closest habitat to the Platform Edge where there were suitable areas of relatively level bottom, appearing as horizontal ledges, to deploy collectors. Below the Lower Wall, the Cemented Rock Slope is mainly hard

limestone substrate with a relatively consistent slope of approximately 30° to 40°. At around 244 m, the bottom is somewhat irregular, with horizontal ridges up to several meters in height, scattered coral debris and sand. Encrusting coralline algae are the most commonly observed organisms in this zone down to around 175 m; below that, little else is observed other than occasional invertebrates, including stalked crinoids. Large “boulders” (some over 10 m in height) are seen at the lower end of the Cemented Rock Slope and are believed to be large chunks of the wall that have broken off and fallen down slope (McNeill and Grammar, 1993). This site offered the advantage of having relatively level surfaces to deploy the collectors, though navigation of the submersible was difficult because of the presence of the large boulders.

### Hypotheses and Objectives

Chapter 1 focuses on defining the faunal composition of benthic molluscs, primarily at the higher taxon level (i.e., total molluscs, bivalves, and gastropods), over depth and relating abundance and diversity to environmental factors that change over the depth gradient. Analyses of the biological characteristics of individual species assemblages with depth from these collections are addressed in Chapter 2.

Since this study does not include an experimental manipulation of the environmental factors, the results are not intended to determine *causative* factors that control species diversity and abundance, but were analyzed quantitatively and qualitatively to determine which factors are *most correlated* with the diversity and abundance of benthic molluscs, and thus are most likely to be important to the molluscan fauna over this depth gradient.

Hypotheses:

- ▶ *Species richness and abundance of benthic gastropod and bivalve molluscs decrease with depth; and,*
- ▶ *Light, temperature, and spatial heterogeneity decrease with depth and are key factors associated with diversity and abundance of the benthic molluscan fauna over the depth gradient (5 - 244 m).*

The objective of the present paper will be to quantitatively assess (1) patterns of abundance and diversity of benthic gastropod and bivalve molluscs and (2) environmental factors that may influence this distribution over a depth gradient of 5 - 244 m off Lee Stocking Island of the Exumas, Bahamas. This depth gradient ranges from a shallow, high energy patch reef environment to prolific reef growth on the well-lit shelf edge, through the transitional zone of decreasing light and more limited abundance of reef organisms, and down to the deeper slope edge with almost no light and no active reef growth. The present research assesses the diversity and abundance of bivalve and gastropod molluscs over the same depth gradient and in the same locations as Maldonado and Young's (1996) study of sponges, Aponte and Ballantine's (2001) study of benthic algae, G Dennis's (pers. comm.) study of fishes, and Liddell et al.'s (1997) study of sessile epifauna. By characterizing the benthic molluscan fauna along this depth gradient off Lee Stocking Island, my study contributes to a more complete understanding of the distribution and diversity of this Bahamian biota, facilitates efforts to understand the processes that govern patterns of diversity and abundance over depth in coastal areas as compared to those that are observed

in the continuum toward the deep sea, and introduces the little known and little explored “twilight zone” (Porter, 1973) of the deep reef environment.

## MATERIALS AND METHODS

### Deployment and Retrieval of Benthic Collectors

Experimental benthic collectors were deployed in the field in December 1993 from shallow to deep water (5 m, 14 m, 46 m, 153 m, 244 m) and retrieved after six months in June 1994. A wide array of motile invertebrates and fishes was found in the collectors. All animals which colonized the collectors were removed, sorted, and preserved. All of the collection was retained, and the non-molluscan species preserved for future research. Only the molluscs were analyzed in the present study.

Benthic collectors were placed off Lee Stocking Island at an inshore site (5 m) at north Norman’s Pond Cay; a mid-shelf site (14 m) at South Perry Reef, and three deep water sites in Exuma Sound at 46 m, 153 m, and 244 m (Figure 1.2). Each collector consisted of layered "hogshair" insulation covered with an outer layer of nylon screen, laced together with monofilament line, with only one open side to allow entry of organisms (Figure 1.4). The hogshair material was chosen because of its successful use in collecting small invertebrates in other studies around Lee Stocking Island and with blue crab postlarvae in Chesapeake Bay (Lipcius et al., 1990). The overall dimensions of the collectors were approximately 43 cm length by 43 cm width by 20 cm height. Each layer of hogshair was spaced with six PVC pipe pieces (3.2 cm length by 1.3 cm diameter) and thin strips of hogshair (6.4 cm width) centered along the inside to provide additional



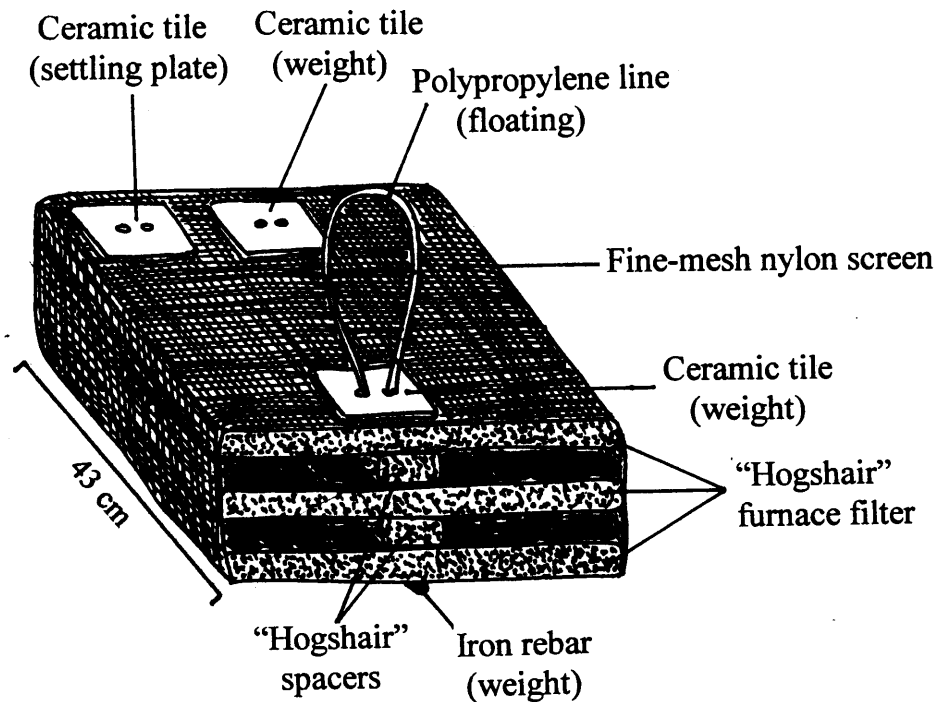


Figure 1.4. Sketch of a benthic collector. The dimensions of the collectors were approximately 43 cm length by 43 cm width by 20 cm height. Collectors were open only on one end to allow entry of organisms through openings of approximately 3 cm. Sections of PVC pipe, not visible in the figure, were embedded vertically through the hogshair spacers for support. (The ceramic tile settling plates attracted sessile biota and were not analyzed in the present study).

support and to help maintain open space of approximately 3 cm between the layers of hogshair.

The collectors were designed to attract motile benthic organisms. The open-spaced layers of hogshair that were separated by spaces of approximately 3 cm limited the entry of organisms larger than a few centimeters and provided artificial habitat suitable for small organisms that inhabit reefs, particularly cryptofauna. An analysis of 960 species of gastropods from the Academy of Natural Sciences (ANS) Western Atlantic Gastropod Database (Chapter 3) showed that nearly three-quarters of the gastropod species in the ANS data set were less than 30 mm. Since the size of the openings in the benthic collectors used in my Lee Stocking Island collections were 3 cm (30 mm), the vast majority of species of gastropods that occur in the Bahamas could have fit into the collectors, even at their maximum size.

Many of the smaller organisms such as bivalve and gastropod molluscs associated with reef environments tend to remain hidden in the refuge of the reef structure and associated sediments and grass beds. Thus the artificial collectors provided the type of habitat that would generally be preferred by these smaller bivalves and gastropod molluscs that use the three-dimensionality of the reef and associated habitats as their natural refuge. Benthic invertebrates used the spaces between the fibers of the hogshair material as refuge once they entered. Thus, the collectors mimicked the smaller crevices and rubble associated with reef habitat and likely provided refuge from predation. The advantage of using the hogshair collectors was that they could be deployed in different habitat types and

depths where other methods such as collecting reef substrate or suction sampling would not have provided as consistent a sampling method along the highly varied habitats along the depth gradient at Lee Stocking Island.

Polypropylene line was attached to the top front of each collector in a hoop fashion to allow retrieval by the submersible manipulator arm. Because the collectors were only slightly negatively buoyant, a length of 1.3 cm iron rebar was fastened to the bottom of each for extra weight. The collectors were designed so that, when picked up by the rope hoop, the opening on the front would face upward and into the water current as the collector was being carried gently to the surface so that organisms would not be lost during retrieval. A total of 45 invertebrate collectors were set out at 5 m, 14 m, 46 m, 153 m, and 244 m on the insular shelf and the slope off the island, as shown in Figure 1.2. Because of possible differences in density and thickness of the hogshair material among manufacturing batches, the traps randomly were assigned numbers from one to 45 using a random number table in the laboratory. The collectors then were deployed according to the corresponding numerical sequence from one to 45 in the field sites.

Collectors were placed randomly at the various depths by setting each one about 9 m apart in a line without regard to bottom type, other than to place the collector on a relatively level surface where it could be adequately secured to the bottom. Thus, at each depth, three replicate collectors were placed 9 m apart from each other in sets of three ( $N = 9/\text{depth}$ ). This distance was selected in order to space the collectors within a reasonable distance of each other so they could be located for retrieval, yet far enough apart (i.e., not immediately adjacent to each other) and without regard to substrate, in as large an area as

possible to ensure independence of the sampling. Collectors at the 46 m, 153 m, and 244 m sites were oriented with openings facing in an approximate southeasterly direction, which is into the predominant direction of density-driven bottom currents in the Exuma Sound side of Lee Stocking Island (W. Head, pers. comm.). Within the Norman's Pond and South Perry Reef sites, the parallel rows were spaced far enough apart (about 6 m) from each other again to ensure independence of the sampling. Because the shallower sites (5 m and 14 m) were higher energy environments influenced by wind-driven currents, tidal currents, and waves, collectors were secured with polypropylene line to adjacent corals by SCUBA divers.

The site at Norman's Pond Cay was selected as the nearest "inshore" habitat with reef (as opposed to level bottom) where collectors could be deployed without being subjected to breaking waves near shore, such as would be the case on the northeast (ocean) side of Lee Stocking Island. At depths of 46 m and greater, the submersible was used to deploy and retrieve the collectors.

Following six months of deployment, all of the collectors were retrieved in June, 1994. Two of the nine deepest collectors (one from each of the three replicates at transect BA and BB at 244 m) were lost, probably due to some disturbance that may have caused the devices to slip down the slope. Three collectors were destroyed by wave action at the 14 m site on South Perry Reef (one lost from each of the three replicates). Two collectors were destroyed by wave action at the 5 m site off Norman's Pond Cay (one lost from each of two replicate sets). All others (38 total) were recovered intact. All collectors were brought gently to the surface where they were carried to the surface boat and immediately

placed in a large plastic bag, tied off and labeled for laboratory examination. In the laboratory, collectors that could not be examined immediately because of time constraints were placed in a walk-in refrigerator to keep specimens fresh. All collectors were disassembled and specimens preserved within 24 hours of retrieval in the field. Specimens were fixed initially in 5% formalin, then later transferred to 70% ethyl alcohol to store for further analysis.

### Habitat Heterogeneity

In September 1995, spatial heterogeneity of the bottom habitats where collectors were placed was estimated. Dives were made off Norman's Pond Cay (5 m), South Perry Reef (14 m), and deep-water transect BA (46 m, 153 m, and 244 m). Three replicate transects (approximately 30 m each) were run at each of the sampling locations listed above. Videotaped horizontal sweeps were made approximately 1.5 m off the bottom at each collection site at a consistent height off the bottom as described below. Dual lasers (6 cm apart) were projected and locations of the lasers on the bottom recorded on the videotape. The distances between the laser dots projected onto the bottom changed with height of the bottom relief, i.e., the dots appeared farther apart as they were projected onto objects closer to the camera. Laser dot distances were calibrated by projecting the dots on a wall approximately 5 m away from the camera and adjusting the lasers so that the projection on the wall was the same 6 cm distance apart as the lasers mounted to the camera housing.

The major limitation in employing the lasers underwater was the amount of ambient lighting. The laser dots, as projected onto the bottom, were not easily seen in full sunlight

in the mid-shelf and inshore locations. Thus, all the shallow water (SCUBA) dives were made at night to provide sufficiently bright and consistent laser projections on the bottom. Videotaping in the deeper (darker) water at the shelf edge (46 m) was successfully accomplished in early morning daylight with the submersible, but the deepest areas (153 m and 244 m) were dark enough to easily see the laser projections anytime the submersible dive occurred. To maintain a consistent height off the bottom at the inshore (5 m) site, we followed a line connected to two weighted PVC poles 1.5 m off the bottom. Best results were achieved by shining a dive light onto the bottom almost out of the field of view of the laser projections on the bottom. This enabled us to orient to the bottom as we proceeded along the transect. Each transect was swum in two sections because, at lengths greater than 15 m, it was difficult to keep the line from bowing with the current.

At the mid-shelf site (14 m), the pole and line method was not used because of the difficulty of moving the weighted poles on the higher relief and slope of the reef. We therefore improvised by counting the number of kicks it took to swim a measured 30 m distance, and then swimming this distance horizontally using a 1.5 m pole to maintain a consistent height of the camera 1.5 m above the 14 m depth contour of the fore reef. We attempted to run all the transects at roughly the same speed. At the depths beyond SCUBA range (46 m, 153 m, and 244 m), distance off the bottom, speed, and distance traveled was accomplished by best possible navigation of the submersible to approximate the methods we employed at the inshore and mid-shelf locations.

The video footage was analyzed subsequently to derive the variance in laser distances for each of three passes of the video camera over each of the collection sites (by

stopping the tape and measuring the distance between laser dot projections every 3 seconds on the videotape). Variances were computed for all values per pass for each depth, then averaged. More variable bottom relief generates more variance with this method, thus providing a quantitative measure of the habitat heterogeneity that is comparable among all of the collection sites.

The formula  $[D = (6N/CX) - N]$  was used to convert the laser dot distances observed on the video screen to actual distance of the camera from the bottom, where “D” (cm) represents the bottom relief, calculated as the camera lens distance to the bottom; 6 (cm) is the distance between lasers; and “C” is the screen conversion. Using a video screen that was 50 cm wide, laser dots were measured as 3 cm apart at a camera height of 1.5 m off “flat bottom.” The screen conversion was obtained by dividing the *real* 6 cm on the screen at closest view by the measured *on screen* distance at 1.5 m, with a screen conversion of 0.125; X = the measured separation of laser dots on the screen in cm; and N = the camera lense distance to the apparent screen (about 10 cm).

#### Identifications of Molluscs

The collectors were disassembled in the laboratory on shore, flushed with running seawater onto a fine-mesh sieve, then closely examined for organisms. The organisms were sorted into broad taxonomic categories. The initial sorting of these organisms in the laboratory indicated a wide array of invertebrates (e.g., sponges, polychaetes, sipunculans, echiurans, crabs, shrimps, isopods, amphipods, brittlestars, urchins, anemones, bryozoans) and several species of fishes.

Bivalve and gastropod molluscs were sorted and identified to species where possible according to Abbott (1974). Name and number of shells were recorded and each measured by width and length as depicted by the standard method for measuring molluscs in Abbott (1974). Current names of all species of molluscs in the collection were verified and updated as appropriate according to Turgeon et al. (1998).

### Statistical Analyses

Statistics were used to test relationships of independent variables (i.e., depth, light, temperature, habitat heterogeneity) to dependent variables (i.e., number of molluscan species, number of molluscan individuals). The statistical tests are not intended to discern conclusively the relationship between the physical and biological parameters within each of the five depths/habitats because there is only one set of data for each of the physical parameters at each depth, which does not provide variability *within* any one habitat to run a rigorous analysis with multiple replicates for the environmental parameters. Thus, the statistical analyses were used to look for “breakpoints” between the abundance and species of molluscs and the different environments found at the five depths. Due to the vastly different numbers of molluscs found in the collectors at the 5 - 46 m depths compared to the 153 m and 244 m depths, data were transformed in the analysis of variance to help overcome the incompatibility of the unequal sample sizes and normalize variance among the various collection sites.

Qualitative descriptions were used to help interpret the results of the statistical tests on the environmental/oceanographic parameters, such as primary productivity and temperature, that do not tend to decrease linearly with depth. For example, water



temperature can be relatively homogeneous down to the insular shelf edge due to mixing, but may show a drop of ten degrees or more from the shelf edge to 244 m; this change also varies with season. While Photosynthetically Available Radiation (PAR) declines with depth, chlorophyll production also is influenced by algae sinking (gravity), nutrient availability, and oceanographic conditions (currents).

The data set for molluscs was first analyzed with a “coarse analysis” of the actual numbers of individuals and species found in the collectors, without accounting for the loss of some collectors at some of the depths. Initial sorting of the mollusc specimens indicated overwhelmingly greater abundance and diversity at the three shallower sites (5 m, 14 m, and 46 m) compared to the deepest sites at 153 m and 244 m. A coarse analysis is presented to provide a synoptic overview of all the data, to highlight the “step function” of abundance and diversity of molluscs between the three shallower sites and the two deeper sites that was immediately apparent in the initial sorting of specimens in the laboratory, to illustrate variation among collectors, and to make collecting gaps easily visible. To further examine differences in species richness between the individual sites, the data were rarefied to simulate equal sample sizes using EcoSim software developed at the University of Vermont (Gotelli and Entsminger, 2001). Sample sizes at the deepest two sites were so small that rarefaction was not possible, with the exception of when numbers of all individuals and species were combined for total molluscs. Since certain types of data such as biomass cannot be rarefied (Gotelli and Entsminger, 2001), the analyses were limited to species richness, evenness and a comparison of key environmental parameters.

One difficulty in making comparisons of species diversity between the various depths in the present study arises from unequal sampling due to the loss of some of the benthic collectors at different depths due to oceanographic conditions. McIntosh (1967) developed the term *species richness* to specify the number of species in a given community. However, in most field studies, it is not possible to assess the *actual* number of species in a natural community, since collections are usually limited to random sampling. The basic problem with field sampling to determine species richness is that the larger the sample size, the larger the expected number of species. Thus, if sampling effort is not consistent among habitats, estimates of species richness tend to be biased. Sanders (1968) proposed a novel method, rarefaction, to standardize collections of different sample sizes of marine benthic communities in order to make more meaningful comparisons among collections from different communities. Sanders' (1968) rarefaction algorithm was correct in principle, though later determined to be technically incorrect, as it tended to overestimate the expected number of species for a random sample (Krebs, 1998), and is only useful when individuals in the collection are uniformly distributed in space (Kobayashi, 1982). The algorithm was corrected independently by Hurlbert (1968) and Simberloff (1972). Gotelli and Graves (1996) provide a summary of the applications of rarefaction based on Sanders (1968) original principle of "rarefying" unequal sample sizes in order to calculate the expected species richness so that rarefied larger samples can be compared directly with smaller collections.

Because the calculations involved in rarefaction are so tedious, Gotelli and Entsminger (2001) developed a computer program known as EcoSim for analysis of

species diversity. EcoSim includes a module for applying the rarefaction algorithm. Thus, the EcoSim species diversity module for rarefaction was used in the present study to analyze species richness of gastropods and bivalves to better interpret the observed differences in species diversity among depths. The numbers of the species and individuals of bivalve molluscs collected at the five depths off Lee Stocking Island are listed in Chapter 2. Rarefaction curves were generated using EcoSim default levels of abundance, where EcoSim sets the levels of abundance necessary to construct a diversity curve that is tailored to the observed levels of abundance levels in the data set.

For a quantitative interpretation of evenness for the molluscan data set, Hurlbert's Probability of an Interspecific Encounter (PIE) index was run using the EcoSim diversity module. Rather than assigning individuals equiprobably to different species, this model is based on rarefaction, i.e., a random sample of individuals is drawn from a given species distribution to estimate sampling effects for the index. The PIE index has a simple interpretation as the probability that two individuals drawn randomly from an assemblage represent different species (Gotelli and Graves, 1996).

There are several advantages of using PIE as a simple index of evenness. First, the index is easily interpreted as a probability. Second, this index is one of the few that is unbiased by sample size, although the variance increases in small sample sizes. For each sub-sample in my analysis, PIE was calculated and the procedure was repeated 100 times to estimate the variance and the 95% confidence intervals for bivalves and gastropods for the 5 m, 14 m, and 46 m sites.

## RESULTS

### Abundance and Diversity of Molluscs with Depth

#### *Total molluscs*

A total of 773 individual molluscs comprising at least 72 taxa were found in the collectors. Thirty-six of the 72 taxa were identified at the species level; 23 were identifiable only to genus; two only to family; and 11 were of unknown affinity. Thus, the 72 taxa include at least 61 species, of which 36 were unequivocally distinguishable with non-overlapping characters. Overwhelmingly higher abundance and diversity was seen in the 5 m, 14 m, and 46 m collection sites, compared to the deeper sites on the slope at 153 m and 244 m. Diversity or species richness was based solely on the number of species that colonized the collectors, and true diversity at the deeper sites may not be represented due to low sample sizes at those sites. Variability between collectors was especially evident at the 5 m depth. For example, one of the collectors at the 5 m depth had 23 species of molluscs and 156 individuals while another collector at the same depth had only eight species and nine individuals.

A series of one-way ANOVAs ( $\alpha = 0.05$ ) were conducted with SAS JMP Statistical Software (SAS Institute, 1995) to determine if depth had any significant effects on the mean number of species and individuals of total molluscs, bivalves, and gastropods per collector at each depth (means of replicate collectors at each depth). Homogeneity of variance tests evaluated whether variances across groups were equal for numbers of total species of molluscs and total numbers of total individual molluscs. Based on the results of O'Brien's homogeneity of variance test in JMP (SAS Institute, 1995), numbers of species

per collector were square-root transformed and number of individuals were log transformed to achieve homogeneity of variance in the ANOVAs. Depths were treated as classes and the biological data assigned roles as continuous variables for the statistical analysis.

The mean and standard error per collector of molluscan species and individuals per collector was computed for each of the five depths (Figure 1.5). The ANOVAs showed that mean number of species and mean number of individuals per collector at the shallower three sites (5 m, 14 m, 46 m) were significantly different from the means of these categories at the two deepest sites (153 m and 244 m) ( $P_{\text{species}} = 0.0001$ ;  $P_{\text{individuals}} = 0.0001$ ). Tukey HSD ( $\alpha = 0.05$ ) tests were used to detect differences between pairs of means at the various depths (Table 1.1).

### *Bivalves*

The total number of bivalves retrieved per collector comprised far less of the total molluscs than gastropods in the collectors (Figure 1.6). The mean and standard error per collector was computed for species of bivalves and individuals with depth (Figure 1.7). As with the total molluscs, the ANOVAs showed that mean number of species and mean number of individuals at the upper three depths (5 m, 14 m, 46 m) were significantly different from the means of these categories at the two deepest depths (153 m and 244 m) ( $P_{\text{species}} = 0.0001$ ;  $P_{\text{individuals}} = 0.0001$ ) (Table 1.2). Tukey HSD ( $\alpha = 0.05$ ) tests were used to detect differences between pairs of means at the various depths.

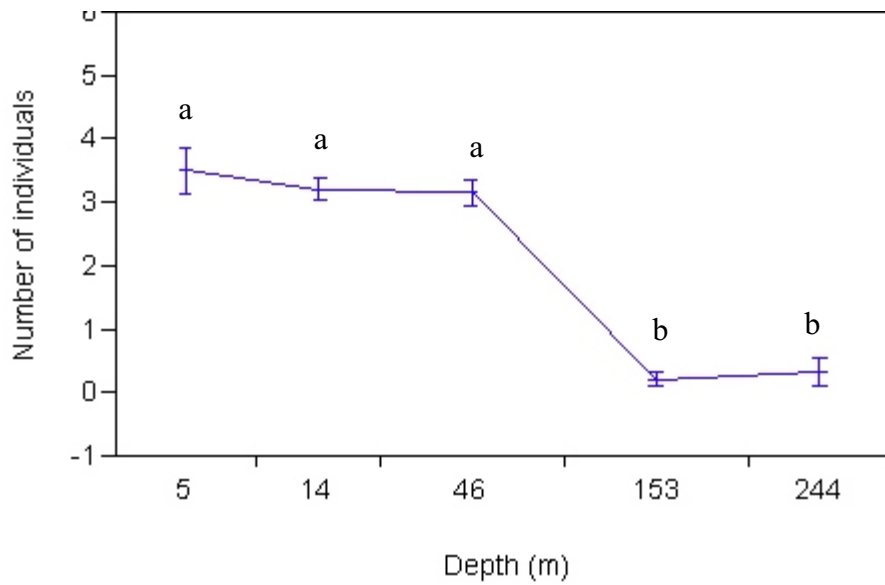
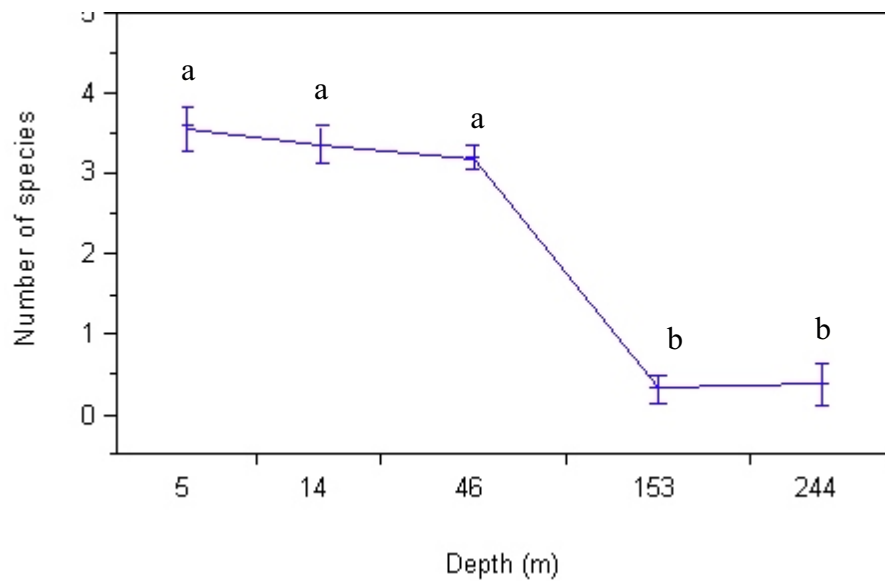


Figure 1.5. Mean ( $\pm$  standard error) of the number of species of molluscs and individuals per collector with depth. Data for species were square-root transformed and for individuals were log transformed to ensure homogeneity of variance. (<sup>ab</sup>Means with same superscript are not significantly different, based on Tukey HSD procedure.)

Table 1.1. One-way ANOVA of mean number of species of molluscs and individuals with depth as a treatment ( $\alpha$  0.05).

| Mollusc category   | Source    | df | Type I SS | F    | r <sup>2</sup> | P        |
|--------------------|-----------|----|-----------|------|----------------|----------|
| No. of Species     | Depth (m) | 4  | 83.78     | 64.7 | 0.88           | < 0.0001 |
|                    | Error     | 33 | 10.67     |      |                |          |
|                    | Total     | 37 | 94.45     |      |                |          |
| No. of Individuals | Depth (m) | 4  | 85.23     | 53.3 | 0.86           | < 0.0001 |
|                    | Error     | 33 | 13.17     |      |                |          |
|                    | Total     | 37 | 98.40     |      |                |          |

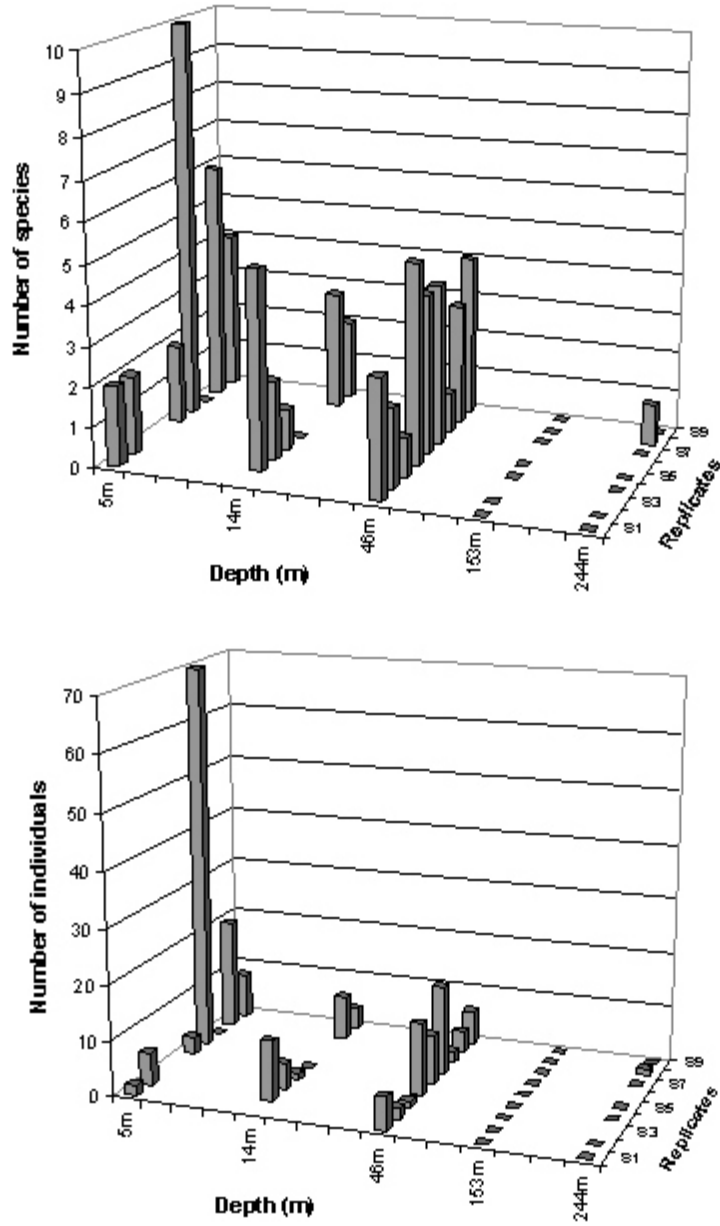


Figure 1.6. Number of species of bivalves and individuals by collector with depth. "S1 - S9" refer to the nine replicate samples taken at each site. Blanks indicate lost collectors.



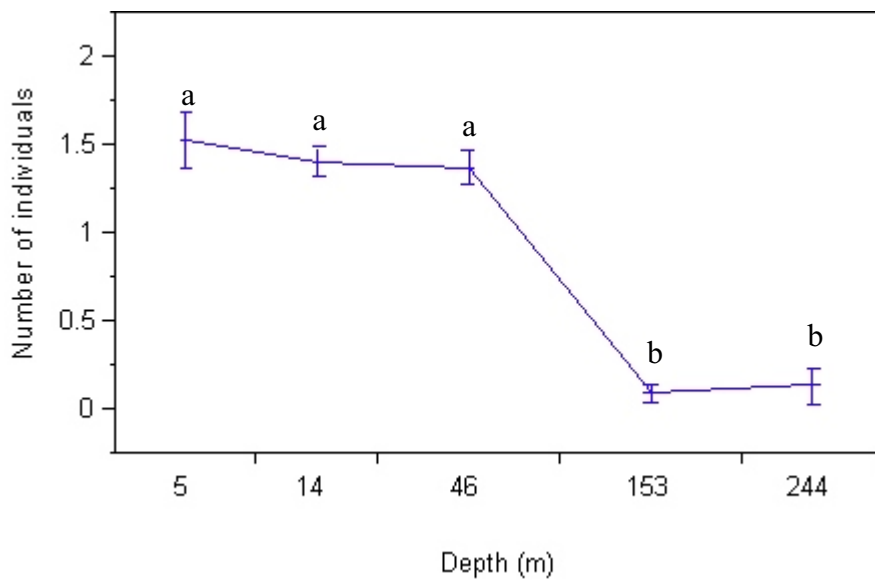
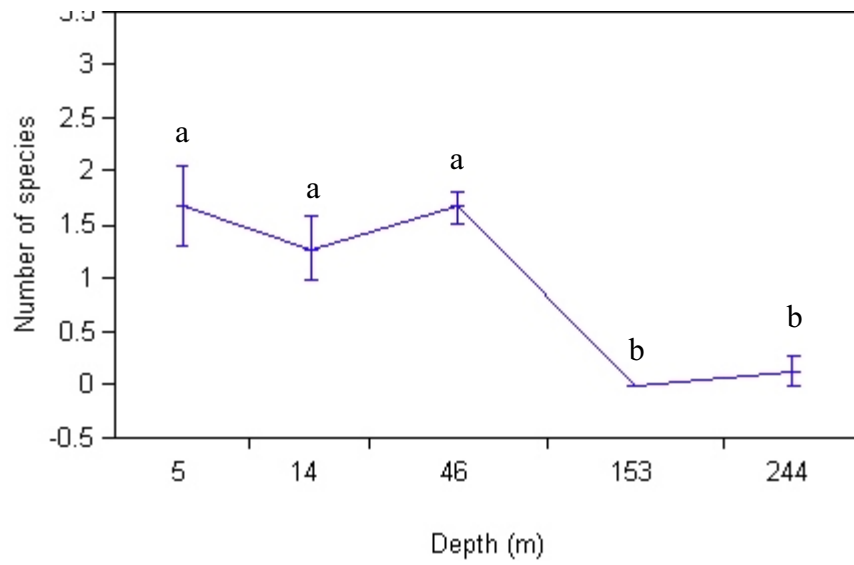


Figure 1.7. Mean number per collector and standard error of species of bivalves and individuals with depth. Species data were square root transformed and individuals were log transformed to ensure homogeneity of variance. (<sup>ab</sup>Means with same superscript are not significantly different based on Tukey HSD procedure.)

Table 1.2. One-way ANOVA of mean number of species of bivalves and individuals with depth as a treatment ( $\alpha$  0.05).

| Mollusc category   | Source    | df | Type I SS | F    | r <sup>2</sup> | P        |
|--------------------|-----------|----|-----------|------|----------------|----------|
| No. of Species     | Depth (m) | 4  | 22.06     | 16.1 | 0.66           | < 0.0001 |
|                    | Error     | 33 | 11.26     |      |                |          |
|                    | Total     | 37 | 33.33     |      |                |          |
| No. of Individuals | Depth (m) | 4  | 16.07     | 53.3 | 0.86           | < 0.0001 |
|                    | Error     | 33 | 2.48      |      |                |          |
|                    | Total     | 37 | 18.56     |      |                |          |

### *Gastropods*

The total number of species and individuals of gastropods per collector comprised far more than the numbers of bivalves in the collectors (Figure 1.8). As with the total molluscs and bivalves, the ANOVA showed that mean number of species and mean number of individuals at the upper three depths (5 m, 14 m, 46 m) was significantly different from the means of these categories at the two deepest depths (153 m and 244 m) ( $P_{\text{species}} = 0.0001$ ;  $P_{\text{individuals}} = 0.0002$ ) (Figure 1.9) (Table 1.3). Tukey HSD ( $\alpha .05$ ) tests were used to detect differences between pairs of means at the various depths.

### *Species diversity*

The Shannon-Wiener index was used to show trends in diversity over depth for total molluscs, gastropods, and bivalves (Figure 1.10). The index incorporates the distribution of individuals among species as well as number of species:  $H' = -\sum[p_i \cdot \ln(p_i)]$  where  $p_i$  is the relative abundance of the  $i$ th species ( $\sum p_i = 1.0$ ). Because the number of species and individuals of bivalves in the collectors were so low at the 153 m and 244 m depths, diversity was much lower relative to the other depths, but could not be reliably estimated at those depths due to very small numbers collected. This index ( $H'$ ) is used here primarily for comparison with other studies over similar depth gradients. For example, Liddell et al. (1997) showed a very similar pattern for species diversity of sessile epifauna over depth, particularly for coral and macro algae, which decline precipitously in deeper habitats beyond the shelf edge. Furthermore, even though Liddell et al's. (1997) methods enabled visual observations on the near vertical relief of the Upper Wall, percent

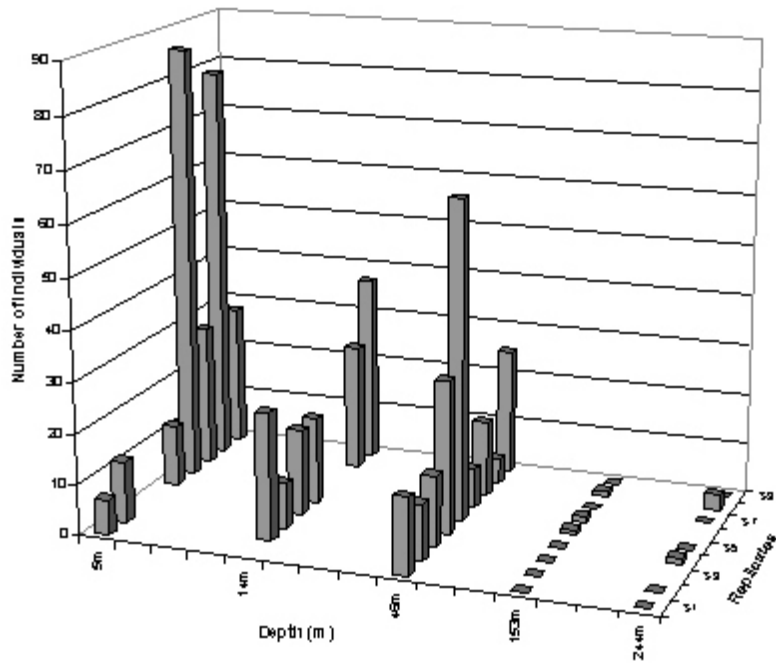
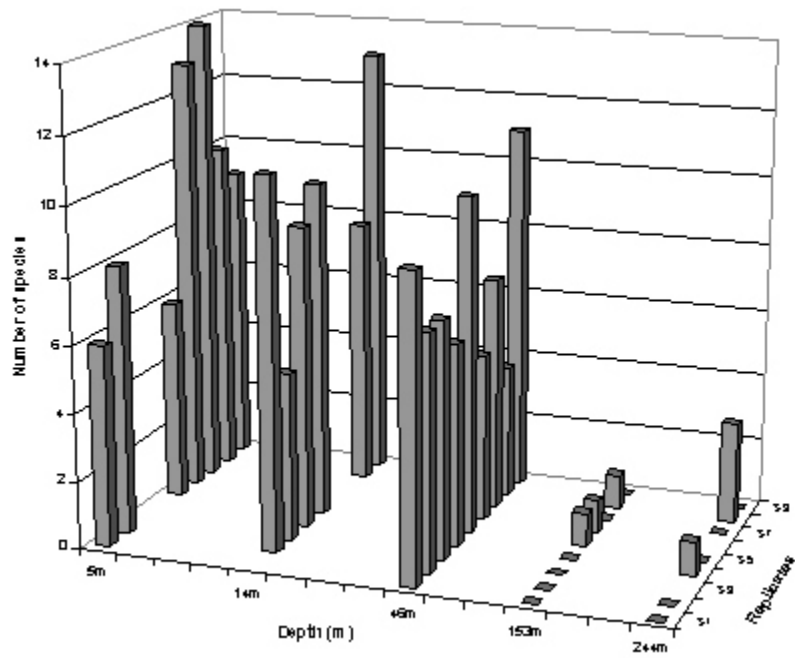


Figure 1.8. Number of species of gastropods and individuals by collector with depth. "S1 - S9" refer to the nine replicate samples taken at each site. Blanks indicate lost collectors.

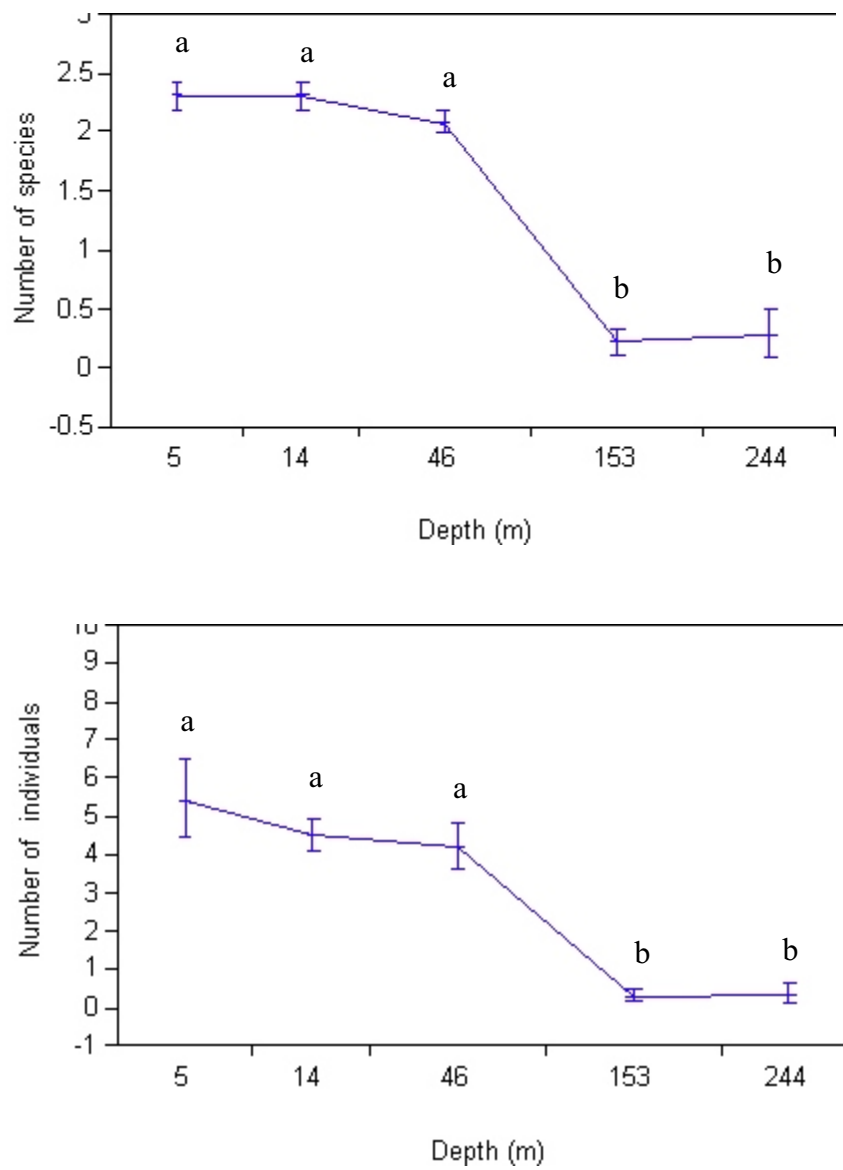


Figure 1.9. Mean number ( $\pm$  standard error) per collector of species of gastropods and individuals with depth. Data were log transformed to ensure homogeneity of variance. (<sup>ab</sup>Means with same superscript are not significantly different based on Tukey HSD procedure.)

Table 1.3. One-way ANOVA of mean number of species of gastropods and individuals with depth as a treatment ( $\alpha$  0.05).

| Mollusc category   | Source    | df | Type I SS | F    | r <sup>2</sup> | P        |
|--------------------|-----------|----|-----------|------|----------------|----------|
| No. of Species     | Depth (m) | 4  | 35.66     | 67.4 | 0.89           | < 0.0001 |
|                    | Error     | 33 | 4.36      |      |                |          |
|                    | Total     | 37 | 40.02     |      |                |          |
| No. of Individuals | Depth (m) | 4  | 71.64     | 46.1 | 0.848          | < 0.0001 |
|                    | Error     | 33 | 12.81     |      |                |          |
|                    | Total     | 37 | 84.46     |      |                |          |

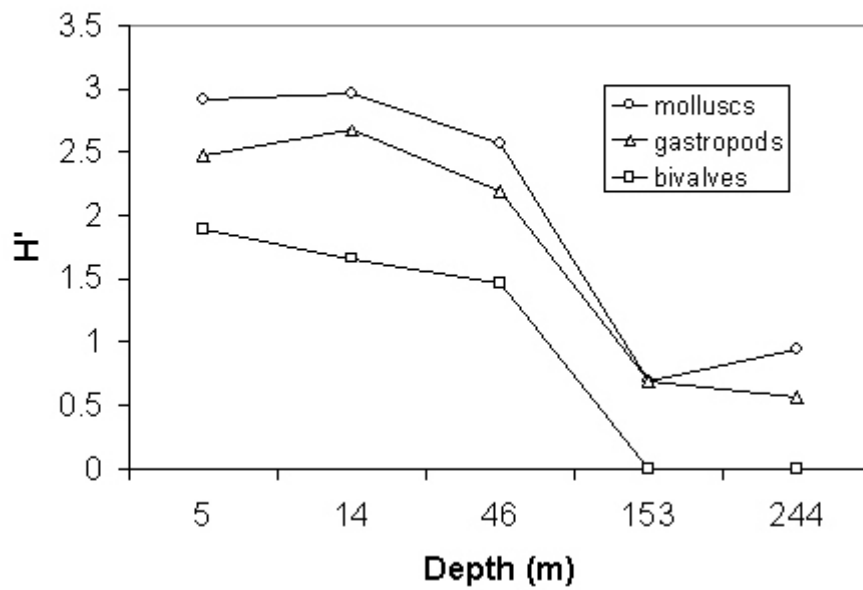


Figure 1.10. Diversity (Shannon-Wiener Index) over depth for total molluscs, gastropods, and bivalves. Because of very low sample sizes, the data for 153 m and 244 m depths are not reliable.

cover for observable species also dropped precipitously from the Platform Edge downward.  $H'$  is not further used in this analysis for statistical interpretation because of the uncertainty of whether the index reflects differences in species richness or species evenness (Gotelli and Entsminger, 2001). Rarefaction analysis in the following section compensates for unequal sample sizes and allows for more meaningful interpretation of the species data.

### Rarefaction

Rarefaction curves for bivalves, gastropods, and total molluscs were computed (Figure 1.11) for the three upper depths, though collections at 153 m and 244 m are not shown for any of the rarefaction analyses because either sample sizes were not large enough to compute rarefaction curves or the rarefaction curves were too small to be seen in the figures. The rarefaction curve for the 46 m depth appears to lie much farther below the 5 m and 14 m curves; there is no overlap in the confidence limits at the upper end of the 46 m curve with the other two curves (Figure 1.12), which suggests that there may be a real difference in species richness between the 5 m and 46 m depths. Confidence limits were superimposed at the abundance level 50 on the bivalve graph in Figure 1.11 to check for overlap. Since confidence limits do not allow for direct testing of hypotheses to detect significant differences between the curves, the EcoSim rarefaction curves were used to simulate random collections of bivalves to compare species richness between the two sites where there appears to be a difference (5 m and 46 m). Fifty-six individuals of seven species were collected from the 46 m depth. Based on the rarefaction analysis with a user-defined specific abundance of 56, a random sample of 56 individuals from the 5 m depth



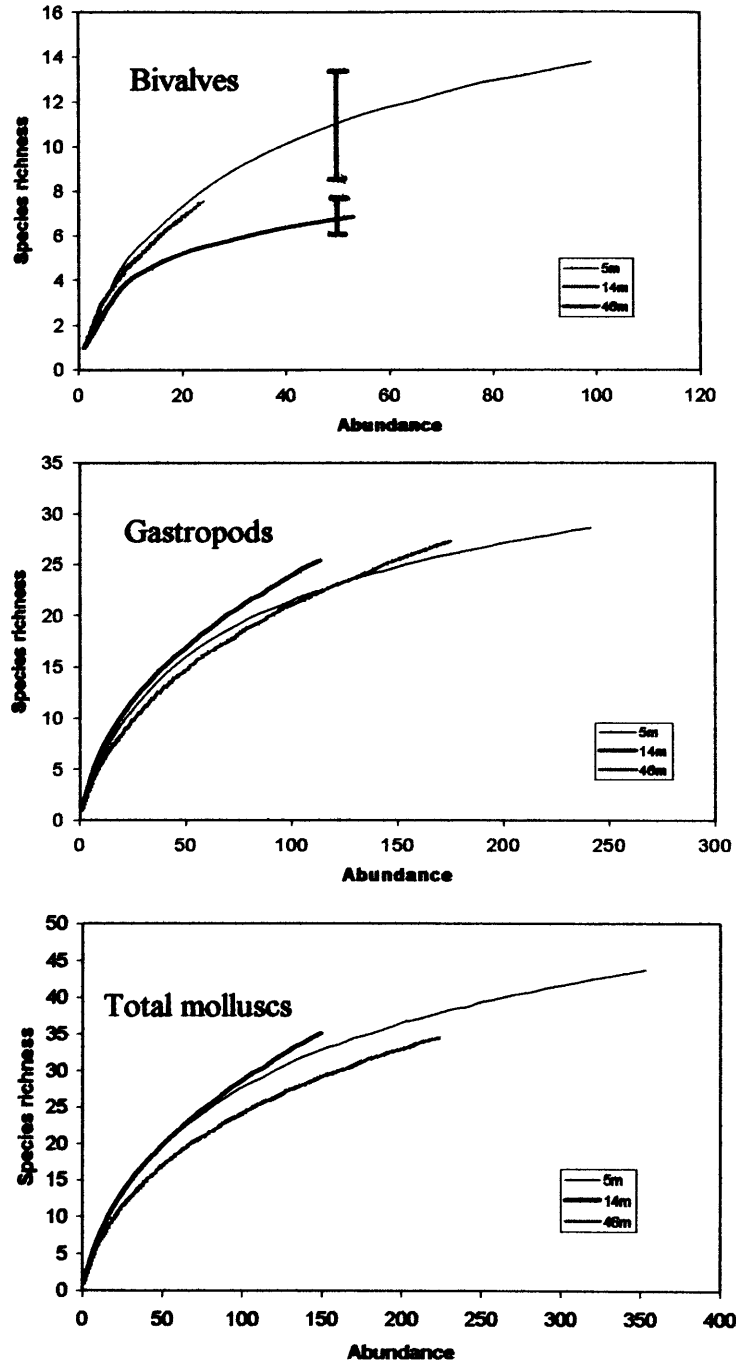


Figure 1.11. Rarefaction curves for collections of bivalves, gastropods, and total molluscs at 5 m, 14 m, and 46 m depths off Lee Stocking Island, Bahamas. The 95% confidence limits shown on the top panel suggested that there may be a real difference in species richness between the 5 m and 46 m depths.

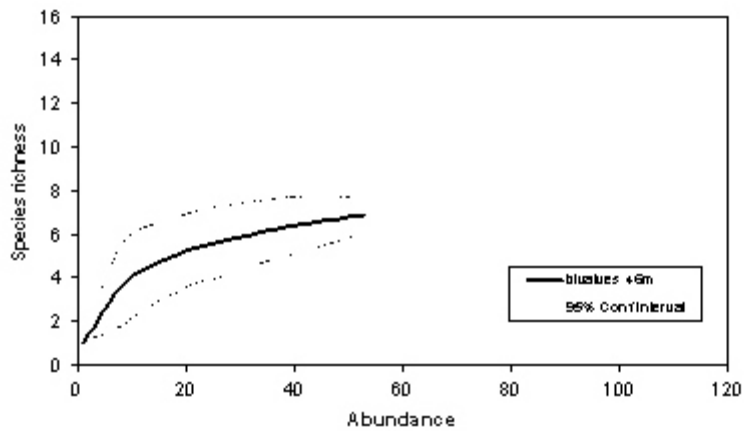
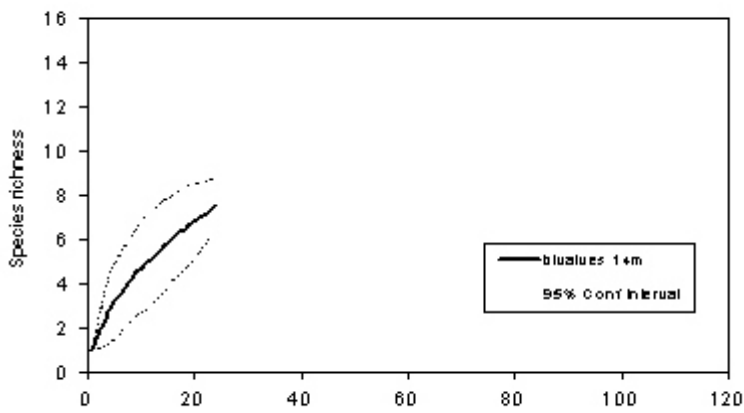
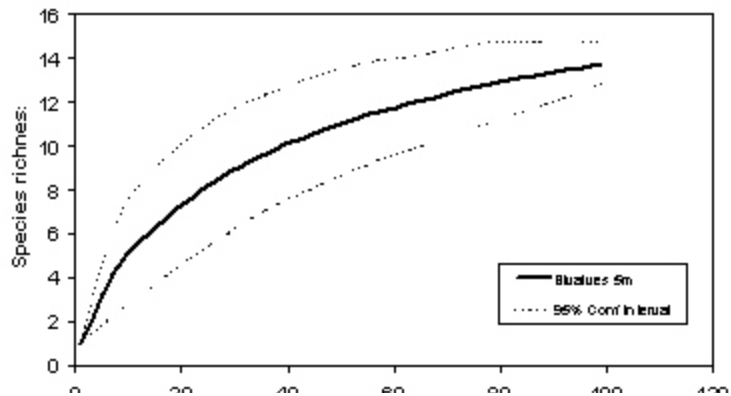


Figure 1.12. Rarefaction curves for collections of bivalves at 5 m, 14 m, and 46 m depths off Lee Stocking Island, Bahamas showing 95% confidence intervals.

would be expected to contain approximately 12 species. Based on the EcoSim analysis, for a random sample of 56 individuals, there was an average of 11.65 species represented, with a variance of 1.35. The 95% confidence interval in this instance (using 56 individuals) ranges from 9.17 to 13.86 species. Therefore, 95% of the time that a random sample of 56 individuals is drawn from the 5 m depth assemblage, one can expect to find between approximately nine and 14 species.

The 56 individuals collected from the 46 m depth assemblage represent only eight species. Thus, the higher species richness of bivalves seen at the 5 m depth collections has a 95% probability of not simply being an artifact of the greater number of individuals collected, and there is likely a difference in species of bivalves diversity between the two sites, i.e., species diversity of bivalves is higher at the 5 m site than at the 46 m site.

Because rarefaction curves reflect the shape of the underlying species abundance distribution (Gotelli and Graves, 1996), an uneven distribution of species (i.e., a few species with a large number of individuals) would yield a curve with a linear increase in number of species with increased number of individuals. In contrast, if all species were evenly distributed, that is, with equal abundance, the rarefaction curve would rise steeply to an asymptote, then level off. Thus, in the bivalve rarefaction curves, the least evenly distributed data can be seen in the curve for 14m depth which appears as the most linear of the three curves. A more quantitative assessment of evenness is provided in this section using Hurlbert's Probability of an Interspecific Encounter .

Rarefaction analysis shows no difference in species richness of gastropods between 5 m, 14 m, and 46 m depths (Figure 1.11). The number of individuals and species of

gastropod molluscs collected at the 5 m, 14 m, and 46 m depths are listed in Chapter 2. In the rarefaction curves for total molluscs (gastropods and bivalves), the additional species and individuals tend to level off more than is seen in the individual bivalve and gastropod rarefaction curves, however, there is again no significant difference in species richness between the three shallowest depths. Since none of the rarefaction curves clearly reach an asymptote, more species are likely to occur in the natural communities at each of the depths where data were rarefied than were collected in this study. This may be due to a number of reasons, including sampling effort, the selectivity of the benthic collectors for a limited size range of organisms, and habitat preference of some species.

However, overwhelmingly more species and individuals were *collected* at the 5 m, 14 m, and 46 m sites compared to the 153 m and 244 m sites with approximately the same collecting effort. On the basis of the statistical analyses provided earlier in Chapter 1, the *abundance* of organisms is likely lower in the deeper sites (153 m and 244 m), though the low numbers there could also be related to differential effectiveness of the benthic collectors in the deep water habitats. Fewer *species* were *collected* in the two deepest sites than in the three shallower sites, and rarefaction analysis shows that the true number of species of bivalves is lower at 46 m than at 5 m. These patterns suggest that true species richness may decline with depth, (at least for bivalves), but definitive conclusions about changes in species numbers over the five depths analyzed in this study can not be made because the small sample sizes at the two deepest sites prevent their analysis by rarefaction.

## Evenness

Since the ranges of the values of the index in both plots (Figure 1.13) are so close together, and the confidence limits overlap, one can not conclude that there are significant differences in evenness among the sites (Gotelli and Graves, 1996).

## Environmental Variation over the Depth Gradient

To identify which parameters are most likely to influence abundance and distribution of molluscs off Lee Stocking Island, data on a suite of environmental variables were obtained for the five depths and habitat types. These parameters were analyzed by depth to determine which appeared to be most relevant to the observed patterns in the mollusc data set.

Salinities average just over 38 parts per thousand (ppt) in the shallow cays around Lee Stocking Island (Pitts and Smith, 1993). High salinity “spikes” occur in shallow water around the inshore cays depending on winds and water temperature. These spikes are episodic, resulting from hypersaline water leaving the shallow Great Bahama Bank with ebb tides, and are associated with density currents on the shelf in the warmer months when evaporation is highest. Just offshore in Exuma Sound, salinities from Conductivity, Temperature, and Depth (CTD) profiles typically show little change (only around one ppt) over the depth range in this study, ranging from around 35.8 - 36.8 ppt from 0 - 500 m (Hickey et al., 1993, 1994, 1995).

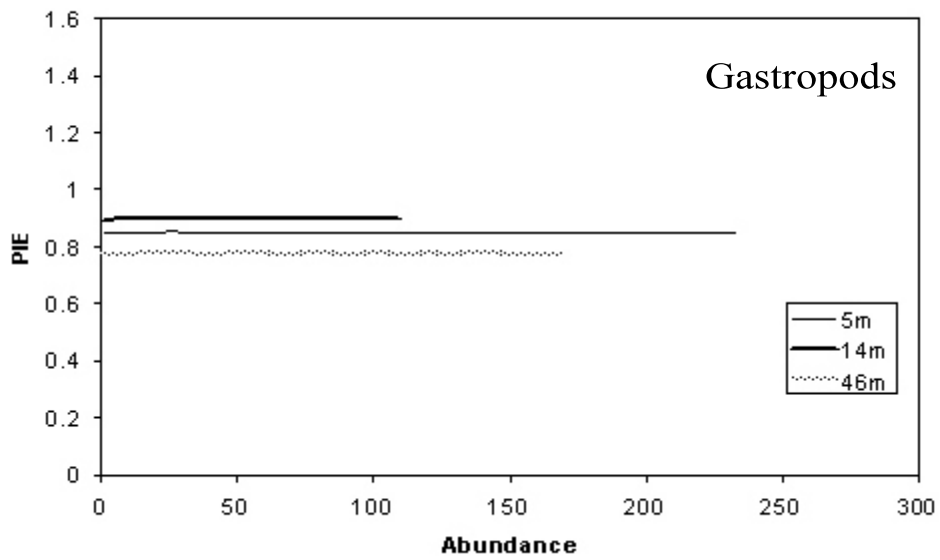
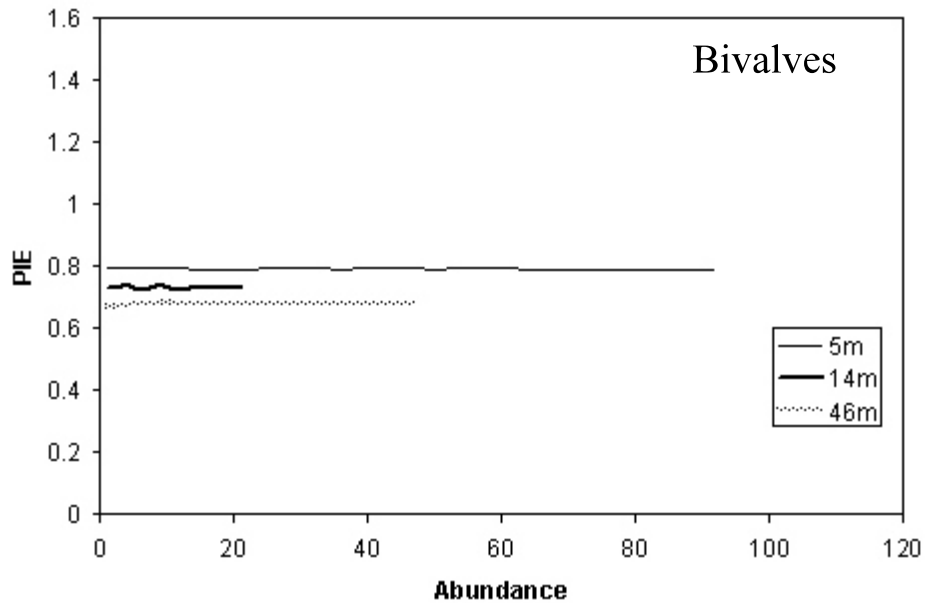


Figure 1.13. Hurlbert's Probability of an Interspecific Encounter (PIE) for bivalves and gastropods at 5 m, 14 m, and 46 m, graphed as a function of abundance in the sample.

CTD profiles in Exuma Sound show that dissolved oxygen varies only between 5 and 10 mg/L, which indicates a relatively well oxygenated environment. These values are significantly above the 2 mg/L limit that is considered hypoxic in marine coastal environments (Rabalais et al., 1999; Rabalais and Turner, 2001). Because of the relatively minor variation other than possibly episodic events over the depth gradient of 244 m in conditions, salinity and dissolved oxygen were not analyzed further.

### *Irradiance*

Photosynthetically Available Radiation (PAR) is the range of wavelengths of the electromagnetic spectrum, peaking in the blue and red regions, that plants use for photosynthesis. PAR often is estimated using only the visible wavelengths, 400 - 700 nm (Mobley, 1994). Data on PAR were available in the immediate vicinity of Lee Stocking Island from submersible CTD recordings from near the surface to around 245 m (Dennis and Proft, 1994). Data on PAR over a similar depth profile from a site off San Salvador Island, Bahamas (Littler et al., 1985) were used as a comparison to help determine whether the profile of PAR off Lee Stocking Island is a reasonable representation of typical irradiance with depth in the generally clear waters of the Bahamas. Photon flux densities for the data on PAR from San Salvador are characteristic of those for extremely clear oceanic water, and are comparable to those at the site off Lee Stocking Island. The water clarity at Lee Stocking is even greater than some other areas of the Bahamas that are considered to have high water clarity, such as northwest Providence Channel (Gordon and Dera, 1969). Subsequent refinement of estimates of water clarity by Jerlov (1976) categorizes water off Lee Stocking Island as falling between Type IA and IB, very close to

conditions in the Sargasso Sea. The area off Lee Stocking Island thus is very oligotrophic, and shows little seasonal variation in water transparency (G. Dennis, pers. comm.).

PAR profiles from 5-245 m were taken by submersible on the deep water transect BA off Lee Stocking Island on December 5, 1993 (Figure 1.14). While not a linear relationship, the greatest change in PAR is seen in the first 20 - 25 m, followed by a more gradual decline to around 45 m, a slower decline to very low values at around 85 m, then relatively little change to 245 m. Because water clarity is minimally influenced by surface runoff in the Bahamas (Sealy, 1994), the values of PAR at the surface of the adjacent Exuma Sound should provide an adequate representation of PAR at the shallow inshore sites around Lee Stocking Island.

#### *Temperature*

Weather data collected over six years at the Caribbean Marine Research Center at Lee Stocking Island show that air temperatures range from 13 - 34°C, with an annual average of 26°C. Inshore water temperatures at Lee Stocking Island range from 20 - 33°C, with an annual average of 27°C. Water and air temperatures are warmest from July through September and coldest from January through March.

A profile of water temperature from 5 - 245 m was taken by submersible on the deep water transect BA off Lee Stocking Island on December 5, 1993 (Figure 1.14). Water temperature in this profile varies less than 1°C from 5 m to around 100 m, then exhibits a gradual decline of about 7°C from 100 - 245 m.



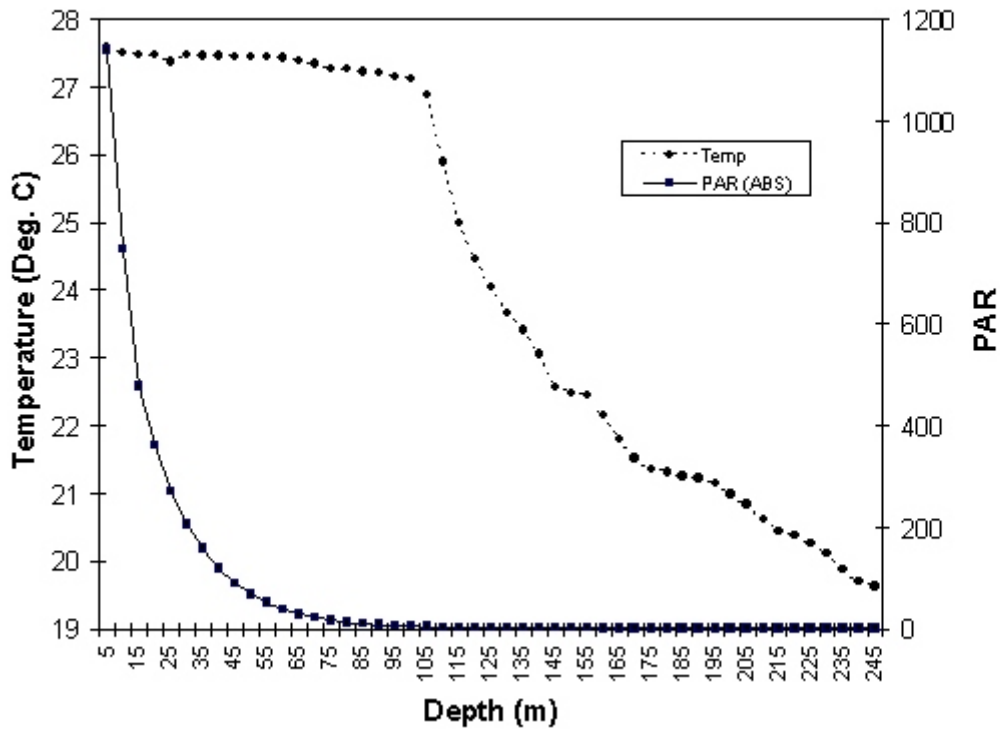


Figure 1.14. Profiles of Photosynthetically Available Radiation (PAR) ( $\mu\text{mol s}^{-1} \text{m}^{-2}$ ) and water temperature ( $^{\circ}\text{C}$ ) from 0 - 245 m, taken by submersible on the deep water transect BA off Lee Stocking Island on December 5, 1993. Data on PAR are denoted as “ABS” (absolute), since PAR occasionally is reported as percent transmission in the water column with depth. The figure is a composite from CTD profiles (NEKTON GAMMA dive # GA272) from Dennis and Proft (1994). Data were taken with a Li-Cor CL-193SA Spherical Quantum Sensor that measured Photosynthetic Flux Fluence Rate (also called Quantum Scalar Irradiance) in  $\mu\text{mol s}^{-1} \text{m}^{-2}$ .

Data on water temperatures also were available from the Caribbean Marine Research Center for the specific study sites at Norman's Pond Cay, South Perry Reef, and from CTD profiles in Exuma Sound for the transects on the deep water slope (Hickey, et al., 1993; 1994; 1995; and Hickey, pers. comm.). Mean annual water temperatures from these data for the five study sites were computed on the raw data (Table 1.4). Hickey's data from repeated annual circulation surveys (cited above) in Exuma Sound exhibit significant seasonal variability, though usually within a 10°C range. Because of the effects of the platform on water temperature around the islands, these site-specific data on water temperature are more representative of conditions at the inshore collection sites at 5 m and 14 m than the CTD profiles off the shelf break in the adjacent Exuma Sound. In both the inshore site-specific data sets for water temperature and in the data from CTDs for Exuma Sound, the mean decline of temperature over 240 m is about 7°C. Below the thermocline (< 50 m off Lee Stocking Island) water temperature becomes more homogeneous with increasing depth (Hickey et al., 1993a; Hickey et al., 1993b).

#### *Habitat Heterogeneity*

Means and ranges of variance in distance from the bottom, when the observer moves along a horizontal line above the sampling site and distance above the bottom is measured by the distances between laser dots, are used here to estimate heterogeneity of the structural environment (see Methods). The 5 m site consists of a large field of patch reefs adjacent to Norman's Cay; the collectors were deployed just inside extensive thickets of *Acropora cervicornis* and adjacent *Thalassia* sp. beds in the deeper seaward channel that extends down to approximately 8-10 m. This area, which is subject to extremely

Table 1.4. Summary of key environmental variables with depth off Lee Stocking Island, Bahamas. Values in parentheses represent the percent of each variable relative to the value observed at 5 m. PAR = Photosynthetically Available Radiation. Micro-habitat heterogeneity was qualitatively assessed by observation.

| Depth (m) | PAR <sup>(1)</sup> (micromols s <sup>-1</sup> m <sup>-2</sup> ) | Mean Water Temperature (°C)   | Macro-habitat Heterogeneity (cm) | Micro-habitat Heterogeneity |
|-----------|---|-------------------------------|----------------------------------|-----------------------------|
| 5         | 1,139.0 (100%)  | 26.61 <sup>(2)</sup> (100%)   | 688 (100%)                       | High                        |
| 14        | 477.5 (41.9%)   | 26.63 <sup>(2)</sup> (100.1%) | 765 (111.2%)                     | High                        |
| 46        | 89.5 (7.9%)   | 26.98 <sup>(3)</sup> (101.4%) | 505 (73.4%)                      | Intermediate                |
| 153       | 1.4 (0.1%)  | 23.04 <sup>(3)</sup> (86.6%)  | 246 (35.8%)                      | Low                         |
| 244       | 0.8 (0.1%)  | 19.81 <sup>(3)</sup> (74.4%)  | 401 (58.4%)                      | Low                         |

<sup>(1)</sup>PAR values were “binned” or rounded to facilitate measurements from a single CTD profile and are considered approximate representations for the five depths used in the present study. <sup>(2)</sup>Annual means were computed from monthly mean water temperatures based on daily observations. SD for 5m is  $\pm 2.0^{\circ}\text{C}$  and SD for 14m is  $\pm 2.1^{\circ}\text{C}$ ; <sup>(3)</sup>Annual means were computed from four discrete CTD seasonal samples within  $10^{\circ}\text{C}$  inter-annual variability with highest variability at the shallowest shelf site of 46m (153m and 244m show less inter-annual variability); macrohabitat heterogeneity values are mean variances.

strong tidal currents in a relatively constricted channel between Norman's Cay and several smaller seaward cays, is characterized by sandy bottom, hard corals, gorgonians, macroalgae, and coral rubble. This patch reef environment showed a relatively high mean variance in distance above a horizontal transect (688 cm), but the variance range (104 cm) was smaller than observed in the other four habitats (Figure 1.15). The low range of variance at the 5 m site can be explained by the moderate but regular relief on the bottom caused by abundant corals and rubble. Mean macro-habitat heterogeneity, is highest at the 14 m site, South Perry Reef (mean variance 765 cm). South Perry Reef is the only one of the five habitat sites that exhibits the structural characteristics and zonation of a typical western Atlantic fringing coral reef (Tryon, 2000). South Perry Reef consists of a spatially complex fore reef, a submerged wave-worn shallow platform and leeward talus slope. The variance range (241 cm), however, is greater at 14 m than at the 5 m site, reflecting the greater irregularity and height of coral formations on the fore reef, but the variance range at this site is lower than that at the 244 m site.

Proceeding seaward towards Exuma Sound, the site at the Platform Edge at approximately 46 m marks the beginning of the drop off of the shelf into deep water. The macrohabitat heterogeneity at this site is moderate, with a mean variance of 505 cm and variance range of 241 cm. The Platform Edge consists of relatively low relief and some evidence of irregular spur and groove formations, with extensive *Lobophora* sp. and plating corals.

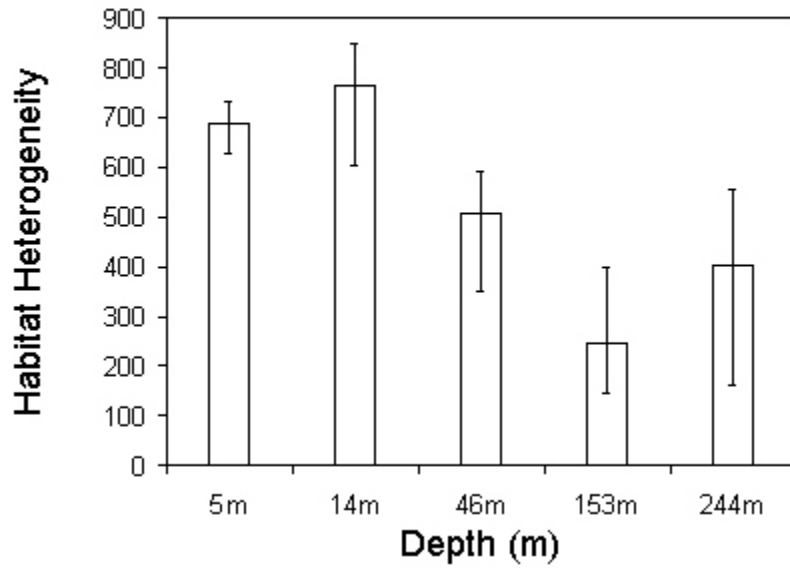


Figure 1.15. Macro-habitat heterogeneity, represented by means of variances in distance of a horizontal transect from the bottom, with variance ranges for five depths off Lee Stocking Island, Bahamas.

Beyond the Platform Edge, the Upper Wall appears nearly vertical with overhangs and occasional ledges, plating corals, sponges, and algae. The nearly vertical relief of the Upper Wall precluded deployment of collectors. More level topography was encountered in the Lower Wall zone, where collectors could be securely deployed by the submersible at about 153 m. This area showed the least macro-habitat heterogeneity (mean variance 246 cm, with a range of 252 cm), reflecting a sediment-dominated slope with occasional hard substrate and boulders that accounted for most of the variability in the bottom topography. Mean variance of the habitat was 64% less than in the shallow (5 m) site and 68% less than the South Perry fore reef (14 m).

The Cemented Rock Slope at 244 m showed moderate structural variability (401 cm mean variance), but the greatest variance range (395 cm) of any of the habitats. Mean variance of the habitat was 42% lower than in the shallow (5 m) site and 48% lower than the South Perry fore reef (14 m). The larger variance range at the 244 m site is caused by a relatively even bottom occasionally punctuated by huge “talus blocks” described by McNeill and Grammar (1993) for this zone.

While the laser method does provide a valuable quantification of the structural diversity of the macro-habitat, it fails to analyze the tiny holes and crevices of the microhabitat that provide refuges for and determine the abundance of the reef cryptofauna, including many molluscs (Moran and Reaka, 1980, 1981; Reaka 1985, 1991). Qualitative assessment of the hard substrate at the two lower depths (153 m and 244 m) showed that it had few holes and crevices, while coral substrate at 5 m and 14 m was riddled with bioeroded holes, providing abundant microhabitat suitable as refuges for benthic animals.

Hard substrate at 46 m appeared to be somewhat bioeroded, with intermediate porosity. Both macro- and micro-habitat heterogeneity are highest at the 5 m and 14 m depths.

Three environmental variables, PAR, water temperature, and habitat heterogeneity (including microhabitat and macrohabitat heterogeneity), likely influence the distribution and abundance of bivalve and gastropod molluscs over depth off Lee Stocking Island, Bahamas (Table 1.4). It is apparent that all three of these parameters exhibit substantial variation among the five habitats in this study. PAR showed the greatest change (almost 100 %) over the depth range of 5-244 m. Water temperature declined only 25%, although the 7°C decline may significantly decrease the metabolic rates of organisms. For comparison, seasonal variability of water temperature is less than the 7°C at the shallowest sites (seasonal range of 6°C at 5 m; 3.5°C at 14 m; and up to a 10°C range at 46 m, with decreasing seasonal range with depth beyond 46 m). Macrohabitat heterogeneity declines 42-68% from the shallowest 2 sites to the deepest 2 sites. Although unquantified, microhabitat heterogeneity also declines over this range of depths. The pattern of decline for both species and abundance in both groups most closely corresponds to the patterns of the decline in temperature and habitat heterogeneity.

## DISCUSSION

Fewer species of molluscs and individuals of molluscs were collected at the two deeper sites (153 m and 244 m) than at the three shallower sites (5 m, 14 m, and 46 m), even though collecting effort (number of traps) was approximately the same at the two deeper sites compared to the shallower sites. Relatively few collectors were lost, and the

loss was generally spread among depths. Although a definitive conclusion of lower diversity at the two deepest sites can not be made because of the small sample sizes at 153 m and 244 m, it is possible to conclude, on the basis of the statistical analyses, and since comparable collecting methods and intensity were used, that the *abundance* of bivalves, gastropods, and total molluscs collected probably was lower in the two deepest sites. Although it is possible that some environmental factor affected the collect-ability of individuals at greater depths, the most likely explanation for the lower numbers of individuals *collected* at greater depths is that *true* abundances and/or recruitment rates are lower in the deeper habitats.

Species richness also declined with depth in some cases. The number of species *collected* for bivalves, gastropods, and total molluscs was significantly lower at 153 m and 244 m than in the three shallower sites. Rarefaction showed that fewer species of bivalves occurred at 46 m than at 5 m. However, rarefaction did not show that the number of species of gastropods or total molluscs declined among 5 m, 14 m, or 46 m depths, and small sample sizes prevented any definite conclusions about patterns of species number down to 153 m and 244 m.

The size of the space available for colonization within the collectors (3 cm) used in the present study may have limited the size of specimens in some cases. However, the largest molluscs collected were typically gastropods that did not exceed a maximum of approximately 2 cm shell height, and most specimens were much smaller. The collectors were effective in attracting numerous species of molluscs in the three shallower sites, though they may have been, to some extent, selective for species that are small in size.



Given that many species of molluscs in the Bahamas are small and cryptic, the collectors likely did attract relatively natural assemblages at the various depths. This assumption is further supported by the findings in Chapter 3 where an analysis of 960 species of gastropods from the Academy of Natural Sciences (ANS) Western Atlantic Gastropod Database showed that nearly three-quarters of the gastropod species in the ANS data set were less than 30 mm. Since the size of the openings in the benthic collectors used in my Lee Stocking Island collections were 3 cm (30 mm), the vast majority of gastropods that occur in the Bahamas could have potentially entered the collectors based on their size. The results in my study reflect only a single collection temporally, due to the inherent difficulties of deep water collecting. Deployment and retrieval of the collectors on a seasonal basis for a full annual cycle would likely provide more insight into the distribution and diversity of benthic molluscs over the depth gradient 5 - 244 m.

Studies of benthic biota have tended to focus on depth (Bergen et al. 1998) without an analysis of the suite of physical parameters that change with depth. I examined five environmental parameters (salinity, oxygen, irradiance, temperature, and habitat heterogeneity) over the depth range studied. The small variations in salinity over the depth gradient (except during episodic spikes due to evaporation on the shallow Great Bahama Bank) were judged to be inconsequential for patterns of diversity and abundance over the depth range studied. Oxygen concentrations also showed relatively minor variation over depth, and were well above hypoxic thresholds that might affect the physiology or ecology of benthic organisms. While at a disadvantage in hypoxic conditions due to their relative lack of motility compared to fishes and crabs that can migrate out of hypoxic areas,

molluscs can endure brief episodes of unfavorable conditions (hypoxia or high salinity) because of their ability to close up, clamp down on the substrate, or retreat into a crevice during inhospitable events.

Although temperature shows the least proportional decline with depth, the decline of 7° C potentially can have important effects on the physiology, activity levels, and interactions among organisms, since metabolic rates decline by at least half with every 10°C decrease in temperature (Giese 1979; Levinton, 2001). Temperature extremes also may affect organisms. During low tides and especially during periods when stagnant water masses remain on the Great Bahama Bank, unusually warm ( $\geq 30\text{-}33^\circ\text{C}$ ) hypersaline water can become entrained in cross-shelf currents, and adversely affect benthic organisms; these events have been observed to cause significant bleaching in corals (B. Hickey, pers. comm.). The effects of these thermal episodes on molluscs, though, are unclear, since molluscs can close themselves off from the environment (this may not entirely insulate them from the effects of external temperature on metabolism, however). Species of molluscs that have surface-dwelling planktonic larvae are likely distributed more rapidly and widely in waters located above the thermocline in deep water adjacent to Lee Stocking Island ( $< 50\text{ m}$  in my study), and possibly have a higher survival rate. The thermocline marks the limit of the well-mixed layer, which also has much higher current velocities due to wind stress (Hickey et al., 1993a; Hickey et al., 1993b). Conversely, molluscs with larvae that are not planktonic, or do not seek surface waters when the larvae are located below the thermocline, will not be dispersed very far (D. Johnson, pers. comm.).

Irradiance and habitat heterogeneity are highly likely to affect abundance and distribution of molluscs over the depth range in this study. This conclusion is consistent with the findings of Liddell et al. (1997) in their study of general patterns of sessile epibenthic community structure in the same area over a 10-250 m depth gradient. Based on observations in other studies of depth gradients in the tropics (Houston, 1985), irradiance appears to be a predominant environmental factor regulating diversity and abundance of biota on deep and shallow coral reefs, and likely is an important parameter affecting productivity, abundance, and diversity over depth in the highly oligotrophic waters of Exuma Sound and adjacent shallow areas in the Bahamas. The paucity of molluscan individuals collected at the two deepest sites (153 m and 244 m), particularly, may reflect the limitation imposed by available light to support primary production. Reduction of primary productivity also may be related to the lower numbers of species found at 46 m than at 5 m by rarefaction. Since none of the rarefaction curves clearly reached an asymptote, more species are likely to occur in the natural communities at each of the depths than were collected in this study. Since benthic molluscs have varied feeding modes depending on species (i.e., carnivores, herbivores, detritivores), it is highly likely that lower primary production is a factor in determining abundance and diversity of the benthic biota at the deeper areas of the slope at Lee Stocking Island.

Numerous studies have shown that a more spatially complex environment can support higher biotic diversity (Kohn, 1967; Valentine and Jablonski, 1991). In the present study, *mean* macro-habitat heterogeneity (highest at South Perry forereef, 14 m) decreased in general with depth. The South Perry forereef is a moderately high energy

environment that exhibits a wave-worn submerged crest and is the shallowest barrier to offshore swells from Exuma Sound. Evidence of wave impact (broken coral and rubble) can be observed down to the 14 m depth where the collectors were deployed. The *range* of macro-habitat heterogeneity (“range of variance”), however, is smallest withing the shallow patch reef site (5 m), where abundant similarly-sized coral colonies and rubble were present. In contrast, the deepest site (244 m) contained the highest *range* of macro-habitat heterogeneity (“range of variance”) due to the intermittent presence of huge outcrops or talus blocks.

Micro-habitat heterogeneity, in the form of holes and crevices in the substrate, has been shown to be particularly important for biodiversity on coral reefs, since field experiments have demonstrated that micro-habitat space, not food, limits populations of motile benthic reef organisms; this micro-habitat structural complexity provides benthic reef organisms safe refuges from predators (Reaka, 1985, 1991; Dominguez and Reaka, 1988). Although only qualitatively assessed in the present study, micro-habitat heterogeneity declined with depth.

When the five major environmental factors are compared, irradiance exhibits the largest percentage decline, followed by habitat heterogeneity, and then by temperature, over the depth gradient studied. While salinity and oxygen concentrations vary relatively little over depth, the percentage change in irradiance, tempearature, and habitat heterogeneity over depth is of considerable magnitude. The *pattern* of decline in species number and abundance of individuals for both gastropods and bivalves over depth, however, most clearly corresponds to the *pattern* of decline of temperature and habitat

heterogeneity suggesting that these factors may be related to diversity and abundance of molluscs over this depth gradient in important ways. Nevertheless, the dramatic drop in light intensity, with its effect upon both phytoplankton and benthic productivity, still may be very significant for benthic organisms throughout the depth gradient. The pattern of the curve for light availability suggests very high levels of productivity at the surface. Dead phytoplankton may fall from the surface to deeper water, and both phytoplankton and benthic production are likely to be passed along the food web and spread into deeper water as particulate and dissolved organic matter. This type of environment would appear to favor gastropods with feeding modes adapted to the available food source. The dissonance between the shapes of the curves for light availability over depth and for the abundance and diversity of molluscs over depth may merely indicate that most of the settling organic matter from the surface is used in the top 50 m and does not reach deeper water. Or, benthic productivity is high above approximately 20 m, but low at other depths.

#### Relation to Other Studies in Deep Reef Habitats

\_\_\_\_\_Liddell et al. (1997) also showed that there is a pronounced dropoff in sessile living cover, particularly corals, beyond the Platform Edge (46 m) in Exuma Sound. Diversity, measured by  $H'$  in their study, was high from 10 m to the Platform Edge, but declined to very low values in his deep water sites (to 250 m), which appears to be consistent with the results of the present study. Liddell et al.'s (1997) study observed pronounced bathymetric zonation of living cover in general (and particularly corals, coralline algae, sponges, and polychaetes) from 10 -150 m.

Benthic algae and sponges have been documented at depths greater than those in the present study in the Bahamas. Littler et al. (1986) reported that certain species of algae have extremely high photosynthetic efficiencies, enabling them to exist at greater depth than sites examined here. Ballantine and Aponte (1995) found that species richness of macroscopically observable species of benthic algae off Lee Stocking Island decrease as a function of depth between 30 and 150 m. Maldonado and Young (1996) observed a bimodal distribution of sponges on the Bahamian slope, with peaks located on the upper slope at around 100 m and between 400 - 500 m, reflecting the adaptations of sponges to greater depths.

Pyle (2000) reported previously undiscovered high fish biodiversity on deep coral reefs from 60 - 150 m on several Pacific Islands. Key findings in his study were that new species assemblages on deep reefs show comparatively low distributional overlap, suggesting higher rates of geographic endemism than for shallow water reef fish assemblages. Based on Pyle's (2000) observations of these patterns, he estimated that as many as 2,000 or more coral reef fish species may still be undiscovered on deep reefs throughout the Indo-Pacific region.

#### Comparison of Coastal Bathymetric Patterns of Biodiversity with those of the Deep Sea

It seems clear from my study and others that coastal coral reef environments show a pattern of highest biodiversity at depths just below their shallowest zone. Lower diversity and abundance in the shallowest zone can be easily understood as the product of harsh environmental conditions, such as wave impact, tidal currents, thermal extremes, salinity changes due to evaporation or occasional fresh water input from storms, exposure

to intense visible and ultraviolet radiation, and occasional nutrient excess from land-based sources leading to eutrophication or increased dominance by a few species. Of these, thermal and salinity extremes from evaporation of water over the extensive shallow Grand Bahama Banks, tidal currents that course on and off the Banks, wave impact from storms, and exposure to visible and ultraviolet radiation through the extraordinarily clear water are most likely to adversely affect biodiversity of intertidal reef flats and immediately subtidal habitats around Lee Stocking Island and in the Bahamas. Somewhere deeper (e.g. 10 - 15 m) reefs exist in the Goldilocks region (conditions that are “just right,” cf. Erwin 2004) and support a luxuriant, flourishing biota of high diversity, structural complexity, and abundance. Below this depth, however, diversity and abundance begin to dwindle, and beneath 100 m the numbers of species and individuals become vanishingly small.

Yet it is now well documented, at least for soft bottom benthos in the North Atlantic, that the shallow coastal region hosts the lowest diversity when comparing relatively shallow shelf ( $\leq$  100 - 200 m) to deeper regions beyond the continental shelf break (e.g., 1,000 - 1,500 m), where diversity peaks. At greater depths (e.g., 2,250 m and beyond), though, diversity withers again (Etter and Mullineaux, 2001). Gastropods show a similar hump-shaped curve over a somewhat broader depth gradient from coastal areas to the deep sea (Rex, 1973; Rex et al., 1997). In contrast to diversity, *abundance* of individuals declines exponentially from the shallow regions outward toward deep water (Etter and Mullineaux, 2001).

The challenge presented here, for the first time anywhere as far as we are aware, is to explain why one should see two humped-shaped curves for diversity: the first as one

progresses down a depth gradient on the coastal shelf (e.g., 0 - 300 m) and a second as one progresses from the shallow shelf out onto the continental slope and into the deep sea (e.g., 100 - 2,500 m). Why should diversity be high near-shore (e.g., 10 - 50 m) but then decline (in most studies) in the deep coastal water (150 - 250 m), only to increase again in much deeper water (1,000 - 1,500 m), but fade again in the very deep, nutrient-impooverished lower abyssal plain environment (to 4,000 m) and beyond?

The present study seeks to provide information on the first dip in the curve, the crucial dip that makes the overall curve bimodal: Why does diversity decline in the deep coastal environment (in this case, deep reef habitat) instead of increase, as it does further along the depth continuum? The analysis presented in previous sections of this paper suggests that a combination of reduced temperature, reduced macro-habitat and micro-habitat heterogeneity, and lack of light and productivity in the deepest reef regions (153 and 244 m) likely contribute substantially to the reduced diversity found in the deep coastal environment. In the deep sea, persistent micro-habitat patch dynamics associated with low temperatures, limited nutrients, long-lived organisms, and reduced reproduction are thought to promote high diversity (Etter and Mullineaux, 2001). Although not as extreme as in the deep sea, reduced temperature and very limited availability of food likely reduce reproduction over the depth gradient studied here (Chapter 2). Body size also declines with depth in the present study, further reducing reproductive output and dispersal ability. Juvenile recruitment clearly did occur in the deep habitats studied (Chapter 2), but numbers of both recruits and adults were extraordinarily low in the two deepest habitats. Very low abundance of individuals means that individual patches of favorable



environment often remain open, which should allow subordinate species to find more patches and persist longer. In the deep sea, however, under-saturation of the habitat and meta-population dynamics are associated with increased, not decreased, diversity. Perhaps temperature (19.8° C at 244 m in contrast to about 5° C at 1,250 m, Levinton, 2001) remains too high in this deep reef environment to allow the patches to endure significantly longer than in the shallow habitats. Perhaps there is less micro-habitat heterogeneity in the deep coastal environment than in deep sea soft sedimentary micro-environments as proposed by Etter and Mullineaux (2001).

The deep reef environment off Lee Stocking Island also is subject to disturbance from bioeroded sediment that cascades off the extensive calcium carbonate banks above. Many areas of hard substrate are covered by deep layers of fine sand and silt that can clog the filtering apparatus of sessile suspension feeders and smother or make locomotion difficult for slow moving benthic organisms. Suspension feeders (such as crinoids) flourish only by standing erect on high boulders or talus blocks where they are exposed to substantial currents (M. Reaka-Kudla, pers. comm.). The deep reef environment clearly experiences periodic disturbances from “current storms.” It is not clear if these plumes sink all the way to the deepest reaches of the study site (153 - 244 m), but the extreme density of the hypersaline water makes that a possibility. If these hot hypersaline waters suddenly flooded organisms at the deeper site, this would present a substantial temperature shock to species acclimated to waters at least 7° C colder than that found in the upper 10 m. Additional physical disturbance results from cliff slides, slope slumps, and the tumbling of house-sized boulders or talus blocks down from the cliffs above. The

consequences of these occasional but severe disturbance events often are observed in submersible dives at the lower two depths of this study (Dennis, G., M. Reaka-Kudla, and R. Wicklund, pers. comm.). It seems likely that many continental shelf edge environments, especially canyons, are subject to at least some of these sources of disturbance. However, according to the intermediate disturbance hypothesis, occasional episodes of disturbance that impact only local patches of deep reef habitat should increase, not decrease, diversity there. On the other hand, when disturbance is pervasive in space and time and also inflicts severe impacts, such as is likely for the carbonate sediment raining down onto the deep reefs off Lee Stocking Island, or for the heavy sedimentation from continental erosion that is characteristic of much of the continental shelf, then diversity can be greatly lowered.

In their study of benthic algae off Lee Stocking Island, Aponte and Ballantine (2001) noted that, at depths below 90 m, the effects of sediment burying was evident particularly on low angled ledges and overhangs and living cover was confined mostly to vertical walls and lower faces of edges not exposed to sedimentation. They concluded that where substrata are low-angled in the deeper reaches of the slope, biota in general are subjected to sediment burial. This observation is consistent with the findings of Liddell and Ohlhorst (1988) where they reported that sedimentation was an important controlling factor on deep Jamaican forereef biota.

A different explanation for the two curves for diversity over depth in deep reef environments and across a broader depth gradient from the continental shelf to deep water (2,250 m) could be simply that two separate types of habitat are being compared.

Information for coastal reef environments is derived from hard substrates, while the diversity curve over the broader continental shelf to continental slope is based on organisms that inhabit soft sediments. The biology of micro-patches may function quite differently in organisms that inhabit hard bottoms and crevices than in those that mine soft sediments. Quantitative and comparable studies on hard substrates across a broader depth gradient (shallow to 2,250 m) have not been done (Etter and Mullineaux, 2001), but they potentially could show a quite different pattern, where the decline in species diversity from a peak at 10 - 30 m continues unabated into the deep sea. Further data are urgently needed to quantify the biology and diversity of organisms that inhabit hard substrates from shallow into deep ocean water (e.g., those that inhabit the hard grounds and canyons of continental margins, mid-ocean ridges, sea mounts, and other deep ocean formations). Only then will the enigma of the apparent double-humped diversity curve from near-shore environments to the deep sea be resolved and the processes that generate and maintain diversity from shallow to deep marine environments be more fully understood. These ecological gradients are appropriately termed “ecoclines” where species assemblages exhibit changes associated with environmental changes over depth. The analyses of the depth gradient off Lee Stocking Island provides a step towards a better understanding of the “coastal curve” in the proposed paradigm of the double-humped diversity curve.

## CHAPTER 2

### BIOLOGICAL ATTRIBUTES OF MOLLUSCAN ASSEMBLAGES FROM SHALLOW TO DEEP REEFS

#### ABSTRACT

Following deployment of benthic collectors at 5 m, 14 m, 46 m, 153 m, and 244 m off Lee Stocking Island in the Exumas, Bahamas, 25 species of gastropods and 11 species of bivalves were recorded; new depth records were established for the bivalves *Brachtechlamys antillarum*, *Spathochlamys benedicti*, and *Laevichlamys multisquamata*, and the gastropods *Zafrona pulchella*, *Bulla occidentalis*, *Columbella mercatoria*, *Ithythythara lanceolata*, *Strombus gigas*, *Tegula fasciata*, *Rubellatoma rubella*, and *Nassarius albus*. Overall depth distributions for most bivalves and gastropods, however, were similar to Redfern's (2001) study in Abaco Island, Bahamas. Although the shape of the larval protoconch has been reported to show a significant relationship to larval dispersal among gastropods, it was not associated with the size of the geographic range (as computed from latitudinal and longitudinal ranges) among species of gastropods in the present study, suggesting either that the shape of the protoconch is not always directly correlated with abbreviated vs. planktotrophic modes of development, that oceanographic conditions or larval behavior may prevent dispersal of long-lived planktotrophic larvae, or that the number of species present did not allow detection of a pattern. The shape of the protoconch also was not related to depth in the present study. Similarly, sizes of geographic ranges did not decline significantly with increased depth among molluscs in this study, even though deep reef species have been shown to have more restricted ranges

than those from shallow reefs in other taxa. Smaller geographic ranges were not associated with smaller ranges of depth distribution among molluscs in the present study. This may be due to sampling, although some evidence argues against the latter interpretation. Herbivorous modes of feeding predominated (52% of species) and carnivorous modes of feeding were common (44% of species) over the range of depths studied at Lee Stocking Island, but mode of feeding did not change significantly over depth. Structural adaptations of the shell against predation also did not change significantly in frequency over depth among species of gastropods. Two species, one bivalve (*Lyropecten antillarum*) and one gastropod (*Tegula fasciata*) showed a significant decline in body size with increasing depth. Tiny colonists suggested that some individuals among both bivalves and gastropod species probably settled as larvae in the collectors, but some individuals of both bivalves and gastropods approximated (or, in the pectinid bivalve, *Spathochlamys benedicti*, exceeded) the largest body sizes known for their species, suggesting that they either grew extremely fast or migrated into the collectors as adults. A juvenile queen conch was found in a collector at 46 m, representing a new depth record for that species and supporting the idea that this species recruits in deep water. Patterns of co-occurrence did not suggest that competitive exclusion occurs among species of gastropods or bivalves. This study therefore provided little evidence that the strength of biotic interactions declined over the depth range studied (5 - 244 m). The low numbers of species and individuals collected at the deepest sites (153 m and 244 m) suggests that at those depths, populations may occur at densities below those at which strong biotic interactions occur among individuals and species.

## INTRODUCTION

### Depth Gradients on Hard Substrates and Deep Reef Molluscan Assemblages

Chapter 1 focuses on defining the faunal composition of benthic molluscs at Lee Stocking Island in the Exumas, Bahamas, primarily at the higher taxonomic level (i.e., total molluscs, bivalves, and gastropods) over depth, relates abundance and diversity to environmental factors that change over a depth gradient of approximately 250 m, and compares patterns of diversity among taxa over coastal shelves with those found over broader depth gradients into the deep sea. The main objective of the present Chapter is to explore biological characteristics of species of bivalves and gastropods over the depths studied off Lee Stocking Island, test several hypotheses about how ecological conditions affect these biological traits over depth, and relate these patterns to the broader context of bivalve and gastropod distribution in the Bahamas.

Before assessing how the biological characteristics of bivalves and gastropods vary from shallow to deep reefs in the Bahamas, however, it is useful to put this study in perspective by briefly reviewing the major findings that have focused scientific attention on deep water communities (including recent interest in sea mounts, deep water corals, and the little-known "twilight zone" of deep reef habitats) and by briefly summarizing what is known about patterns of distribution and abundance of molluscs over depth.

In 1872, the H. M. S. Challenger Expedition revealed that the previously thought barren sea floor had extensive marine life below 200 m. Deep sea exploration later found that life extends to hadal depths greater than 10,000 m. Hessler and Sanders' (1967), Sanders' (1968), and Sanders and Hessler's (1969) work electrified the scientific

community with its demonstration of extraordinarily high benthic diversity on a transect that ranged from the shallow shelf off Massachusetts across the continental slope and onto the abyssal plain toward Bermuda.

Over the last several decades, improvements in submersible, ROV, and diving technology have provided major new discoveries of unexpected biota from deep water hard substrates that are less accessible to sampling than sedimentary environments. For example, the unique biology of organisms that inhabit hydrothermal vents and cold seeps has attracted widespread public and scientific attention (Grassle et al., 1985). Lack of knowledge about the ocean's ubiquitous deep sea mounts and ridges, combined with the realization that fishing and trawling activities are wreaking havoc on the isolated, frequently endemic, and often unprotected benthic populations associated with these structures, has galvanized scientific and policy-making bodies to document and attempt to protect the biota associated with these oceanic features (Malakoff, 2003). Remarkable beds of hexacorals, octacorals, and hydrocorals also have been discovered during the last few years in deep water in the North Atlantic (Roberts and Hirshfield, 2003) and in the Northeast Pacific Ocean and Bering Sea (Etnoyer and Morgan, 2003). Evidence suggests that these communities flourish from the Bering Sea south to the equator and west to the Hawaiian Islands. Depth ranges extend from as shallow as 9 m to as deep as 3,880 m, depending on location and the biology of individual species, but few if any have been systematically sampled over depth. The beds are sufficiently large and dense that they provide substantial habitat complexity and refuge for associated species, and likely are important in maintaining sustainable fisheries (Etnoyer and Morgan, 2003). Deep sea

coral communities already have been badly damaged due to new fishing technology such as "rock hopper" trawls that cut swaths through the beds. The implications of their destruction for marine biodiversity and for fisheries has propelled deep sea corals to the forefront of contemporary concerns among marine scientists and policy-makers.

Tropical coral reefs also extend into deep water, and interest in the little known "twilight zone" that extends beyond scuba diving capability has been high for several decades (Porter, 1973). On shallow reefs, the diversity of sessile organisms increases to around 20 m and then decreases as light becomes increasingly attenuated in deeper water (Loya, 1972; Sheppard, 1981; Huston, 1985). Only recently have we begun to assess by submersible the sessile organisms in deeper reef habitats that are inaccessible to scuba diving, but knowledge of diversity and biological characteristics of these deep communities remains meager (G. Dennis, pers. comm.; Avery, 1998; Aponte and Ballantine, 2001). Even less is known about gradients of diversity and biological attributes of motile organisms on deep reefs, especially beyond 50 m, although diving, submersible, and ROV innovations are beginning to yield exciting new information about high percentages of undocumented and endemic species in some sites (Pyle, 2000).

Only a few studies have examined the distribution and abundance of molluscs across depth gradients on reefs and hard bottoms, since most such studies in coastal and shelf habitats have examined soft bottom assemblages. Most of these studies show decreasing species richness with depth from shore to the shelf edge or beyond (reviewed in Chapter 1). However, in a study from the intertidal to 40 m depths in the Red Sea, Zuschin et al. (2000) concluded that type of substrate was more important than depth in



the distribution of molluscs, and, in a study that included both soft and hard reef substrates off the east and west coasts of Florida, Allmon et al. (1993), found that the number of gastropod species *increased* from the shore down to about 100-200 m before leveling off.

Therefore, in spite of intense recent interest in deep hard bottom communities, we remain mostly ignorant of how diversity and biological attributes of species change over depth in both coastal and deep sea hard bottom environments. Understanding these patterns is important because it allows us to assess the different ways in which species interact with their physical and biotic environment and provides insight into the factors that delimit (and modify) the spatial distribution of species. This should enhance our ability to protect and manage species in a rapidly changing seascape.

#### Biological Attributes of Species: Reflections of History and Management Implications

A number of biological attributes, such as morphological features, body size, and life history traits (reproductive and larval mode, growth trajectory, longevity) reflect the history of interactions between a species and its environment. In particular, the history of interactions with other species (predators, competitors) as well as the nature of the physical environment (e.g., depth-related factors such as light, pressure, temperature; level and predictability of primary productivity; chemistry and structural complexity of the habitat; predictability and intensity of disturbance) can influence body size and architecture (Vermeij 1978). Vermeij (1978) pointed out that many deep sea species lack morphological specializations for strong biotic interactions such as predation and competition, reflecting either low abundance and few specialized biotic interactions, physio-chemical constraints, or the persistence of ancient lineages. Indeed, Paleozoic

relicts, including stalked crinoids, epibenthic brachiopods, bryozoans, primitive nautiloids, and coelocanth fish persist today primarily in refugial habitats, such as deep water, that are comparatively safe from the pervasive predators that diversified during the Mesozoic, and especially the Coenozoic, in shallow water (Vermeij 1987).

Body size often is strongly related to the size and number of offspring produced, type of larval development, and the potential for dispersal (Reaka, 1980, 1986; Strathmann and Strathmann, 1982; Jablonski and Lutz, 1983). High dispersal capability of larvae affects the predictability of recruitment in local communities and the genetic connectivity among populations, and usually is associated with larger geographic distributions (Thorson, 1950; Mileikovsky, 1981; Scheltema, 1977). Size of the geographic range in turn is inversely correlated with both diversification and extinction (Hansen 1978; 1980; Jablonski, 1986; Reaka and Manning, 1987).

This study examines how a number of ecological and evolutionary traits such as body size, larval mode, geographic range, feeding habits, adaptations against predation, and co-occurrence vary in species of gastropod and bivalve molluscs over a depth gradient of 245 m off Lee Stocking Island in the Exumas, Bahamas. This conveys information about what types of biotic and physical environments these species have encountered in their recent evolutionary history, and provides information about the distribution of these species. Such data improve our management capability. For example, do deep dwelling species have more restricted ranges and are they more vulnerable to anthropogenic disturbance and exploitation than those living on shallow reefs?

Central hypotheses included:

- ▶ *Species of gastropods and bivalves in this study reach larger body sizes in shallow than deep habitats and sizes are comparable to those reported for these species from other geographic regions;*
- ▶ *Dispersal and size of the geographic range are greater in shallow than in deep reef habitats;*
  - *The shape of the protoconch is associated with the size of the geographic range in gastropods in this study (i.e., gastropods with elongated, sculptured protoconchs have lecithotrophic larvae vs. gastropods with globose, unornamented protoconchs have planktotrophic larvae);*
  - *The number of species of gastropods with globose protoconchs increases with depth; and the number of species with pointed spires decreases with depth;*
  - *Geographic ranges of gastropod molluscs are larger for species in shallow than deep habitats;*
- ▶ *The number of herbivorous and carnivorous species of gastropods decreases with depth, while the number of detritivorous gastropods increases with depth;*
- ▶ *Shallow reef gastropods are adapted for strong biotic interactions while those from deep reef environments are not;*
  - *Shell adaptations against predation occur on more species of gastropods from shallow than deep habitats;*
  - *Co-occurrence of certain species of gastropods and bivalves is greater than expected in shallow but not deep habitats, thus the potential for competitive interactions among certain species (per collector) is greater in shallow than deep environments; and,*
- ▶ *Depth ranges of species of gastropods and bivalves in this study are equivalent to those known for these species in other geographic areas.*

## MATERIALS AND METHODS

### Summary of Field Collection Methods

Artificial benthic collectors (Figure 1.3, Chapter 1) were deployed in December, 1993, at five depths (5 m, 14 m, 46 m, 153 m, and 244 m) off Lee Stocking Island, Bahamas, and retrieved after six months. The openings on the collectors were approximately 3 cm by 25 cm (with a total of four openings on the front of each collector), which limited the size of the organisms that could enter the collectors to about 3 cm or less. The collectors were constructed of “hogshair” furnace filter material. The openings between layers and in the spaces between the relatively large fibers of the artificial material were intended to mimic holes and crevices that occur naturally in reef substrate. The advantage of using the artificial collectors rather than other methods such as dredging, suction, collecting reef substrate, etc., was that they could be deployed over a wide range of habitats (i.e., patch reef, deep reef, and deep hard bottom), thus using a consistent method over all five depths. Further details on the construction, deployment, and retrieval of the collectors are provided in Chapter 1. Upon retrieval of the collectors after deployment for six months in the field, bivalve and gastropod molluscs found in the collectors were sorted and preserved, then measured and identified to family, genus, or species according to Abbott (1974). The taxonomic status of each species was checked for most current nomenclature in the literature. “Width” and “height” of the shells were measured according to methods in Abbott (1974). Gastropod height was measured from tip of spire to lowest point on the lower axis of shell; width was measured from the broadest peripheries of the body whorls. Bivalve height was measured from the valve

hinge line to the farthest point of the ventral margin; width was measured from the widest horizontal distance of the shell perpendicular to the height.

#### Assembling Biological Attributes

Taxonomic categories of molluscs by depth were arranged according to family, genus, and species; mean abundance and standard deviation per collector were calculated for each taxon. Depth ranges and habitat preferences were obtained from the literature. Geographic ranges for individual species of gastropods were obtained from the Academy of Natural Sciences' database on western Atlantic gastropods (Academy of Natural Sciences, 2003). Surface distances for geographic ranges were computed between latitudes and between longitudes as a set of "crosshair" ranges and added together to obtain a relative index of the range of the individual species so they could be compared with one another (km latitudinal range + km longitudinal range). The index then was compared between gastropods that were scored as either lecithotrophic (short-lived larvae) or planktotrophic (long-lived larvae) by the shape of their protoconchs, as illustrated by Shuto (1974) (Figure 2.1). The protoconch is the remnant of the pre-metamorphic larval shell, retained as the small tip of the spire in the adult. Species with planktotrophic larvae tend to have elongated, sculptured protoconchs, while species with lecithotrophic larvae tend to have globose, unornamented protoconchs (Powell, 1942; Thorson, 1950; Shuto, 1974). Shapes of protoconchs were assessed according to photographs and physical descriptions of the protoconch for individual species (in many cases, high-resolution photographs of the spire



A. Elongated, sculptured protoconch = “planktotrophic”



B. Globose, unornamented protoconch = “lecithotrophic”

Figure 2.1. Illustration of protoconch shapes in gastropod molluscs. Adapted from Shuto (1974) to show the contrast between the form of the protoconchs.

tip were available) in Redfern (2001) and Abbott (1974). Inferred capability for larval dispersal and size of the geographic range then were analyzed statistically across depths.

Feeding modes for molluscs were divided into four categories: herbivores, carnivores, detritivores, and planktivores. All bivalves were categorized as planktivores, and gastropods were categorized as either herbivores, carnivores, or detritivores, primarily according to descriptions provided by Boss (1982) and supplemented by information on various species where available in the literature. Feeding modes were not available for some species and were listed as unknown. Body sizes of species of both bivalves and gastropods collected in the present study were compared to the maximum body size reported in the literature to attempt to determine if larvae settled, or juveniles or adults crawled into the benthic collectors, and if there were any evident patterns of body size with depth. Key adaptations against predation were selected for analysis in gastropods according to Vermeij (1978): 1) a high spire (which enables the gastropod to retract into the shell), 2) a thick shell, 3) a thick lip, 4) compact spines, 5) ribs, and 6) a heavily beaded shell. These results were evaluated for possible environmental influences.

### Statistical Analyses

The sizes of the geographic ranges for each species was computed using the Geographic Range Index formula:

$$\sqrt{^{\circ}\text{latitude}^2 + ^{\circ}\text{longitude}^2}$$

The Geographic Range Index (GRI) formula is described in more detail in Chapter 3 where it was applied to a much larger gastropod data set from the Academy of Natural Sciences (ANS). The inputs to the formula were latitudinal and longitudinal ranges for 960 species of gastropods. The formula was used in this chapter to analyze geographic range within the larger context of the ANS data set. This was done in order to distinguish species of gastropods with small geographic ranges from those with large geographic ranges. A frequency distribution of the GRI data for the 960 species ranged from 4.72 to 132.55, with a median of 57.40. Ranges for small, medium, and large GRI's were based on the frequency distribution of the full ANS data set, which was divided into three equal parts: small = 4.74-47.33; medium = 47.34-89.94, and large = 89.95-132.55.

Also analyzed in this chapter were potential for larval dispersal, feeding modes, and adaptations against predation of molluscs in the collection were analyzed statistically using contingency tables to detect patterns in these characteristics from shallow to deep reef habitats. Because of the relatively small sample sizes for gastropods and bivalves at the various depths, Fisher's Exact Test (Sokal and Rohlf, 1987; Steel and Torrie, 1980) was used. Fisher's Exact Tests (for  $r \times c$  table sizes) were run on all contingency tables using SAS Statistical Software according to SAS/STAT User's Guide (1989), p. 882, at the  $p < 0.05$  significance level.

For an analysis of species co-occurrence, a presence-absence matrix was constructed for gastropods and bivalves using EcoSim software (Gotelli and Entsminger, 2001) and modeled after an example in Gotelli and Graves (1996). A co-occurrence module in the EcoSim program provides statistical tests for non-random patterns of



species co-occurrence in the presence-absence matrix. Of four available indices that test for non-random patterns, Stone and Roberts' (1990) C-score measures the average compared to the expected number of "checkerboard units" (see definition below) between all possible pairs of species in the matrix, and was selected for analysis of the distribution of molluscan species at the five depths in the present study. The number of checkerboard units (CUs) for each species is calculated as  $CU = (r_i - S)(r_j - S)$ , where S is the number of shared sites (depths containing both species) and  $r_i$  and  $r_j$  are the row totals for species i and j. The C-score is the average of all possible checkerboard pairs, calculated for species that occur at least once in the matrix. A classic "checkerboard" pattern is where one of two species, but not both, occurs at a given site. In a community where species interactions are affecting the presence or absence of species, there is a non-random pattern and the C-score should be significantly larger than expected by chance.

## RESULTS

### Taxonomic Categories of Molluscs by Depth

Bivalve and gastropod taxa were arranged by family for five sampling depths off Lee Stocking Island with number of individuals per collector and standard deviations (Tables 2.1 and 2.2). Nine families of bivalves and 27 families of gastropods are represented in the collection from Lee Stocking Island. Overwhelmingly higher abundance and species richness was observed in both bivalves and gastropods at the shallower depths of 5 m, 14 m, and 46 m, compared to the deeper depths of 153 m and 244 m (also see Chapter 1).

Table 2.1. Bivalve taxa arranged by family for five sampling depths off Lee Stocking Island, with feeding mode (Boss, 1982), mean number of individuals per collector and standard deviations (brackets). All taxa listed are planktivores.

| Family<br>Species, Author, Common Name  | Individuals per collector (mean ± SD) |                |                |      |      |
|---|---------------------------------------|----------------|----------------|------|------|
|   | 5m                                    | 14m            | 46m            | 153m | 244m |
| <b>Arcidae</b>  |                                       |                |                |      |      |
| <i>Arca</i> sp.   | 0                                     | 0.33<br>[0.52] | 0              | 0    | 0    |
| <i>Barbatia cancellaria</i> , (Lamarck, 1819)<br>Red-brown ark                | 0                                     | 0.17<br>[0.41] | 0              | 0    | 0    |
| <b>Cardiidae</b>  |                                       |                |                |      |      |
| <i>Papyridea soleniformis</i> , (Bruguier, 1789)<br>Spiny paper cockle        | 0.71<br>[1.89]                        | 0.17<br>[0.41] | 0              | 0    | 0    |
| <b>Juliidae</b>   |                                       |                |                |      |      |
| <i>Berthelinia</i> sp.  | 0.14<br>[0.38]                        | 0              | 0              | 0    | 0    |
| <b>Laevicardinae</b>  |                                       |                |                |      |      |
| <i>Laevicardium</i> sp.   | 0.14<br>[0.38]                        | 0              | 0              | 0    | 0    |
| <b>Limadae</b>  |                                       |                |                |      |      |
| <i>Lima</i> sp.   | 0.57<br>[1.51]                        | 1.00<br>[2.45] | 0              | 0    | 0    |
| <i>Limaria pellucida</i> , (C. B. Adams, 1846)<br>Antillean lima              | 3.57<br>[9.02]                        | 0.17<br>[0.41] | 0              | 0    | 0    |
| <i>Ctenoides scabra</i> , (Born, 1778)<br>Rough lima                          | 0.86<br>[1.46]                        | 2.17<br>[2.56] | 3.33<br>[4.53] | 0    | 0    |
| <b>Limopsidae</b>   |                                       |                |                |      |      |
| <i>Limopsis sulcata</i> , Verrill and Bush, 1898<br>Sulcate limposis          | 0                                     | 0              | 0.44<br>[0.53] | 0    | 0    |
| <b>Noetiidae</b>  |                                       |                |                |      |      |
| <i>Arcopsis adamsi</i> , (Dall, 1886)<br>Adam's ark                           | 0.29<br>[0.49]                        | 0              | 0              | 0    | 0    |
| <b>Pectinidae</b>   |                                       |                |                |      |      |
| <i>Spathochlamys benedicti</i> , (Verrill and<br>Bush, 1897, Benedict scallop | 0.14<br>[0.38]                        | 0              | 1.33<br>[1.32] | 0    | 0    |
| <i>Carbachlamys imbricata</i> , (Gmelin, 1791)<br>Little knobby scallop       | 0.43<br>[1.13]                        | 0              | 0              | 0    | 0    |
| <i>Laevichlamys multisquamata</i> , (Dunker, 1864)<br>Many-ribbed scallop     | 0.14<br>[0.38]                        | 0              | 0              | 0    | 0    |

Table 2.1 (cont'd). Bivalves arranged by family for five sampling depths off Lee Stocking Island, with feeding mode (Boss, 1982), mean number of individuals per collector and standard deviations (brackets). All taxa listed are planktivores.

| Family<br>Species, Author, Common Name                                 | Individuals per collector (mean ± SD) |                |                |      |                |
|--|---------------------------------------|----------------|----------------|------|----------------|
|  | 5m                                    | 14m            | 46m            | 153m | 244m           |
| <i>Caribachlamys ornata</i> , (Lamarck, 1819)<br>Ornate scallop        | 4.86<br>[8.09]                        | 0.33<br>[0.52] | 0              | 0    | 0              |
| <i>Brachtechlamys antillarum</i> , (Recluz, 1853)<br>Antillean scallop | 1.29<br>[3.40]                        | 0.17<br>[0.41] | 0.78<br>[0.67] | 0    | 0.14<br>[0.38] |
| <b>Pinnidae</b>  |                                       |                |                |      |                |
| <i>Atrina</i> sp.  | 0.57<br>[1.13]                        | 0              | 0.11<br>[0.33] | 0    | 0              |
| <b>Unknown</b>   |                                       |                |                |      |                |
| Unknown scallop sp. #1   | 0                                     | 0              | 0.11<br>[0.35] | 0    | 0              |
| Unknown scallop sp. #2   | 0                                     | 0              | 0.11<br>[0.33] | 0    | 0              |

Table 2.2. Gastropod taxa arranged by family for five sampling depths off Lee Stocking Island, with feeding mode (Boss, 1982), mean number of individuals per collector and standard deviations (brackets). C = Carnivore; H = herbivore; D = detritivore.

| Family<br>Species, Author, Common Name   | Feeding Mode | Depth           |                |                |                |      |
|--|--------------|-----------------|----------------|----------------|----------------|------|
|  |              | 5m              | 14m            | 46m            | 153m           | 244m |
| <b>Architectonicidae</b>   |              |                 |                |                |                |      |
| <i>Pseudomalaxis</i> sp., Fischer, 1885<br>False dial                                  | C            | 0               | 0.17<br>[0.41] | 0              | 0              | 0    |
| <b>Bullidae</b>  |              |                 |                |                |                |      |
| <i>Bulla occidentalis</i> ,* Adams, 1850<br>Striate bubble                             | H            | 0.57<br>[0.79]  | 0              | 0.33<br>[0.50] | 0              | 0    |
| Unknown bubble shell   | H            | 1.14<br>[1.86]  | 0.17<br>[0.41] | 0.22<br>[0.44] | 0              | 0    |
| <b>Cerithiidae</b>   |              |                 |                |                |                |      |
| <i>Bittium</i> sp.   | H            | 0.14<br>[0.38]  | 0.17<br>[0.40] | 0.22<br>[0.67] | 0.11<br>[0.33] | 0    |
| <i>Cerithium eburneum</i> , Bruguiere, 1792<br>Ivory cerith                            | H            | 1.00<br>[1.41]  | 0.17<br>[0.41] | 0              | 0              | 0    |
| <i>Cerithium litteratum</i> , (Born, 1778)<br>Stocky cerith                            | H            | 7.86<br>[12.46] | 0.33<br>[0.82] | 0              | 0              | 0    |
| <i>Cerithium lutosum</i> , Menke, 1828<br>Variable cerith                              | H            | 0.29<br>[0.76]  | 0              | 0              | 0              | 0    |
| <i>Cerithium</i> sp.   | H            | 1.71<br>[3.68]  | 2.67<br>[4.13] | 2.00<br>[1.5]  | 0              | 0    |
| <b>Columbellidae</b>   |              |                 |                |                |                |      |
| <i>Costoanachis lafresnayi</i> , (Fischer and<br>Bernardi, 1856) Well-ribbed dovesnail | C            | 0               | 0.17<br>[0.41] | 0              | 0              | 0    |
| <i>Zafrona pulchella</i> , (de Blainville, 1829)<br>Beautiful dovesnail                | C            | 1<br>[1.53]     | 4.83<br>[2.40] | 2.56<br>[4.19] | 0              | 0    |
| <i>Columbella mercatoria</i> , (Linne, 1758)<br>West Indian dovesnail                  | C            | 1.86<br>[3.29]  | 0.17<br>[0.41] | 0              | 0              | 0    |
| <i>Columbellopsis nycteis</i> , (Duclos, 1846)<br>Fenestrate dove shell                | C            | 0               | 0              | 0.44<br>[1.01] | 0              | 0    |
| Unknown dove shell   | U            | 0.57<br>[0.79]  | 0.83<br>[1.17] | 0              | 0              | 0    |

\**Bulla occidentalis* is referred to by some workers as *Bulla striata* Bruguiere, 1792 (Redfern, 2001).

Table 2.2 (cont'd). Gastropods arranged by family for five sampling depths off Lee Stocking Island, with feeding mode (Boss, 1982), mean number of individuals per collector and standard deviations (brackets). C = Carnivore; H = herbivore; D = detritivore.

| Family<br>Species, Author, Common Name                             | Feeding Mode | Depth          |                |                |                |                |
|--|--------------|----------------|----------------|----------------|----------------|----------------|
|  |              | 5m             | 14m            | 46m            | 153m           | 244m           |
| <b>Cymatiidae</b>  |              |                |                |                |                |                |
| <i>Triton sp.</i>  | C            | 0              | 0.17<br>[0.41] | 0.22<br>[0.44] | 0              | 0              |
| <b>Eratoidea</b>   |              |                |                |                |                |                |
| <i>Trivia sp.</i>  | U            | 0.71<br>[0.79] | 0              | 0              | 0              | 0              |
| <b>Fasciolariidae</b>  |              |                |                |                |                |                |
| <i>Fusinus sp.</i>   | C            | 0.71<br>[1.41] | 0              | 0.22<br>[0.44] | 0              | 0              |
| <i>Latirus sp. #1</i>  | C            | 0              | 0              | 0              | 0.11<br>[0.33] | 0.43<br>[0.79] |
| <i>Latirus sp. #2</i>  | C            | 0.14<br>[0.38] | 0              | 0.11<br>[0.33] | 0              | 0              |
| <b>Haminoeidae</b>   |              |                |                |                |                |                |
| <i>Haminoea petiti</i> , (d'Orbigny, 1841)<br>Petit's paper bubble | U            | 0.29<br>[0.76] | 0              | 0              | 0              | 0              |
| <b>Marginellidae</b>   |              |                |                |                |                |                |
| <i>Hyalina sp.</i>   | C            | 0.29<br>[0.49] | 0.50<br>[0.55] | 0.67<br>[1.32] | 0              | 0              |
| <i>Prunum carneum</i> , (Storer, 1837)<br>Orange marginella        | C            | 0              | 0.17<br>[0.41] | 0              | 0              | 0              |
| <i>Marginella sp.</i>  | C            | 1.71<br>[1.89] | 0.83<br>[1.60] | 0.11<br>[0.33] | 0              | 0              |
| <b>Melanellidae</b>  |              |                |                |                |                |                |
| <i>Melanella sp.</i>   | U            | 1.71<br>[1.70] | 1.33<br>[0.89] | 0.11<br>[0.33] | 0              | 0              |
| <b>Mitridae</b>  |              |                |                |                |                |                |
| <i>Vexillum sp.</i>  | C            | 0              | 0              | 0.11<br>[0.33] | 0              | 0              |
| <b>Modulidae</b>   |              |                |                |                |                |                |
| <i>Modulus modiolus</i> , (Linne, 1758)<br>Atlantic modiolus       | H            | 0.14<br>[0.38] | 0.33<br>[0.52] | 0              | 0              | 0              |

Table 2.2 (cont'd). Gastropods arranged by family for five sampling depths off Lee Stocking Island, with feeding mode (Boss, 1982), mean number of individuals per collector and standard deviations (brackets). C = Carnivore; H = herbivore; D = detritivore.

| Family<br>Species, Author, Common Name                                  | Feeding Mode | Depth            |                |                 |                |      |
|---|--------------|------------------|----------------|-----------------|----------------|------|
|   |              | 5m               | 14m            | 46m             | 153m           | 244m |
| <b>Muricidae</b>  |              |                  |                |                 |                |      |
| <i>Murex sp. #1</i>   | C            | 0                | 0.33<br>[0.52] | 0               | 0              | 0    |
| <i>Murex sp. #2</i>   | C            | 0                | 0.17<br>[0.41] | 0.11<br>[0.52]  | 0              | 0    |
| <b>Nassariidae</b>  |              |                  |                |                 |                |      |
| <i>Nassarius albus</i> , (Say, 1826)<br>Variable nassa                  | C            | 0.14<br>[0.38]   | 0.17<br>[0.41] | 0.33<br>[0.71]  | 0              | 0    |
| <b>Naticidae</b>  |              |                  |                |                 |                |      |
| <i>Polinices lacteus</i> , (Guilding, 1834)<br>Milk moon snail          | U            | 0                | 0.17<br>[0.41] | 0               | 0              | 0    |
| <b>Neritidae</b>  |              |                  |                |                 |                |      |
| <i>Smaragdia viridis</i> , (Linnaeus, 1758)<br>Emerald nerite           | H            | 0.29<br>[.049]   | 0              | 0               | 0              | 0    |
| <b>Rissoinidae</b>  |              |                  |                |                 |                |      |
| <i>Rissoina sp.</i>   | D            | 0.57<br>[0.53]   | 3.00<br>[4.98] | 9.11<br>[16.64] | 0              | 0    |
| <b>Strombidae</b>   |              |                  |                |                 |                |      |
| <i>Strombus gigas</i> , Linnaeus, 1758<br>Queen conch                   | H            | 0                | 0              | 0.11<br>[0.33]  | 0              | 0    |
| <b>Triphoridae</b>  |              |                  |                |                 |                |      |
| <i>Nototriphora decorata</i> , (C. B. Adams, 1850)<br>Mottled triphora  | U            | 0.14<br>[0.38]   | 0              | 0               | 0              | 0    |
| <i>Iniforis turrithomae</i> , (Holten, 1802)<br>Thomas' trifora         | U            | 0                | 0.50<br>[0.84] | 0               | 0              | 0    |
| <b>Trochidae</b>  |              |                  |                |                 |                |      |
| <i>Tegula fasciata</i> , (Born, 1778)<br>Smooth Atlantic tegula         | H            | 11.00<br>[18.37] | 2.17<br>[1.51] | 0.44<br>[0.33]  | 0              | 0    |
| <i>Tegula lividomaculata</i> , (C.B. Adams, 1845)<br>West Indian tegula | H            | 0.57<br>[1.51]   | 0              | 0.11<br>[0.33]  | 0              | 0    |
| <b>Liotiidae</b>  |              |                  |                |                 |                |      |
| <i>Arene briareus</i> , (Dall, 1881)<br>Briar arene                     | H            | 0                | 0              | 0               | 0.11<br>[0.33] | 0    |
| <i>Arene cruentata</i> , (von Muhlfeld, 1829)<br>Star cyclostreme       | H            | 0.14<br>[0.38]   | 0              | 0               | 0              | 0    |

Table 2.2 (cont'd). Gastropods arranged by family for five sampling depths off Lee Stocking Island, with feeding mode (Boss, 1982), mean number of individuals per collector and standard deviations (brackets). C = Carnivore; H = herbivore; D = detritivore; U = unknown.

| Family<br>Species, Author, Common Name                                      | Feeding Mode | Depth          |                |                |      |                |
|---|--------------|----------------|----------------|----------------|------|----------------|
|   |              | 5m             | 14m            | 46m            | 153m | 244m           |
| <b>Turbonillidae</b>  |              |                |                |                |      |                |
| <i>Turbonilla sp.</i>   | U            | 0              | 0              | 0.11<br>[0.33] | 0    | 0              |
| <b>Turridae</b>   |              |                |                |                |      |                |
| <i>Ithythyra lanceolata</i> , (C.B. Adams, 1850)<br>Spear turret            | C            | 0              | 0              | 0.11<br>[0.33] | 0    | 0              |
| <i>Agathotoma candidissima</i> , (C.B. Adams, 1845)<br>Cox's turrid         | C            | 0.29<br>[0.76] | 0.17<br>[0.41] | 0.78<br>[0.83] | 0    | 0              |
| <i>Rubellatoma rubella</i> ,** (Kurtz & Stimpson, 1851)<br>Reddish mangelia | C            | 0.43<br>[1.13] | 0.17<br>[0.41] | 0.33<br>[0.71] | 0    | 0              |
| <b>Turritellidae</b>  |              |                |                |                |      |                |
| <i>Torcula exoleta</i> , (Linne, 1758)<br>Eastern turret shell              | C            | 0              | 0.33<br>[0.52] | 0.44<br>[1.13] | 0    | 0              |
| <i>Vermicularia sp.</i>   | C            | 0              | 0              | 0.11<br>[0.33] | 0    | 0.14<br>[0.38] |
| <b>Vitrinellidae</b>  |              |                |                |                |      |                |
| <i>Teinostoma sp.</i>   | U            | 0.14<br>[0.38] | 0              | 0.44<br>[0.53] | 0    | 0              |
| <b>Unknown (limpets)</b>  |              |                |                |                |      |                |
| Unknown limpet  | H            | 0.14<br>[0.38] | 0              | 0              | 0    | 0              |
| <b>Unknown</b>  |              |                |                |                |      |                |
| Unknown sp. #1  | U            | 0.86<br>[0.38] | 1.17<br>[0.52] | 0.89<br>[0.73] | 0    | 0              |
| <b>Unknown</b>  |              |                |                |                |      |                |
| Unknown sp. #2  | U            | 0              | 0              | 0.11<br>[0.33] | 0    | 0              |
| <b>Unknown</b>  |              |                |                |                |      |                |
| Unknown sp. #3  | U            | 0              | 0.17<br>[0.41] | 0              | 0    | 0              |
| <b>Unknown</b>  |              |                |                |                |      |                |
| Unknown sp. #4  | U            | 0              | 0.17<br>[0.41] | 0              | 0    | 0              |
| <b>Unknown</b>  |              |                |                |                |      |                |
| Unknown sp. #5  | U            | 0.14<br>[0.38] | 0              | 0              | 0    | 0              |

\*\*Noted as a rare species by Abbott (1974).

Table 2.2 (cont'd). Gastropods arranged by family for five sampling depths off Lee Stocking Island, with feeding mode (Boss, 1982), mean number of individuals per collector and standard deviations (brackets). C = Carnivore; H = herbivore; D = detritivore.

| Family                       |              |    | Depth          |                |      |      |  |
|------------------------------|--------------|----|----------------|----------------|------|------|--|
| Species, Author, Common Name | Feeding Mode | 5m | 14m            | 46m            | 153m | 244m |  |
| Unknown                      |              |    |                |                |      |      |  |
| Unknown sp. #6               | U            | 0  | 0              | 0.11<br>[0.33] | 0    | 0    |  |
| Unknown                      |              |    |                |                |      |      |  |
| Unknown sp. #7               | U            | 0  | 0.17<br>[0.41] | 0              | 0    | 0    |  |
| Unknown                      |              |    |                |                |      |      |  |
| Unknown sp. #8               | U            | 0  | 0.17<br>[0.41] | 0              | 0    | 0    |  |



A study by Redfern (2001) at Abaco Island, representing more than 108,000 shells collected over 30 years of intensive collecting with a variety of techniques, is the most comprehensive collection of molluscs reported from the Bahamas to date, and can be used for comparison to the results of the present study. Proportionately, the number of bivalve and gastropod families collected at Lee Stocking Island were very similar to those collected at Abaco Island. Redfern's (2001) study reported 45 families of bivalves and 120 families of gastropods. The present study collected 20% of the bivalve families and 22.5% of the gastropod families that Redfern (2001) reported from Abaco. Bivalves represented 25% and gastropods represented 75% of the total number of families collected in this study, while bivalves represented 27%, and gastropods represented 73% of the total number of families for these two classes in Redfern's (2001) study. These data suggest that the present study represents a fairly typical subset of the families found in the Bahamas.

In addition to the collections by Redfern (2001), relatively small numbers of species of gastropods reported from various collections at several of the main Bahamian Islands are listed on a malacology website, maintained by the Academy of Natural Sciences (ANS) in Philadelphia, PA. (<http://data.acnatsci.org/wasp/index.php>). The full data set of species that occur in the Bahamas as part of the ANS data set are analyzed separately in Chapter 3. The analyses of the Lee Stocking Island data in the present chapter are focused on the bivalve and gastropod fauna of Lee Stocking Island over a depth gradient, to add to a more complete understanding of various characteristics of species that inhabit that area.

### Depth Ranges and Habitat Preferences

The species reported from Abaco Island were collected from beach and shoreline to 295 m (Redfern, 2001). Specimens from shallow water were collected by beach-combing, wading, and snorkeling. Depths of about 2 - 6 m were dredged, and other material was obtained by SCUBA to a depth of around 15 m. Sediment samples from deeper water were obtained using La Motte, Ekman, and Petite Ponar grabs. Little trapping was done, though the use of a crab trap in 295 m added several species to the collection. Depths from which species of bivalve and gastropod molluscs were collected at Lee Stocking Island, along with their reported depth range from Redfern (2001), Abbott (1974), and Allmon (1988) are summarized in Tables 2.3 and 2.4. Habitat preferences also are listed for each species.

There are three new depth records for bivalves in the collection from Lee Stocking Island (Table 2.3). *Brachteclamys antillarum* has not been previously reported beyond 52 m, but was found at 244 m off Lee Stocking Island. *Spathochlamys benedicti* and *Laevichlamys multisquamata* typically have been found offshore in deep water in sediment. At Lee Stocking Island, they both occurred at the shallowest site off Norman's Pond patch reef at 5 m, thus providing a new shallow depth record for each species in the Bahamas.

Table 2.3. Occurrence at depth (m) for species of bivalves collected at Lee Stocking Island and reported depth ranges (m) and habitat preferences from Redfern (2001) and Abbott (1974).

| Species                           | Occurrence     |    |    |     |                | Reported    |                              |
|-----------------------------------|----------------|----|----|-----|----------------|-------------|------------------------------|
|                                   | 5              | 14 | 46 | 153 | 244            | Depth Range | Habitat Preference           |
| <i>Arcopsis adamsi</i>            |                | X  |    |     |                | 0 - 35      | Rocks, sediment              |
| <i>Barbatia cancellaria</i>       |                | X  |    |     |                | 0 - 45      | Rocks, sediment              |
| <i>Brachtechlamys antillarum</i>  | X              | X  | X  |     | X <sup>#</sup> | 0 - 52      | Rocks, sediment              |
| <i>Spathochlamys benedicti</i>    | X <sup>#</sup> |    | X  |     |                | 35 - 52     | Sediment                     |
| <i>Caribachlamys ornata</i>       | X              | X  |    |     |                | 1 - 15      | Underside of rocks           |
| <i>Laevichlamys multisquamata</i> | X <sup>#</sup> |    |    |     |                | 52 - ?      | Sediment                     |
| <i>Carbachlamys imbricata</i>     | X              |    |    |     |                | 9 - 14      | Underside of rocks           |
| <i>Ctenoides scabra</i>           | X              | X  | X  |     |                | .5 - 52     | Underside of rocks, sediment |
| <i>Limaria pellucida</i>          | X              | X  |    |     |                | 1.5 - 52    | Rocks, sediment              |
| <i>Limopsis sulcata</i>           |                |    | X  |     |                | ? - 636*    | Sediment                     |
| <i>Papyridea soleniformis</i>     | X              | X  |    |     |                | 2 - 10      | Sand, grassbeds              |

<sup>#</sup> Significant new depth record (> 10 m from reported).

New depth records were established for nine species of gastropods from the Lee Stocking Island collections (Table 2.4). *Zafrona pulchella* was previously known only from depths less than 12 m, though this species was found at 46 m in the present study. The habitat at the shelf edge (46 m) is considerably different from the habitats near shore around Lee Stocking Island, particularly from the shallower areas off Norman's Pond, which are largely patch reefs and grass beds, as described in Chapter 1. *Bulla occidentalis*, *Columbella mercatoria*, *Ithycthyara lanceolata*, *Strombus gigas*, and *Tegula fasciata* all were found at 46 m, exceeding the shallower depths for these species reported by Redfern (2001). Two species, *Rubellatoma rubella*, and *Nassarius albus*, were found in shallower water than previously reported. Contingency tables were constructed to statistically compare the numbers of species found at the long-term Abaco Island study and the results of the present study. It is apparent that the vast majority of bivalves and gastropods reported by Redfern (2001) occur in the shallow and mid- water depths, which is also similar to the results of the present study. For comparison to the collection by Redfern (2001), the species found at Lee Stocking Island also are aggregated into three depth categories (0 - 15 m, 16 -50 m, and >50 m. The analysis shows that the numbers of species of bivalves (Table 2.5) and of gastropods (Table 2.6) found at different depths at Lee Stocking Island do not vary from those found by Redfern (2001), further confirming that this study provides a reliable subset of his larger study. In addition, there is no significant difference in the decline in number of species of bivalves versus gastropods over depth at Lee Stocking Island (Table 2.7).

Table 2.4. Depth ranges (m) for species of gastropods collected at Lee Stocking Island, and reported depth ranges (m) and habitat preferences from Redfern (2001), and other authors (\*, \*\*\*, \*\*\*\*).

| Species                          | Depth Occurrence LSI |                |                |     |     | Reported<br>Depth Range | Habitat Preference       |
|----------------------------------|----------------------|----------------|----------------|-----|-----|-------------------------|--------------------------|
|                                  | 5                    | 14             | 46             | 153 | 244 |                         |                          |
| <i>Costoanachis lafresnayi</i> * |                      | X              |                |     |     | ? - 48                  | Rocks, shelly bottoms    |
| <i>Zafra pulchella</i>           | X                    | X              | X <sup>#</sup> |     |     | ? - 12 - ?              | Underside of rocks       |
| <i>Arene briareus</i>            |                      |                |                | X   |     | 32 - 154                | Sediment                 |
| <i>Arene cruentata</i>           | X                    |                |                |     |     | 1 - 12                  | Underside of rocks, reef |
| <i>Bulla occidentalis</i>        | X                    |                | X <sup>#</sup> |     |     | Inshore                 | Sand to thick mud        |
| <i>Cerithium lutosum</i>         | X                    |                |                |     |     | Intertidal              | Rocks, sand              |
| <i>Cerithium litteratum</i>      | X                    | X              |                |     |     | 1 - 12                  | Sediment, grassbeds      |
| <i>Cerithium eburneum</i> **     | X                    | X              |                |     |     | 2.5 - 52                | Sediment, grassbeds      |
| <i>Columbella mercatoria</i>     | X                    | X              | X <sup>#</sup> |     |     | 1 - 9                   | Under rocks, grassbeds   |
| <i>Haminoea petiti</i>           | X                    |                |                |     |     | Shallow                 | Unknown                  |
| <i>Rubellatoma rubella</i> ***   | X <sup>#</sup>       | X              | X              |     |     | 16 - 145                | Sediment                 |
| <i>Ithythythara lanceolata</i>   |                      |                | X <sup>#</sup> |     |     | 3 - 23                  | Sediment                 |
| <i>Prunum carneum</i>            |                      | X              |                |     |     | 1 - 16                  | Grassbeds, sediment      |
| <i>Columbellopsis nycteis</i>    |                      |                | X              |     |     | 1.5 - 45                | Grassbeds, sediment      |
| <i>Modulus modulus</i>           | X                    | X              |                |     |     | Shallow                 | Grassbeds, sand          |
| <i>Nassarius albus</i>           | X <sup>#</sup>       | X              | X              |     |     | 23 - 60                 | Sediment                 |
| <i>Polinices lacteus</i>         |                      | X              |                |     |     | .5 - 7.5                | Coarse sand              |
| <i>Agathotoma candidissima</i>   | X                    | X              | X              |     |     | 2 - 55                  | Unknown                  |
| <i>Smaragdia viridis</i>         | X                    |                |                |     |     | Shallow                 | Grassbeds                |
| <i>Strombus gigas</i>            |                      |                | X <sup>#</sup> |     |     | 2 - 12                  | Grassbeds, sand          |
| <i>Tegula lividomaculata</i>     | X                    |                | X <sup>#</sup> |     |     | Shallow                 | Under rocks              |
| <i>Tegula fasciata</i>           | X                    | X <sup>#</sup> | X <sup>#</sup> |     |     | 1 - 1.5                 | Under rocks, grassbeds   |
| <i>Nototriphora decorata</i>     | X                    |                |                |     |     | 14 - 45                 | Rocks, sediment          |
| <i>Iniforis turrithomae</i>      |                      | X              |                |     |     | 4.5 - 52                | Rocks, sediment          |
| <i>Torcula exoleta</i> ****      |                      | X              | X              |     |     | 2 - 340                 | Sediment                 |

\**Costoanachis lafresnayi* is not reported from Abaco Island, depth range from Abbott (1974).

\*\*Adults are known from 2.5 - 12 m, juveniles occur in sediment down to 52 m.

\*\*\**Rubellatoma rubella* is not reported from Abaco Island, depth range is from Abbott (1974); noted as a rare species.

\*\*\*\*Depth is reported by Allmon (1988).

<sup>#</sup>Significant new depth record (> 10 m from reported)

Table 2.5. Number of species of bivalves over depth at Abaco Island and Lee Stocking Island. Depths are binned as three categories for comparison to data on molluscs from Abaco Island. Number of species of bivalves at Abaco and Lee Stocking Islands do not differ significantly over depth ( $p = 0.914$ ).

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| <u>Depth (m)</u> | <u>Abaco Island</u> | <u>Lee Stocking Island</u> |
|------------------|---------------------|----------------------------|
| 0 - 15           | 110                 | 10                         |
| 16 - 50          | 64                  | 4                          |
| > 50             | 16                  | 1                          |

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Table 2.6. Number of species of gastropods over depth at Abaco Island and Lee Stocking Island. Depths are binned as three categories for comparison to data on molluscs from Abaco Island. Number of species of gastropods at Abaco and Lee Stocking Islands do not differ significantly over depth ( $p = 0.348$ ).

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| <u>Depth (m)</u> | <u>Abaco Island</u> | <u>Lee Stocking Island</u> |
|------------------|---------------------|----------------------------|
| 0 - 15           | 502                 | 20                         |
| 16 - 50          | 208                 | 12                         |
| > 50             | 67                  | 1                          |

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Table 2.7. Number of species of gastropods and bivalves over depth at Lee Stocking Island. Depths are binned as three categories for comparison to data on molluscs from Abaco Island. Numbers of species of bivalves and gastropods do not differ significantly over depths ( $p = 0.661$ ).

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| <u>Depth (m)</u> | <u>Bivalves</u> | <u>Gastropods</u> |
|------------------|-----------------|-------------------|
| 0 - 15           | 10              | 20                |
| 16 - 50          | 4               | 12                |
| > 50             | 1               | 1                 |

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### Depth, Geographic Range, and Potential for Dispersal of Gastropod Molluscs

Species of gastropods collected from Lee Stocking Island were analyzed with the size of their geographic ranges and shape of the protoconch (Table 2.8). The sizes of the geographic ranges, as computed with a standardized index described later, are sorted into small, medium, and large classes. The shape of the protoconch is categorized as globose, elongate and sculptured, or indefinite (Figure 2.1; see discussion in Methods). The type of protoconch was not significantly associated with size of the geographic range ( $p = 0.573$ , Table 2.9). Thus, the hypothesis that type of protoconch, and probable larval dispersal, is related to the size of the geographic range is rejected for these gastropods from Lee Stocking Island. Similarly, there is not a significant relationship between the type of protoconch and the depth distribution for gastropods from Lee Stocking Island when species are counted once each time they occur at each depth ( $p = 0.697$ , Table 2.10). A similar qualitative pattern is found when species that occur only in one depth zone are analyzed: for species that occur only in habitats  $< 15$  m deep, five had globose and seven had elongated protoconchs; for species living only in environments  $> 15$  m deep, one had a globose and two had elongate protoconchs (five species whose depth ranges overlap these depth categories are excluded from the latter analysis).

Table 2.8. Species of gastropods collected from Lee Stocking Island, Geographic Range Index\* (in parentheses), and type of protoconch (E = elongated, sculptured spire; G = globose, and/or low profile protoconch; I = indistinct). Species were placed into three categories by size of the Geographic Range Index.

| <u>Species</u>                 | <u>Geographic Range Index</u> | <u>Protoconch Type</u> |
|--------------------------------|-------------------------------|------------------------|
| <i>Smaragdia viridis</i>       | L (132.55)                    | G                      |
| <i>Polinices lacteus</i>       | L (115.94)                    | G                      |
| <i>Bulla occidentalis</i>      | L (113.47)                    | I                      |
| <i>Nototriphora decorata</i>   | L (94.27)                     | E                      |
| <i>Modulus modulus</i>         | M (89.81)                     | I                      |
| <i>Torcula exoleta</i>         | M (87.72)                     | E                      |
| <i>Cerithium litteratum</i>    | M (87.38)                     | E                      |
| <i>Ithythythara lanceolata</i> | M (87.21)                     | E                      |
| <i>Nassarius albus</i>         | M (86.66)                     | E                      |
| <i>Agathotoma candidissima</i> | M (85.26)                     | G                      |
| <i>Columbella mercatoria</i>   | M (85.17)                     | E                      |
| <i>Tegula fasciata</i>         | M (80.53)                     | I                      |
| <i>Rubellatoma rubella</i>     | M (76.26)                     | E                      |
| <i>Cerithium eburneum</i>      | M (76.06)                     | E                      |
| <i>Iniforis turrithomae</i>    | M (75.72)                     | E                      |
| <i>Haminoea petiti</i>         | M (55.56)                     | G                      |
| <i>Arene briareus</i>          | M (52.85)                     | G                      |
| <i>Cerithium lutosum</i>       | S (44.86)                     | E                      |
| <i>Costoanachis lafresnayi</i> | S (44.82)                     | E                      |
| <i>Strombus gigas</i>          | S (41.37)                     | E                      |
| <i>Zafrona pulchella</i>       | S (38.54)                     | E                      |
| <i>Tegula lividomaculata</i>   | S (37.80)                     | I                      |
| <i>Arene cruentata</i>         | S (37.57)                     | G                      |
| <i>Prunum carneum</i>          | S (33.77)                     | G                      |
| <i>Columbellopsis nycteis</i>  | S (32.25)                     | I                      |

\*Information on geographic ranges provided with the permission of The Academy of Natural Sciences, Philadelphia, PA (G. Rosenberg, pers. comm.). Geographic Range Index was computed from latitudinal and longitudinal ranges with the formula:

$$\sqrt{^{\circ}\text{latitude}^2 + ^{\circ}\text{longitude}^2}$$



Table 2.9. Geographic Range Index (GRI) and type of protoconch for species of gastropods collected from Lee Stocking Island. Small GRI = 4.72 - 47.33; medium GRI = 47.34 - 89.94; large GRI = 89.95 - 132.55. There is no significant association between size of GRI and type of protoconch ( $p = 0.573$ ).

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| <u>Geographic<br/>Range Index</u> | <u>Elongate spire</u> | <u>Globose spire</u> |
|-----------------------------------|-----------------------|----------------------|
| Small                             | 4                     | 2                    |
| Medium                            | 8                     | 3                    |
| Large                             | 1                     | 2                    |

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Table 2.10. Depth and type of protoconch for species of gastropods collected at Lee Stocking Island. There is no association between depth and type of protoconch ( $p = 0.697$ ). Species were counted once each time they occurred at each depth.

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| <u>Depth (m)</u> | <u>Elongate</u> | <u>Globose</u> |
|------------------|-----------------|----------------|
| 5                | 8               | 4              |
| 14               | 9               | 3              |
| 46               | 7               | 1              |

---

Furthermore, the *width* of the depth distribution (number of different depths at Lee Stocking Island from which a species is collected) was not associated with type of protoconch ( $p = 0.223$ , Table 2.11). Width of the depth distribution, was also not significantly associated with size of the geographic range ( $p = 1.000$ , Table 2.12). This, however, may be due to sampling, whereby a rare species is likely to be collected both from few depths and from few geographic localities. A plot of mean abundance of individuals per collector (data in Table 2.2) against number of depths from which species were collected showed, however, that most species are relatively rare ( $\leq 1$  individual per collector); these occurred in either one, two, or three depths, arguing against the idea that narrow depth distributions were associated with rarity or lack of sampling. The few common species were found in two to three different depths. When abundance is plotted against size of the geographic range, again rare species were observed in all three categories of range size; the few abundant species are characterized by either small or medium-sized ranges, however, again suggesting that the an association between narrow depth ranges and small geographic ranges would not be an artifact of sampling. Because of small sample sizes, however, this analysis does not rule out a possible association between width of the depth distribution and size of the geographic range as was seen in the analysis of the far larger data set in Chapter 3.

The size of the geographic range is not associated significantly with the depth at which the species is found ( $p = 0.837$ , Table 2.13). Thus, the hypothesis that species

Table 2.11. Width of depth distribution (number of depths from which species are recorded) and type of protoconch for gastropods collected at Lee Stocking Island. There was no association between width of depth distribution and type of protoconch ( $p = 0.223$ ).

| <u>Width of<br/>Depth distribution</u> | <u>Elongate</u> | <u>Globose</u> |
|--|-----------------|----------------|
| 1                                      | 6               | 6              |
| 2                                      | 3               | 0              |
| 3                                      | 4               | 1              |

Table 2.12. Width of depth distribution (number of depths from which species are recorded) versus small Geographic Range Index (GRI) (4.72 - 47.33) and large GRI (89.95-132.55) for gastropods collected at Lee Stocking Island. There was no significant association between width of depth distribution and the size of the geographic range ( $p = 1.000$ ).

| <u>Width of<br/>Depth distribution</u> | <u>Geographic Range Index</u> |              |
|--|-------------------------------|--------------|
|  | <u>Small</u>                  | <u>Large</u> |
| 1                                      | 7                             | 3            |
| 2                                      | 1                             | 1            |
| 3                                      | 1                             | 0            |

Table 2.13. Depth distribution and Geographic Range Index (GRI) for species of gastropods collected from Lee Stocking Island. Sizes of GRI are as in Table 2.9. There was no significant association between depth distribution and size of geographic range ( $p = 0.837$ ).

| <u>Depth (m)</u> | <u>Geographic Range Index</u> |               |              |
|------------------|-------------------------------|---------------|--------------|
|                  | <u>Small</u>                  | <u>Medium</u> | <u>Large</u> |
| 5                | 4                             | 9             | 4            |
| 14               | 3                             | 10            | 2            |
| 46               | 4                             | 7             | 1            |

from deep reef environments have narrower geographic distributions than those from shallow reef habitats can be rejected for gastropods from Lee Stocking Island.

### Modes of Feeding

Tables 2.1 and 2.2 show modes of feeding for bivalve and gastropod molluscs, respectively, collected at the five depths. Bivalves, which are usually planktivores, were represented at all depths except 153 m, though very few species of either bivalve or gastropod molluscs were collected at the two deeper depths, 153 m and 244 m. A one-sample chi-square test on planktivores at the 5 m, 14m, and 46 m depths (using only number of species with type of feeding mode values > 5) shows that the number of planktivores at 5 m was not significantly higher than at 14 m or 46 m (Table 2.14).

Modes of feeding for gastropods are summarized by depth, and number of species in Table 2.2. There was no significant association between mode of feeding and depth ( $p = 0.742$ ) (Table 2.15). Among all species of gastropods in the present study, 44% were carnivores, 52% were herbivores, and the remainder detritivores. In a study of intertidal reef environments in the western Indian Ocean and Caribbean, McClanahan (2002) found that 64 to 72% of the species were carnivores, the remaining third being a mixture of herbivores and detritivores.

Table 2.14. Number of species of planktivorous bivalves by depth. A one-sample chi-square test on data from 5 m, 14m, and 46 m (using only values > 5) showed that the number of planktivores at 5 m was not significantly higher than at 14 m or 46 m ( $\chi^2 = 1.67$ ,  $df = 2$ ,  $p = 0.50$ ).

---

| <u>Depth (m)</u> | <u>Planktivores</u> |
|------------------|---------------------|
| 5                | 12                  |
| 14               | 8                   |
| 46               | 8                   |
| 153 + 244        | 1                   |

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Table 2.15. Depth and modes of feeding for species of gastropods. There was no significant association between mode of feeding and depth ( $p = 0.742$ ).

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| <u>Depth (m)</u> | <u>Herbivores</u> | <u>Carnivores</u> | <u>Detritivores</u> |
|------------------|-------------------|-------------------|---------------------|
| 5                | 13                | 10                | 1                   |
| 14               | 7                 | 12                | 1                   |
| 46               | 7                 | 14                | 1                   |
| 153 + 244        | 2                 | 4                 | 0                   |

---

### Adaptations Against Predation

Species of gastropod molluscs show a variety of architectural modifications of the shell that can be interpreted as adaptations against predation. Six categories of architectural modifications that can be readily identified on gastropods include: 1) a high spire, 2) a thick shell, 3) compact spines, 4) a ribbed shell, 5) a thick lip, and 6) a heavily beaded shell. When these adaptations are ranked as High (three or more adaptations); Medium (two adaptations); or Low (none or one adaptation), it is possible to test whether these architectural features of shells vary over depth among species of gastropods at Lee Stocking Island (Table 2.16). When tested statistically using Fisher's Exact Test, the hypothesis that species of gastropods show more adaptations against predation in shallow than deep water is rejected ( $p = 0.733$ , Table 2.17).

Table 2.16. Species of gastropods found at five depths off Lee Stocking Island, with shell adaptations against predation and ranking for number of adaptations per species.

| <u>Species</u>                 | <u>Shell Adaptations</u> | <u>Rank</u> |
|--------------------------------|--------------------------|-------------|
| <i>Cerithium litteratum</i>    | ts, cs, tl               | H           |
| <i>Cerithium eburneum</i>      | hs, ts, tl               | H           |
| <i>Strombus gigas</i>          | ts, cs, rs, tl           | H           |
| <i>Ithycthyara lanceolata</i>  | ts, tl, rs               | H           |
| <i>Cerithium lutosum</i>       | ts, tl                   | M           |
| <i>Prunum carneum</i>          | ts, tl                   | M           |
| <i>Modulus modulus</i>         | ts, cs                   | M           |
| <i>Agathotoma candidissima</i> | ts, rs                   | M           |
| <i>Columbella mercatoria</i>   | ts, tl                   | M           |
| <i>Rubellatoma rubella</i>     | ts, rs                   | M           |
| <i>Nototriphora decorata</i>   | hs, hb                   | M           |
| <i>Iniforis turrithomae</i>    | hs, rs                   | M           |
| <i>Costoanachis lafresnayi</i> | hs, rs                   | M           |
| <i>Arene briareus</i>          | ts, cs                   | M           |
| <i>Arene cruentata</i>         | ts, cs                   | M           |
| <i>Bulla occidentalis</i>      | ts                       | L           |
| <i>Torcula exoleta</i>         | hs                       | L           |
| <i>Zafrona puchella</i>        | none                     | L           |
| <i>Tegula lividomaculata</i>   | ts                       | L           |
| <i>Tegula fasciata</i>         | ts                       | L           |
| <i>Haminoea petiti</i>         | none                     | L           |
| <i>Smaragdia viridis</i>       | none                     | L           |
| <i>Nassarius albus</i>         | rs                       | L           |
| <i>Polinices lacteus</i>       | ts                       | L           |
| <i>Columbellopsis nycteis</i>  | ts                       | L           |

| <b>LEGEND</b>                      |                                  |
|------------------------------------|----------------------------------|
| <u>Shell adaptations; Ranking:</u> |                                  |
| hs = high spire                    | H = High (3 or more adaptations) |
| ts = thick shell                   | M = Medium (2 adaptations)       |
| cs = compact spines                | L = Low (none or 1 adaptation)   |
| rs = ribbed shell                  |                                  |
| tl = thick lip                     |                                  |
| hb = heavily beaded                |                                  |

Table 2.17. Number of species of gastropods with adaptations against predation (ranked as high, medium, low) by depth off Lee Stocking Island. Adaptations of the shell were not significantly associated with depth ( $p = 0.733$ ).

---

| <u>Depth (m)</u> | <u>Shell Adaptations</u> |               |            |
|------------------|--------------------------|---------------|------------|
|                  | <u>High</u>              | <u>Medium</u> | <u>Low</u> |
| 5                | 1                        | 7             | 6          |
| 14               | 1                        | 8             | 6          |
| 46               | 2                        | 3             | 6          |

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## Body Size

Median body size, size range, number of individuals, and maximum reported size from Abbott (1974) were summarized for bivalve and gastropod molluscs, respectively, from Lee Stocking Island (Tables 2.18, 2.19). Unfortunately, maximum body size is the only metric available for body sizes of molluscan populations in the literature. It is unclear exactly how many of the bivalves or gastropods in the present study were juveniles, since growth rates of these species are not available. For some species such as the Queen Conch, *Strombus gigas*, the one individual at 16.8 mm was clearly a juvenile, when compared with the maximum reported size of 352.0 mm. Interestingly, the juvenile *S. gigas*, was found at 46 m (Table 2.4), representing a new depth record for that species (previously reported only to around 12 m). This observation supports suggestions in the literature (Stoner, 1996) that the Queen Conch recruits at depth then migrates inshore. Nine of the 11 species of bivalves and 14 of the 25 species of gastropods are represented by at least one individual that is less than 30% of the maximum reported size of the species. The median sizes (N>2) of seven species of bivalves and eight species of gastropods collected were less than 30% of the maximum body size known for the species (Tables 2.18, 2.19). Furthermore, in two species of bivalves (*Papyridea soleniformis* and *Ctenoides scabra*) and five species of gastropods (*Bulla occidentalis*, *Cerithium eburneum*, *Modulus modulus*, *Tegula lividomaculata*, and *Torcula exoleta*), the median (N>2) sizes of individuals collected were less than 20% of the maximum size reported for the species, suggesting either that these individuals were juveniles (and possibly had recruited as larvae) or that body sizes of deep populations from Lee Stocking Island were

Table 2.18. Median body size (mm), size range, and number of individuals for bivalve molluscs collected at Lee Stocking Island compared to maximum reported body sizes.

| <u>Species (by family)</u>        | <u>Median size</u> | <u>Size Range</u>           | <u>Number of Individuals</u> | <u>Maximum Size*</u> |
|-----------------------------------|--------------------|-----------------------------|------------------------------|----------------------|
| Arcidae                           |                    |                             |                              |                      |
| <i>Barbatia cancellaria</i>       | 9.5 <sup>(2)</sup> | –                           | 1                            | 45.0                 |
| Cardiidae                         |                    |                             |                              |                      |
| <i>Papyridea soleniformis</i>     | 4.3 <sup>(3)</sup> | 3.5 - 6.6                   | 6                            | 37.0                 |
| Limadae                           |                    |                             |                              |                      |
| <i>Limaria pellucida</i>          | 7.2 <sup>(2)</sup> | 3.3 - 14.3 <sup>(1)</sup>   | 34                           | 26.0                 |
| <i>Ctenoides scabra</i>           | 3.2 <sup>(3)</sup> | 1.4 - 9.6                   | 49                           | 67.0                 |
| Limposidae                        |                    |                             |                              |                      |
| <i>Limopsis sulcata</i>           | 3.2 <sup>(2)</sup> | 2.4 - 3.9                   | 4                            | 13.0                 |
| Noetiidae                         |                    |                             |                              |                      |
| <i>Arcopsis adamsi</i>            | 6.9 <sup>(1)</sup> | –                           | 1                            | 13.0                 |
| Pectinidae                        |                    |                             |                              |                      |
| <i>Spathochlamys benedicti</i> ** | 4.8 <sup>(1)</sup> | 2.8 - 9.9 <sup>(1,2)</sup>  | 13                           | 9.3                  |
| <i>Caribachlamys ornata</i>       | 7.1 <sup>(2)</sup> | 3.7 - 14.5 <sup>(1)</sup>   | 36                           | 25.0                 |
| <i>Laevichlamys multisquamata</i> | 14.5               | –                           | 1                            | 30.0                 |
| <i>Carbachlamys imbricata</i>     | 7.8 <sup>(2)</sup> | 6.6 - 8.1                   | 3                            | 37.0                 |
| <i>Brachtechlamys antillarum</i>  | 9.0                | 3.1 - 16.3 <sup>(1,3)</sup> | 18                           | 20.0                 |

\*Source: Redfern (2001), except for *Limopsis sulcata*, which is from Abbott (1974).

\*\*New record for body size.

<sup>(1)</sup> ≥ 50% of maximum reported size.

<sup>(2)</sup> ≤ 30% of maximum reported size.

<sup>(3)</sup> ≤ 20% of maximum reported size.

Table 2.19. Median body size (mm), size range, and number of individuals for gastropod molluscs collected at Lee Stocking Island compared to maximum reported body sizes.

| <u>Species (by family)</u>     | <u>Median size</u>  | <u>Size Range</u>          | <u>Number of Individuals</u> | <u>Maximum Size*</u> |
|--------------------------------|---------------------|----------------------------|------------------------------|----------------------|
| Bullidae                       |                     |                            |                              |                      |
| <i>Bulla occidentalis</i>      | 5.2 <sup>(3)</sup>  | 2.3 - 8.2                  | 7                            | 44.0                 |
| Cerithidae                     |                     |                            |                              |                      |
| <i>Cerithium eburneum</i>      | 6.3 <sup>(3)</sup>  | 4.3 - 15.2                 | 8                            | 43.0                 |
| <i>Cerithium litteratum</i>    | 8.6 <sup>(2)</sup>  | 2.7 - 21.2 <sup>(1)</sup>  | 57                           | 34.0                 |
| <i>Cerithium lutosum</i>       | 9.9                 | 7.8 - 12.0 <sup>(1)</sup>  | 2                            | 20.0                 |
| Columbellidae                  |                     |                            |                              |                      |
| <i>Costoanachis lafresnayi</i> | 15.1 <sup>(1)</sup> | –                          | 1                            | 18.0                 |
| <i>Zafrona pulchella</i>       | 6.1 <sup>(1)</sup>  | 3.2 - 9.0 <sup>(1,2)</sup> | 59                           | 12.0                 |
| <i>Columbella mercatoria</i>   | 7.1 <sup>(2)</sup>  | 2.3 - 12.3 <sup>(1)</sup>  | 14                           | 24.0                 |
| <i>Columbellopsis nycteis</i>  | 5.5 <sup>(1)</sup>  | 5.2 - 6.6 <sup>(1)</sup>   | 4                            | 8.1                  |
| Haminoeidae                    |                     |                            |                              |                      |
| <i>Haminoea petiti</i>         | 4.2                 | 3.1 - 7.7 <sup>(1,2)</sup> | 2                            | 11.5                 |
| Marginellidae                  |                     |                            |                              |                      |
| <i>Prunum carneum</i>          | 13.4 <sup>(1)</sup> | –                          | 1                            | 18.0                 |
| Modulidae                      |                     |                            |                              |                      |
| <i>Modulus modulus</i>         | 2.5 <sup>(3)</sup>  | 2.4 - 5.3                  | 3                            | 16.5                 |
| Nassariidae                    |                     |                            |                              |                      |
| <i>Nassarius albus</i>         | 4.5                 | 3.4 - 5.5                  | 5                            | 12.8                 |
| Naticidae                      |                     |                            |                              |                      |
| <i>Polinices lacteus</i>       | 3.7 <sup>(3)</sup>  | –                          | 1                            | 40.0                 |
| Neritidae                      |                     |                            |                              |                      |
| <i>Smaragdia viridis</i>       | 3.45                | 3.4 - 3.5                  | 2                            | 8.0                  |
| Strombidae                     |                     |                            |                              |                      |
| <i>Strombus gigas</i>          | 16.8 <sup>(3)</sup> | –                          | 1                            | 352.0                |
| Triphoridae                    |                     |                            |                              |                      |
| <i>Nototriphora decorata</i>   | 7.5 <sup>(1)</sup>  | –                          | 1                            | 12.0                 |
| <i>Iniforis turrithomae</i>    | 5.3 <sup>(1)</sup>  | 5.1 - 5.4 <sup>(1)</sup>   | 3                            | 9.0                  |

\*Information provided with the permission of The Academy of Natural Sciences, Philadelphia, PA.

<sup>(1)</sup> ≥ 50% of maximum reported size.

<sup>(2)</sup> ≤ 30% of maximum reported size.

<sup>(3)</sup> ≤ 20% of maximum reported size.

Table 2.19 (cont'd). Median and range for size (mm) of gastropod molluscs collected at Lee Stocking Island compared to maximum reported body sizes.

| <u>Species (by family)</u>     | <u>Median size</u> | <u>Size Range</u>          | <u>Number of Individuals</u> | <u>Maximum Size*</u> |
|--------------------------------|--------------------|----------------------------|------------------------------|----------------------|
| Trochidae                      |                    |                            |                              |                      |
| <i>Tegula fasciata</i>         | 5.3 <sup>(2)</sup> | 1.0 - 10.7 <sup>(1)</sup>  | 94                           | 20.0                 |
| <i>Tegula lividomaculata</i>   | 2.0 <sup>(3)</sup> | 1.5 - 2.7                  | 5                            | 20.0                 |
| Liotiidae                      |                    |                            |                              |                      |
| <i>Arene briareus</i>          | 5.3 <sup>(1)</sup> | –                          | 1                            | 9.0                  |
| <i>Arene cruentata</i>         | 2.5 <sup>(3)</sup> | –                          | 1                            | 16.3                 |
| Turridae                       |                    |                            |                              |                      |
| <i>Ithythythara lanceolata</i> | 4.5                | –                          | 1                            | 12.0                 |
| <i>Agathotoma candidissima</i> | 5.4                | 3.2 - 6.7 <sup>(1,2)</sup> | 10                           | 11.0                 |
| <i>Rubellatoma rubella</i>     | 7.2 <sup>(1)</sup> | 5.4 - 9.6 <sup>(1)</sup>   | 7                            | 11.0                 |
| Turritellidae                  |                    |                            |                              |                      |
| <i>Torcula exoleta</i>         | 5.2 <sup>(3)</sup> | 4.2 -21.5                  | 7                            | 75.0                 |

\*Information provided with the permission of The Academy of Natural Sciences, Philadelphia,PA.

<sup>(1)</sup>  $\geq$  50% of maximum reported size.

<sup>(2)</sup>  $\leq$  30% of maximum reported size.

<sup>(3)</sup>  $\leq$  20% of maximum reported size.

smaller than those reported for these species in the literature (most of which probably come from shallow populations).

However, four species of bivalves and 14 species of gastropods were represented by at least one individual in the collection that exceeded 50% of the maximum body size reported for the species (Tables 2.18, 2.19). Among bivalves, the median body size (N=13) of *Spathochlamys benedicti* was greater than half of the maximum reported size for the species, and one individual was larger than any member of this species reported in the literature. Among gastropods, the median (N>2) body size collected exceeded 50% of the maximum reported size in *Zafrona pulchella*, *Columbellopsis nycteis*, *Iniforis turristhoniae*, and *Rhubellatoma rubella*. At least some species, therefore, appeared to be represented by adult individuals.

Median body sizes (mm ) and size ranges for species of bivalves and gastropods that occur at least at two different depths were analyzed from 5 - 46 m at Lee Stocking Island. Of these species, species were selected for statistical analysis of size vs. depth for any species that had at least three individuals at a minimum of two depths ((Table 2.20). Species that fit this criteria, but had less than three individuals at a given depth, that depth was excluded from the analysis. ANOVA's were run in JMP on two bivalves, *Ctenoides scabra* and *Lyropecten antillarum*, and four gastropods, *Tegula fasciata*, *Rubellatoma rubella*, *Bulla occidentalis*, and *Zafrona pulchella*. Of the bivalves, *C. scabra* body sizes showed an insignificant relationship with depth ( $p = 0.145$ ), while the decline in body size over depth for *L. antillarum* was highly significant ( $p=0.0004$ ). Of the gastropods, only *T. fasciata* body sizes declined significantly with depth ( $p=0.0001$ ).

Table 2.20. Median body sizes (body size range in parentheses) in mm for species of bivalves and gastropods that occurred at least at two different depths from 5 - 46 m at Lee Stocking Island. Sample sizes for each species at the individual depths are given in brackets.

| <u>Species of bivalves</u>       | Depth               |                     |                    |
|----------------------------------|---------------------|---------------------|--------------------|
|                                  | <u>5m</u>           | <u>14m</u>          | <u>46m</u>         |
| <i>Spathochlamys benedicti</i>   | 14.7 [1]            | 0                   | 4.5 (2.8-9.9) [12] |
| <i>Caribachlamys ornata</i>      | 7.1 (3.7-14.5) [34] | 4.0 (6.1-7.7) [2]   | 0                  |
| <i>Lyropecten antillarum</i>     | 13.3 (8.5-16.4) [9] | 5.1 [1]             | 4.2 (3.7-11.0) [7] |
| <i>Papyridea soleniformis</i>    | 4.3 (3.5-6.6) [5]   | 4.4 [1]             | 0                  |
| <i>Limaria pellucida</i>         | 7.3 (3.3-12.1) [33] | 6.2 [1]             | 0                  |
| <i>Ctenoides scabra</i>          | 4.3 (2.8-9.2) [6]   | 3.0 (2.2-5.5) [13]  | 3.1 (1.4-9.6) [30] |
| <u>Species of gastropods</u>     |                     |                     |                    |
| <i>Zafrona pulchella</i>         | 6.1 (3.7-9.4) [7]   | 6.2 (3.1-8.5) [29]  | 6.1 (3.2-9.0) [23] |
| <i>Bulla occidentalis</i>        | 5.4 (4.5-6.8) [4]   | 0                   | 4.0 (2.3-8.2) [3]  |
| <i>Cerithium eburneum</i>        | 7.0 (4.3-15.2) [7]  | 3.5 [1]             | 0                  |
| <i>Cerithium litteratum</i>      | 8.6 (2.7-21.2) [55] | 10.0 (6.6-13.4) [2] | 0                  |
| <i>Columbella mercatoria</i>     | 7.4 (4.4-13.0) [13] | 2.3 [1]             | 0                  |
| <i>Modulus modulus</i>           | 2.4 [1]             | 2.5 (2.4-5.3) [2]   | 0                  |
| <i>Nassarius albus</i>           | 5.5 [1]             | 5.3 [1]             | 3.9 (3.4-4.5) [3]  |
| <i>Pyrgocythara candidissimi</i> | 5.9 (5.4-6.4) [2]   | 4.6 [1]             | 5.4 (3.2-6.7) [7]  |
| <i>Tegula fasciata</i>           | 5.5 (1.4-10.7) [77] | 3.2 (1.3-6.1) [13]  | 1.2 (1.0-3.9) [4]  |
| <i>Tegula lividomaculata</i>     | 2.1 (1.5)-2.7) [4]  | 0                   | 2.0 [1]            |
| <i>Torcula exoleta</i>           | 0                   | 5.9 (4.6-7.1) [2]   | 5.2 (4.6-21.5) [4] |
| <i>Rubellatoma rubella</i>       | 7.4 (6.0-9.6) [3]   | 5.4 [1]             | 7.2 (5.4-7.7) [3]  |

The other three gastropods showed an insignificant relationship of body size with depth (*R. rubella*,  $p=0.607$ ; *B. occidentalis*,  $p=0.689$ , and *Z. pulchella*,  $p=0.812$ .)

### Species Co-occurrence

In a description of possible approaches to the analysis of co-occurrence, Gotelli and Graves (1996) note the importance of interspecific interactions in determining which species are found in a particular assemblage. The classic checkerboard pattern is where only one of two species, but not both, occur at a given site, indicating that the presence of one species may preclude the occurrence of another species (Diamond, 1975). The presence of many checkerboard pairs of species in a community (where species occur at a site in a non-random manner) is evidence of “deterministic assembly rules.” Two key deterministic assembly rules are 1) where species that overlap “too much” in resource use or other niche dimensions cannot coexist; and, 2) species that do coexist must differ in body size or trophic morphology in such a way that allows them to use different resources in the same site or habitat area (Gotelli and Graves, 1996). As part of the analysis, presence-absence matrices were constructed for species of bivalves and gastropods collected at five depths off Lee Stocking Island, Bahamas.

Because of the phylogenetic, morphological, and ecological differences between bivalves and gastropods, reflected in their categorization as different molluscan classes, each was analyzed separately for co-occurrence. For bivalves, the “C-score,” or checkerboard index, as computed with EcoSim, resulted in an observed C-score of 0.32. The observed number of checkerboard units was not significantly different from the expected ( $p>0.05$ ), indicating that the C-score was not significantly larger than expected

by chance. For gastropods, the “C-score,” or checkerboard index, resulted in an observed C-score index of 0.45. Here also, the observed number of checkerboard units was not significantly different from the expected ( $p > 0.05$ ), indicating that the C-score was not significantly larger than expected by chance. These results imply that, of the bivalve and gastropod species of molluscs assemblages found in the collectors at the five depths, there were no significant non-random patterns of species co-occurrence detected among the five depths. An important caveat to this result is that the species that colonized the artificial benthic collectors do not likely reflect the full spectrum of species of bivalves and gastropods in the natural environment, when compared to the much larger numbers of species in long-term collections such as Redfern (2001) from Abaco Island, Bahamas (Redfern collected over 108,000 specimens over a 30 year period).

## DISCUSSION

The present study documents 25 species of gastropods and 11 species of bivalves living on reef framework over a depth gradient of 5 - 244 m off Lee Stocking Island in the Exumas, Bahamas. The total number of species of bivalves and gastropods in the Bahamas is unknown. Robertson (1994) reported that approximately 650-700 species of bivalves and gastropods, mostly small in size, have been found in the Bahamas. Redfern (2001) later documented, from over 30 years of collecting, a total of 866 species of bivalves and gastropods (89 and 777 species of each group, respectively) from his study at Abaco Island, Bahamas. The true number of species of bivalves and gastropods on Abaco is likely even higher than the number reported by Redfern (2001), given that only



approximately 27% of the 50,000 - 100,000 species of global molluscs have been described (Brusca and Brusca, 1990; Kozloff, 1989; Ruppert and Barnes, 1994; Systematic Agenda 2000, 1994) and the fact that greater depths (e.g., > 50 m) are known to contain a high proportion of undescribed species of some taxa (Wilson and Kaufman, 1987; Pyne, 2000). Thus, the species in the present study represent a relatively small subset of the total gastropod and bivalve fauna that occurs in the Bahamas.

The results in the present study nevertheless contribute to a better understanding of the bivalve and gastropod fauna of the Exumas, and ultimately towards a more complete assessment of the total number of species that inhabit the broader Bahamas. Although this study sampled considerably fewer species, several types of analyses showed that the proportion of families of gastropods and bivalves collected were very similar to, and that the depth distributions of bivalves and gastropods were not significantly different from, those of Redfern's (2001) extensive study of molluscs at Abaco Island. Chiappone et al. (1997) reported that they did not find any consistent latitudinal pattern in common species in their studies of reef invertebrates of the Exuma Cays, and noted the apparent environmental uniformity throughout much of the Bahamas.

Despite extensive studies on molluscs in the Bahamas, such as Abbott (1974) and Redfern (2001), it is apparent that much work still needs to be done to better assess the species assemblages of bivalves and gastropods that exist in the Bahamas, particularly with respect to species that live deeper. Three new depth records were established for bivalves and ten for gastropods in the present study. When considering the difficulties of sampling deeper reef habitats, and that even the larger macrofauna, such as fishes, may be

as much as 70% undescribed at 90 m (Pyle, 2000), a large number of small and cryptic species of bivalves and gastropods likely remains unknown on deep reefs.

The benthic collectors used in this study offer a consistent method that could be used to assess gastropod and bivalve molluscan assemblages over depth in a wide range of habitat types. Contrasting with other widely used methods such as dredging, baiting and trapping, and suction, the benthic collectors provide artificial habitat that has proven suitable for collecting both bivalves and gastropods, and the habitat is not damaged by their use. Limitations of the collectors are that they may exclude species larger than a few centimeters because of the relatively small openings and they are difficult to deploy and secure on slopes that exceed much greater than a 40 to 45 degree angle.

The type of protoconch was not significantly associated with size of the geographic range, or with depth distribution among species of gastropods at Lee Stocking Island. Similarly, type of protoconch does not differ significantly with width of the depth distribution. Although narrow depth distributions were not associated with narrow geographic ranges in gastropods from Lee Stocking Island, this may be associated with sampling effects (rare species, however, are found across all depths and among all sizes of geographic ranges). These findings suggest that, while the shape of the protoconch can be used as a predictor of the potential for larval dispersal in some species of gastropods, this relationship does not always hold true, either because the protoconch is not *consistently* associated with length of larval life, or because larval behaviors or oceanographic conditions disrupt the usual correlation between length of larval life and extent of the geographic range. This finding supports the need to understand the reproductive life

history and larval biology of individual species along with the shape of the protoconch, and argues that the shape of the protoconch should not be used alone to predict wide or restricted larval dispersal.

The early observations by numerous authors such as Powell (1942) and Thorson (1950) that the shape of the protoconch on gastropods can be used to infer planktotrophic or lecithotrophic modes of larval development has been used by various researchers such as Shuto (1974), Hansen (1980), and Jablonksi (1986) to infer mode of larval development in extinct species, or in extant deep-sea species whose planktonic development and dispersal is otherwise unknown. This concept has been generalized and used as an assumption to formulate biogeographical and speciation models for gastropods (Grant and da Silva-Tatley, 1997). Species with long-lived larvae logically would then have large geographic ranges, which allows for widespread distribution, and possibly a hedge against extinction, when compared to species with lecithotrophic larvae. The results of the present study of species of gastropods in the Bahamas, which did not show a significant relationship between shape of the protoconch and geographic range, are consistent with the preliminary results of a long-term investigation of protoconch form and geographic range at the Academy of Natural Sciences, where no direct correlation is evident within faunal provinces; definitive conclusions await completion of the project, however (G. Rosenberg, pers. comm.). Since the hypothesis that geographic ranges of gastropod molluscs are larger in shallow than deep water habitats at Lee Stocking Island was rejected, the present study suggests that dispersal capability of gastropods does not decline with greater depth over the range of depths (5 m - 46 m) analyzed at Lee Stocking Island. Reaka (1980) and

Pyle (2001), however, did find smaller geographic ranges among reef stomatopods (>10 m) and deep-dwelling reef fishes (>90 m), respectively, than those living in shallow habitats, and Wilson and Kaufman (1987) reported a high incidence of endemism for fishes on some southwestern Pacific sea mounts. Greater endemism in deep reef habitats suggests that threats to these habitats should be carefully assessed and controlled.

Gastropods, however, do not appear to be as much at risk of anthropogenic disturbance on deep reefs as some other groups. The deep reef nevertheless may represent a unique environment with its own set of environmental and biotic characteristics. Porter (1973) suggested that deep reefs represent a sort of “twilight zone” inhabited by species that are specific to this environment and different from those in both shallower *and* deeper water. Deeper reef areas, including those in the Bahamas, increasingly are subject to commercial exploitation and increasingly are being recognized as a unique and poorly understood habitat. Recent dredging from deep water (300 - 400 m) on the Bimini Shelf of the Great Bahama Bank has revealed the presence of a benthic community that includes at least 28 species of gastropods (Petuch, 2002). At least three of the deep-water species collected by Petuch are represented in the present study (two species of the genus *Cerithium* and one *Trivia*). Petuch (2002) notes that the great range of depths found on the Bahamas Platform makes it one of only about four areas in the Caribbean and Gulf of Mexico regions that is largely unexplored and may contain a rich molluscan fauna with new and undescribed species.

The newly discovered molluscan fauna from these “deep-reef” environments live on ancient limestone that was once near the surface as actively growing coral reefs.

Studying a range of habitats from 10- 250 m off Lee Stocking Island, Avery (1998) observed that living cover is high above 100 m, declines markedly below 100 m, and is replaced by increasing amounts of bare rock and sediment-covered rock surfaces (see Chapter 1). The dominant motile organisms in the deep environment beyond 100 m are polychaetes. Many organisms in the deeper and dark areas of the slope off Lee Stocking Island depend on detritus falling from above. Liddell et al. (1997) observed that the amount of hard substrate available for colonization by epi- and endo-benthos declines significantly below 100 -125 m off Lee Stocking Island. This sedimentary environment provides little microhabitat for refuge from predation, and little hard substrate for settlement of larvae, which may partly explain the lower abundance, and possibly lower diversity, of bivalves and gastropods at the deeper depths of the present study at Lee Stocking Island.

Avery (1998) noted that peak recruitment for most taxa of sessile organisms occurs on the substrate between 20 m and 50 m off Lee Stocking Island. The occurrence of a juvenile queen conch at 46 m in the present study is consistent with other research in the Bahamas which suggests that recruitment for some species of molluscs, such as the queen conch, may occur in deep water, whereas adults of these species are found in shallower habitats. Two species in the present study, one bivalve and one gastropod, showed a highly significant decline in body size with increasing depth: the bivalve *Lyropecten antillarum* ( $p=0.0004$ ), and the gastropod, *Tegula fasciata* ( $p=0.0001$ ). Other bivalves and gastropods that had at least three individuals at two or more depths also were analyzed, though results were insignificant.

Glynn (1990) reported a steady decline in herbivory by invertebrates and fishes with increasing depth on reefs. Also, in his study of deep-water fishes off Lee Stocking Island, G. Dennis (pers. comm.) noted a significant drop in fish abundance and diversity below 150 m. At least twelve families of carnivorous fishes (particularly nocturnal species) consume benthic or epibenthic organisms, including molluscs, in coral reef environments (Hobson, 1974). Carnivorous species were shown in a study by McClanahan (2002) of intertidal reef environments to comprise 64-72% of the species, yet despite the high percentage of carnivorous species, carnivores never comprised more than 25% of the individuals.

The present study did not show significant changes in the mode of feeding or adaptations against predation over the range of depths examined here. The present study offers little evidence that biological interactions differentially structure benthic molluscan communities in shallow vs. deep reef environments. More comprehensive studies might demonstrate such interactions, or other factors, such as recruitment limitation, low productivity, or episodic disturbance, may keep populations below densities that necessitate extensive interactions among individuals and species. Further studies of the diversity and abundance of deep reef organisms such as benthic molluscs are needed, particularly at depths beyond 150 m (Pyle, 2000). A summary of relatively recent available data do not suggest that there are clear gradients of species diversity from shallow water to the deep sea (Gray, 2001). Comprehensive assessments of molluscan species richness and abundance are urgently needed to draw together the increasing numbers of point samples and habitat surveys from shallow and deep water, and to define

species assemblages and the processes that regulate them, particularly in tropical areas such as the Bahamas where threats to biodiversity are likely to increase.

## CHAPTER 3

### BIOGEOGRAPHIC PATTERNS OF BAHAMIAN GASTROPOD MOLLUSCS

#### ABSTRACT

Analysis of data on 960 species of gastropod molluscs from the Western Atlantic Gastropod Database of the Academy of Natural Sciences (ANS) showed a positive relationship between the body size of species of gastropods and both the size of their geographic ranges and the extent of their depth range. This finding is consistent with similar studies of other taxa such as coral-dwelling mantis shrimps. Minimum depth was negatively correlated with the size of the geographic range, indicating that, generally, species occurring in shallower water occur over wider areas. Species with more shallow minimum depths had small depth ranges, while species with deeper minimum depths tended to have broader depth ranges. Interestingly, maximum depth showed a positive relationship with the size of the geographic range, indicating that species inhabiting deeper waters also occurred over wider geographic areas. Species of gastropods with large depth ranges had larger geographic ranges, which suggested that depth range influenced species having large geographic ranges on both ends of the depth spectrum. Western Atlantic gastropods in general have very large geographic ranges compared to some other taxa. The numbers of species of Bahamian gastropods in the ANS data set whose ranges extended into the Eastern Pacific region (350 species, 37% of total) and Brazilian province (480 species, 50% of total) were relatively high, considering that the Eastern Pacific is separated by the physical barrier of the Isthmus of Panama, and the relative distance,



geographically, of the Brazilian province from the Caribbean. The commonality of the species reported from either side of the Isthmus of Panama likely reflect historical factors in that both are descendants of Tethyan fauna. The species in the Bahamas that have geographic ranges extending to the Eastern Atlantic (83 species, 8.6% of total) also reflect historical affinities with the Western Atlantic.

## INTRODUCTION

### Background

The broad biogeographic divisions that are generally accepted for the tropical oceans include the Indo-West Pacific, Eastern Pacific, Western Atlantic, and Eastern Atlantic (Ekman, 1953; Briggs, 1974, and Vermeij, 1978). Sub-divisions of these broad biogeographic regions are based on endemic faunas that have formed as a result of physical barriers (e.g., Isthmus of Panama) and environmental influences (e.g., changes in oceanic circulation, temperature, productivity). Global biogeographic patterns have been described in considerable detail for some taxa such as corals (Veron, 1995) and fishes (Bellwood and Wainright, 2002). The history of the movement of corals from the Old World (Tethys Sea) to the New World (Caribbean region) is one of the best documented in paleobiology (Veron, 1995). The current state of understanding of biogeographical patterns for molluscs in the tropical Western Atlantic is improving with continued sampling and new discoveries, particularly for poorly understood distributions of species that occur in deeper waters. While Briggs (1995) described general provincial patterns for the tropical Western Atlantic, Petuch (2004) proposed provincial structure of even higher

resolution, specifically for tropical Western Atlantic molluscs. Petuch's (2004) proposal is based largely on the arrangement of endemic faunas as seen in fossil gastropod molluscs in the late Pleistocene. Petuch (2004) suggested that this "final arrangement" in the late Pleistocene also holds for present-day distributions of molluscan species.

The purpose of this chapter is to further investigate biogeographical patterns in the tropical Western Atlantic by analyzing the distributions of gastropod molluscs whose geographic ranges extend into the Bahama Islands that are reported in the Western Atlantic Gastropod Database of the Academy of Natural Sciences (ANS). The data also are discussed as they relate to other Western Atlantic, Eastern Atlantic, and Eastern Pacific molluscan faunas. The ANS dataset is the most comprehensive dataset of its kind for species of gastropod molluscs, and contains information on maximum size, minimum and maximum depth, and latitudinal and longitudinal ranges. These parameters were analyzed to provide a better understanding of the geographic distributions and affinities of species of gastropods in the tropical Western Atlantic, and to describe relationships that exist between the reported sizes, depths, and geographic ranges of the species. The geological origin and environmental conditions of the Bahamas, along with a brief overview of the global and regional biogeography are described in the following two sections to provide context for the patterns that were seen in the analysis of the ANS gastropod dataset.

#### Geological Origin and Environment of the Bahamas

The Bahama Islands are low-lying carbonate islands that stretch from 27°N off the coast of Florida to 21°N north of Haiti, resting on two large bank systems, the Great Bahama Bank in the south and the Little Bahama Bank in the north (Figure 3.1). The

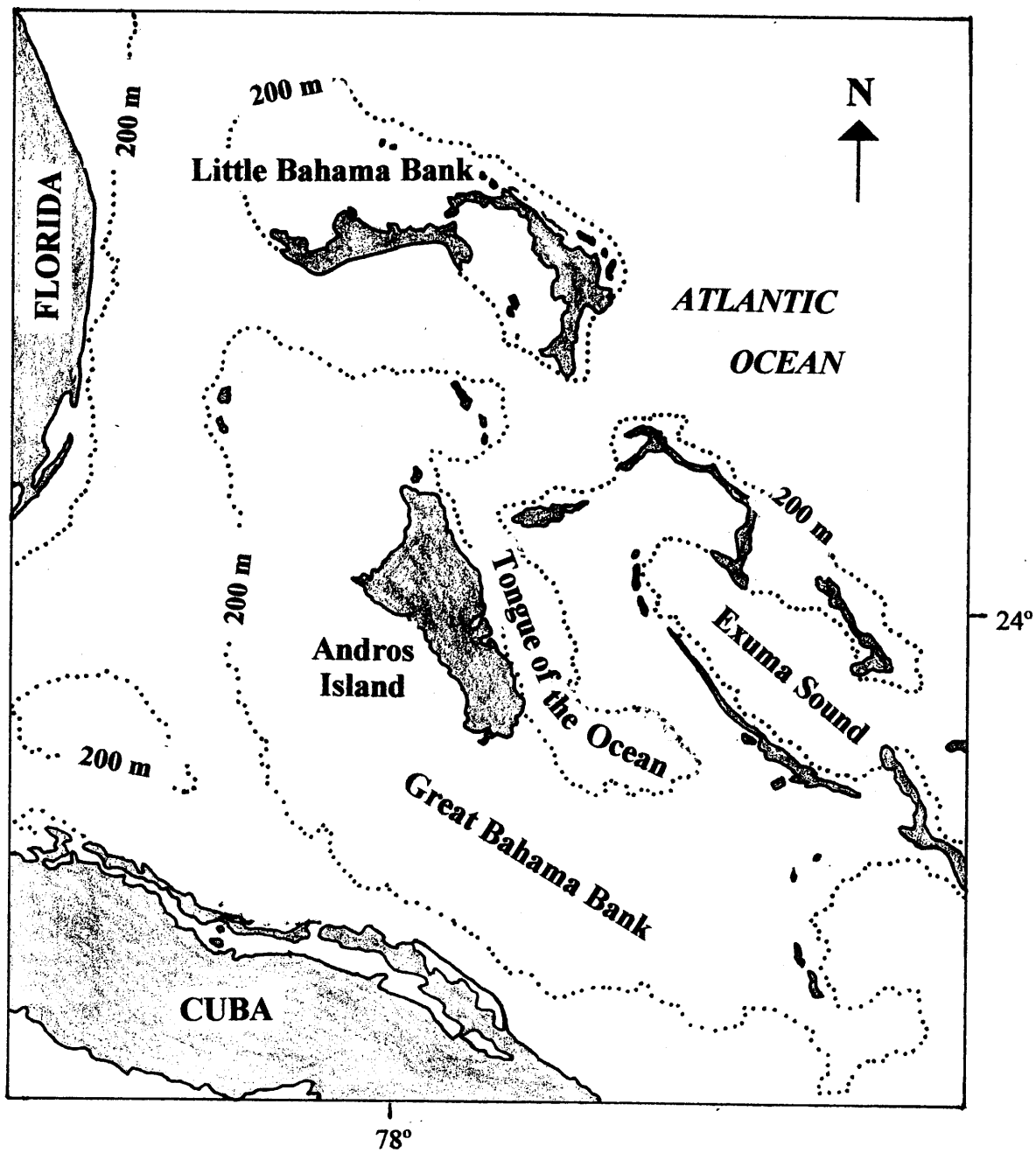


Figure 3.1. Bathymetric map of the Bahamas banks delineated by 200 m isobaths.

island group consists of about 2,750 islands, cays, and islets totaling 4,400 square miles (7,085 km<sup>2</sup>) of currently exposed surface (Storr, 1964).

The Little Bahama Bank to the north and the Great Bahama Bank to the south are delineated by the 200 m depth contour, though water depths over most of the banks are less than 10 m. The vast expanses of sand that occur in these areas reflect the heavy sedimentary environment which is a major factor affecting the shallow water biota. These shallow seas give the Bahamas its name, from the Spanish “Baja Mar.”

The origin of the Bahamas has been a subject of debate among geologists over the last 100 years, and remains controversial. Mullins and Lynts (1977) proposed that the Bahamas are a result of plate tectonic activity, which formed as a “horst graben.” Horst and graben pairs can occur in areas of rifting, where the crust of the Earth is being pulled apart. Horsts are relatively high-standing fault blocks, whereas graben refers to a relatively low-standing fault block. Meyerhoff and Hatten (1974) described the Bahamas as a remnant of a much larger platform.

About 200 mya, at the boundary of North America and Africa, the continental crust was stretched and thinned as Africa pulled away from it (Sealy, 1994). The thinning crust (which has now stopped thinning) gradually was flooded by the surrounding ocean and overlain with sediments. It is believed that the Bahamas and its neighbors (present day Cuba and Florida), were nearly at sea level, and formed a vast marine “plain” dotted with islands. As sediments accumulated on the thin crust, sinking occurred. This process probably varied with location. For instance, in areas of the Bahamas where the

sedimentation rate was less than the rate of sinking, troughs may have formed, but these are not directly relatable to present morphology.

About 80 mya towards the end of the Cretaceous, a major event occurred in the Western Atlantic as the Americas distanced themselves from Europe and Africa. This event drowned the Blake Plateau, separated the Bahamas from Cuba and Florida, and created the extensive troughs and channels among the Bahama Banks (Sealy, 1994). The nature of the event is unknown, though it is clear that a major change in the environment had occurred.

Theories abound on the evolution of the Bahamas Banks once they were separated from Cuba and Florida. Mullins and Hines (1989) suggested processes such as step-faulting and rifting that created troughs and channels, filling in of troughs by lateral (current-borne) sedimentation, and scalloping (erosion) of the Bank margins. Despite the uncertainties about the early formation of the Bahamas in the context of plate tectonics, most authors concur on the general sedimentary processes that created and maintain the carbonate banks. The grouping of the Bahamas into banks provides enormous atoll-like structures that resulted from the lithification of coral sand and reef debris (Storr, 1964). Sediment cores as deep as 5,800 m have shown that the carbonate structure of the Bahamian platform was formed in place. No rock was found which was older than 135 million years (Cretaceous period) with one exception. In "Great Isaac's Well," limestones and marine shales dated to the earlier Jurassic period were found, along with some volcanic debris which may have come from the North American continent.

The rock layers of the Bahamian platform are all shallow-water carbonates, which could only have been formed by calcifying organisms such as corals near the surface (Sealy, 1994). For comparison, extensive studies of sediment cores on Eniwetok Atoll showed that Eniwetok is formed by 1.25 km of shallow-water coral limestone, dating back to the Eocene, resting on top of a 3.2 km basalt volcano on the ocean floor (Stoddart, 1969). It has been suggested that the Bahamas may have formed in a manner similar to the Pacific atolls, though, despite the deep drilling in the Bahamas, evidence of *in situ* volcanism has not been encountered.

The underlying beds of limestone which comprise the Bahamian platform are believed to slope seaward towards the Atlantic where they are at their thickest (Sealy, 1994). Numerous deep-water channels and straights, including the Tongue of the Ocean, occur within and between the Bahama Banks. The origins of the deep-water channels in the Bahamas such as the Tongue of the Ocean are not completely understood in the context of sedimentary processes that would seem to favor accretion rather than troughing (Sealy, 1994). Changes in sea level tied to glaciations in the Late Quaternary played a large role in shaping the present day emergent land formations in the Bahamas (Hearty, 1998). The exposed “rockland” of the Bahamas, being composed of limestone, is subject to weathering or dissolving by rainwater (which is slightly acidic from passing through the atmosphere). This weathering is apparent in caves and other erosional formations throughout the Bahamas and is considered a type of karst topography that is characteristic of the tropics (Sealy, 1994). In the context of changing sea levels, the amount of emergent

landscape peaked at or above present levels at least three times since 0.45 mya (Hearty and Kaufman, 2000).

### *Currents*

Regionally, the Bahamian islands are “sandwiched” between two major currents: the Antilles Current to the east and the Florida Current to the west. The Antilles Current transports warm tropical waters from the North Equatorial Current northwestward (Rowe, et al., 2002), but does not show a continuous flow along the Antilles island chain and the Bahamas (Lee, et al., 1996), appearing more as an eddy field than as a continuous jet (Gunn and Watt, 1982). Receiving input both from the Loop Current in the Gulf of Mexico and the Antilles Current, the Florida Current flows consistently northward after it passes through the Straits of Florida, although it shows significant seasonal variation in flow rate (Niiler and Richardson, 1973).

Circulation within the Bahamas is influenced by the island configurations, the varied deep and shallow topography, winds, water density, and tides. Generally, surface currents flow to the northwest due to the influence of the trade winds that blow from the southeast across the Bahamas. The northeasterly direction of the trade winds in the north Atlantic is deflected by the temperature effect of the North American continent that “bends” the northeast trade winds so they blow from the southeast to the northwest on their way into the continent (Sealy, 1994). Tides pump water onto and off the platforms, causing reversible flows through the scattered islands and cays of the Bahamas; these tidal currents can be very strong in shallow constricted channels.

Major surface current patterns for the wider Caribbean region indicate a general pattern of connectivity beginning with the Lesser Antilles, through the Caribbean Basin, and on to the Gulf Stream. In the context of this connectivity via surface currents, Roberts (1997) analyzed dispersal routes of pelagic fish larvae from 18 sites in the Caribbean region and found that the sites varied considerably, both as sources and recipients of larvae. Roberts (1997) used two categories of dispersal periods, one and two months, to examine the potential for recruitment between upstream and downstream locations in the Caribbean. While Roberts' (1997) findings may not be directly applicable to many species of gastropods, the implications of transport within the Caribbean do help explain the relative homogeneity of many taxa in the region. Local retention mechanisms, and the ability of certain larvae to influence their own dispersal, suggested the existence of population-isolating mechanisms in the region. Local retention mechanisms were seen as an impediment to wide distribution, depending on the upstream or downstream location of the study site. The effectiveness of local retention mechanisms and the behavior of some species to enhance local retention were seen as factors that would likely increase the number of generations required for species to circuit the region.

### *Climate*

The Bahamian climate is generally considered sub-tropical (Sealy, 1994). Positioned on the boundary between temperate and tropical zones, the Bahamas have a warm temperate winter and tropical summer. The islands are directly in the path of the year-round trade winds and thus have a "trade wind climate." The Bahamas occasionally are influenced by cold fronts from North America in winter, and by hurricanes from the



Atlantic in summer (Sealy, 1994). The Antilles Current and the Florida Current, both consisting of warm water, tend to buffer the Bahamas from temperature extremes, even in the most severe conditions.

The shallow banks of the Bahamas provide conditions that result in the bank waters generally being more dense than those in the adjacent and deeper Exuma Sound. Evaporation on the shallow platforms can be extensive, and dense, high salinity currents often cascade off the platform, especially during the spring and summer months (Hickey, 2000; Smith, 2001). During periods of low rainfall and low wind speeds in spring and summer, evaporative cooling is reduced over the shallow banks, resulting in a “downwelling” pattern where hyperpycnal, unusually warm water floods the adjacent shelf. These localized density currents have been implicated in coral bleaching (Smith, 2001), and alter local circulation patterns of the along-shelf bank water.

#### Biogeographical Relationships of the Bahamian Marine Fauna

##### *Global Marine Biogeography*

The origins of present-day marine biogeographical patterns can be traced to the formation of the Tethys Sea which formed two relatively uniform zoogeographical provinces, the Indo-European in the east, and the American province to the west (Ekman, 1953). The closure of the Tethys Sea was marked by the relatively early connection of the landbridge between Asia and Africa in the east and the relatively recent formation of the Isthmus of Panama in the west. Many of the similarities in present day taxa are due to the relative homogeneity of the Tethys fauna. The relative paucity of warm water species in

the Atlantic today compared to the Indo-West Pacific can be attributed in large part to a deterioration in climate and extinctions that began with cooling in the early Tertiary.

The four major biogeographic regions in the present-day tropical ocean are: the Indo-West Pacific, Eastern Pacific, Western Atlantic, and Eastern Atlantic (Briggs, 1974). In turn, each of these regions can be subdivided into provinces, based on barriers that have promoted, at the species level, endemic faunas. The Western Atlantic region has been sub-divided provincially in various ways, depending on individual taxa and the state of understanding of the number and distribution of species. For example, within the Caribbean, a north-south division within the Caribbean with further subdivisions was proposed by Domeier (1994) based on the genus *Hypoplectrus*, a reef-associated serranid (sea bass) fish. Subsequent authors also have subdivided the Caribbean based on distributions of various fish species. Provincial configurations and sub-groupings within provinces in the western Atlantic typically are modified with finer resolution as more data become available.

Two major historical events dominated the late Pliocene to Pleistocene environments of the tropical Americas (Jackson and Budd, 1996): 1) isolation and oceanographic separation of the eastern Pacific and Caribbean due to the formation of the Central American Isthmus about 3.1-2.8 mya (Coates and Obando, 1996), and 2) changes in sea level and oceanographic conditions associated with the intensification of glaciation in the Northern Hemisphere about 2.4 mya. The timing of these events remains an area of controversy, particularly with respect to the oceanographic response (e.g., water temperature, primary productivity) to climate change. The precision of regional

stratigraphic records is only about  $\pm$  one million years, thus it is not possible to conclude that major environmental and biological events were synchronous across the Caribbean region (Allmon et al., 1996; Dowsett and Cotton, 1996).

The study of the effects of the formation of the Isthmus of Panama has led to a better understanding of biogeographic patterns because the isolation created by the emergence of the Isthmus essentially divided the ancestral species into two large sub-populations (Collins, 1996). For example, Bellwood and Wainwright (2002) note that, for fishes, there remain about a dozen species that span both sides of the Isthmus of Panama with little or no morphological differentiation. These “geminate species” pairs suggest that the rise of the Isthmus of Panama centrally divided the broad geographic range of some ancestral species into two sub-populations, rather than creating small “peripheral isolates” (Collins, 1996).

*a. Molluscs*

Molluscan faunas of the Caribbean and southeastern North America experienced a major pulse of extinction and origination about 2 mya in the late Pliocene (Allmon et al., 1996). In general, extinction occurs because no member of a population can survive or because the population cannot recover from a particular event (Vermeij, 2001). Thus, as long as there are refuges during rare environmental events, species can persist.

Areas where continuous upwelling occurred, such as those in the tropical eastern Pacific and mainland coasts of Central and South America, were characterized by continuously high planktonic productivity. These areas likely served as refuges during periods where extinctions occurred. Among the various explanations that have been

described for causing extinctions are changes in productivity, cooling associated with the onset of glaciation, reduction in shallow coastal habitat area, and changes in world-wide circulation brought about by events such as the closing of the Isthmus of Panama. Vermeij (2001) suggested that oceanographic changes in circulation in the Pliocene that brought about changes in primary productivity may have been the *primary* cause of extinctions.

Following the rise of the Isthmus of Panama, molluscs in the Caribbean with Pacific affinities, which represented around 10% of the “Neogene” (Miocene, Pliocene, and Pleistocene) Caribbean fauna, became extinct in the Caribbean at the end of the Pliocene but radiated to a great extent in the Pacific at approximately the same time (Jackson and Budd, 1996). Paulay (1990) estimated that about one-third of the bivalve species that inhabited shallow areas of central Pacific islands were lost during episodes of glaciations, and bivalves that were soft-bottom dwellers tended to be more affected than those in hard-bottom habitats, possibly due to the area of soft bottom being a more restricted coastal habitat type. During Pleistocene low sea-levels, the area of shallow water in the greater Caribbean region was reduced by about 89% (Bellwood and Wainright, 2002).

Scheltema (1995) noted the importance of passive larval dispersal in sublittoral species of molluscs with wide distributions in the tropical Atlantic. Passive larval transport and in some instances rafting have extended geographic ranges of tropical Atlantic molluscs over wide geographic ranges. Fixed life spans of larvae that are too short to account for long-distance dispersal and the loss of the ability, over time, to metamorphose have long been believed to limit distributions of molluscs. However,

Scheltema (1995) believed these assertions to be mistaken, based on laboratory and field data. Surface and density-driven currents within the Caribbean Basin, in a very general sense, tend to reflect the geographical pattern of the Antillean island arc and the trade winds, resulting in the greatest amount of flow towards the northwest up to the Yucatan Peninsula, but with isolated eddies and local currents moving northward sporadically through the Bahamas to the north. Thus, larval advection in the mixed and surface layer likely follows a predominantly northwesterly pattern toward the Gulf of Mexico, as reflected by the relative uniformity of the biota in the Caribbean Basin. The life histories of the deep-water (i.e., > 100 m) molluscan fauna of the region are not well known, so it is not yet possible to assign influences.

*b. Fishes*

The shallow water (0 - 50 m) molluscan fauna of the Bahamas was likely shaped by the same physical and environmental processes that led to the present day distributions of coral reef fish faunas of the Bahamas described by Bellwood and Wainright (2002). While climate change has been regarded as an important factor in evolutionary history and biogeographical patterns in marine systems, there is evidence that organisms can adapt to environmental temperature changes relatively quickly (Clarke, 1993). Thus, the oceanographic effects of climate change by temperature *per se* are unlikely to have caused extinction by direct physiological impact; rather, temperature change is but one factor of many that may contribute to environmental changes (e.g., also changes in circulation, productivity, rises and falls in sea level which cause changes in the amount and type of habitat available, etc.) that are the more direct causes of extinction. Simple cause and

effect relationships are difficult to determine because the biological response to environmental conditions is more complex than just the magnitude of the environmental event itself, and marine biota likely respond to changes in regional environmental processes that take place over longer time scales (Ricklefs, 1987).

*c. Corals*

In the Caribbean, the Plio-Pleistocene was a time of significant faunal turnover for corals (Veron, 1995). The key changes in coral composition were as follows: extinctions in most zooxanthellate families were approximately simultaneous, although most genera that became extinct in the Caribbean remain extant in the Indo-Pacific. Modern distributions of corals, as described by Veron (1995), show that, at the family level, the Caribbean is almost as diverse as the Indo-Pacific, with no clear center of diversity in the Indo-Pacific. However, at the species level, diversity in the Caribbean is similar to the most depauperate provinces of the Indo-Pacific. According to Veron (1995), the present-day corals of the Caribbean are relicts of a far more diverse fauna that may have rivaled the equatorial West Pacific if it were not for the deterioration in climate and glaciation that impacted the Caribbean. Budd et al. (1996) noted the approximately synchronous extinctions in the Caribbean region of corals and molluscs, and that the extinctions were accompanied by roughly equal numbers of originations (Jackson, et al., 1993).

Biogeography of the Western Atlantic Marine Fauna

Cairns (2001), in his analysis of biogeographic affinities of north Atlantic deep water scleractinian corals, reported a strikingly similar pattern to that reported by Petuch (1988) in the provincial divisions of molluscs in the western Atlantic (i.e., faunal regions

were divided into the Brazilian, Caribbean, and the east coast of the U.S./Gulf of Mexico). Cluster analysis of deep water corals showed that the Bahamas and Caribbean were part of the same supercluster (Cairns, 2001). This is consistent with the findings of Petuch (2004), where the Bahamas are considered to be a sub-province of the Caribbean Province. Further, Cairns (2000) reported that, of 73 shallow-water species of azooxanthellate scleractinian corals in the western Atlantic region, 41 (56%) occurred in the Bahamas.

Vermeij (1978) broadly described the Bahamas as part of a marine biogeographic province, the Tropical Western Atlantic, which includes the area from Palm Beach, Florida to Bermuda, the Bahamas, the east coast of the Yucatan Peninsula, the Greater Antilles through the Lesser Antilles, and south to near Rio de Janeiro, Brazil. Later, Petuch (1988) applied a system for classification of molluscan faunal regions that consisted of a provincial arrangement based on the “50% rule” devised by Valentine (1973). Under this system, two adjacent geographical areas are considered separate provinces if at least 50% of the species-level taxa are endemic to each area. Further, if at least 30% endemism at the species level exists within a provincial boundary, that area is designated as a “subprovince.” This approach is based on the earlier major divisions of large molluscan faunal regions referred to as “provinces” by Briggs (1974). Petuch (2004) also applied this classic provincial framework to bivalve and gastropod molluscs of the western Atlantic. Petuch (2004) noted that, as demonstrated by Valentine (1973) and Briggs (1995), the provinces of other marine organisms such as echinoderms, corals, and fishes tend to conform to the geographical limits of molluscan faunal provinces. Assuming that the final provincial reorganization, and associated extinctions, took place

during the Aftonian Inter-glacial Stage (1.6 to .01 mya) of the Pleistocene, Petuch (2004) divided the western Atlantic into three main provinces and 17 sub-provinces (Table 3.1, Figure 3.2). Figure 3.2 shows the outline of the three Western Atlantic provinces described by Petuch (2004). The Brazilian Province was only recently recognized as having full provincial status (Petuch, 1988), as previously it had been considered part of the Caribbean Province. More detailed studies by Petuch (1987, 1988), and Rios (1994) demonstrated the presence of a large endemic component of molluscs in the Brazilian Province.

The Caribbean Province contains the *only* eutropical molluscan fauna in the western Atlantic (Petuch, 1988). Many eurythermal Caribbean molluscan species have extended ranges into the southern part of the Carolinian Province and the northern part of the Brazilian Province. The inshore waters off North Carolina become cold in winter months, though the offshore waters remain warm from the intrusion of the Gulf Stream, enabling a relatively stable warm-water fauna to exist. This is why the Carolinian Province is extended northward in a rather narrow band as seen in Figure 3.2.



Table 3.1. Late Pleistocene and Recent marine molluscan provinces and sub-provinces of the western Atlantic (Petuch, 2004).

| Provinces     | CAROLINIAN   | CARIBBEAN   | BRAZILIAN  |
|---------------|--|---|--|
| Sub-provinces | <i>Virginian</i><br><i>Georgian</i><br><i>Floridian</i><br><i>Suwannean</i><br><i>Texan</i><br><i>Yucatanean</i> | <i>Bahamian</i><br><i>Bermudan</i><br><i>Antillean</i><br><i>Nicaraguan</i><br><i>Venezualan</i><br><i>Grenadian</i><br><i>Surinamian</i> | <i>Cearaian</i><br><i>Bahian</i><br><i>Paulinian</i><br><i>Uruguayan</i> |

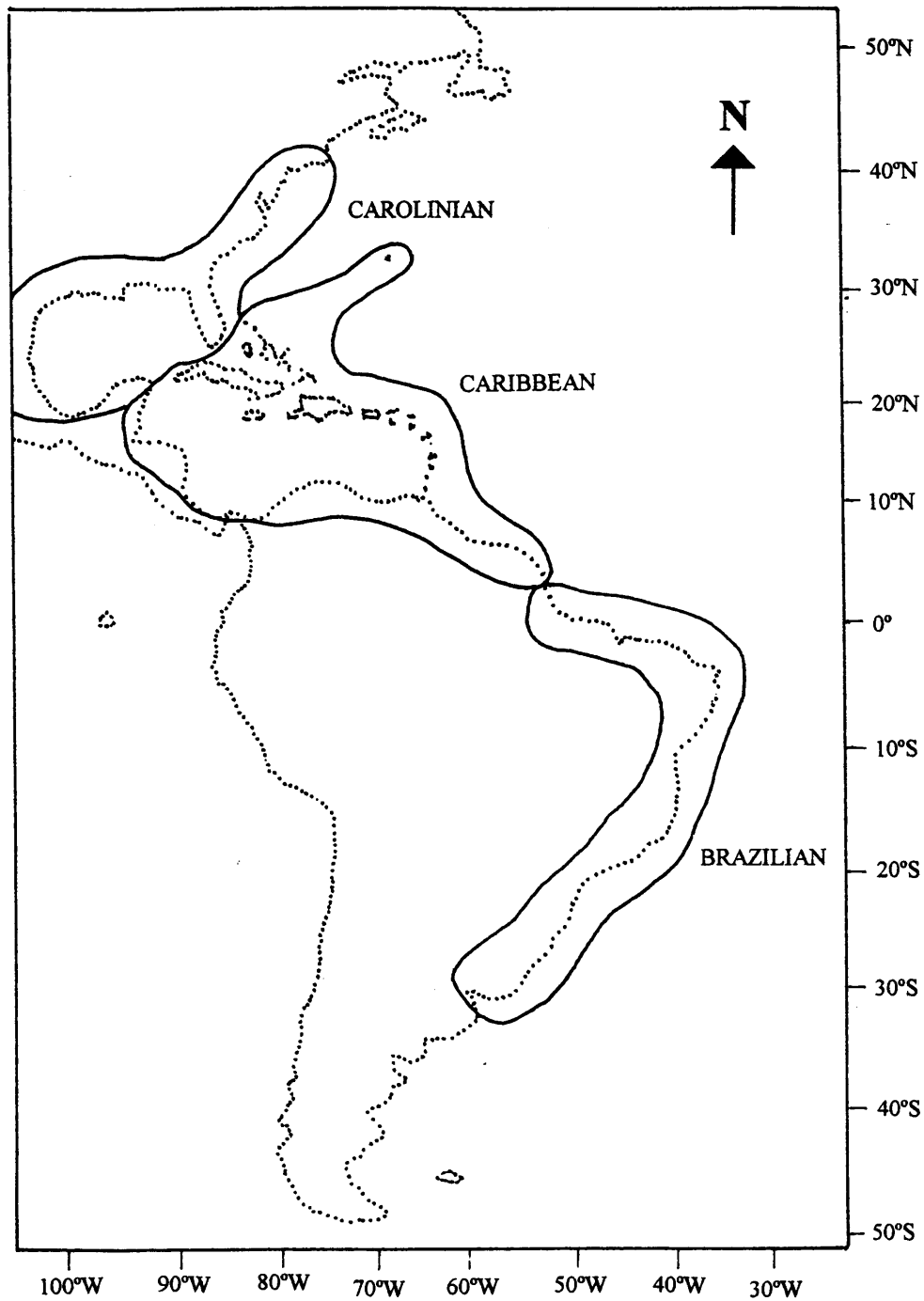


Figure 3.2. Molluscan faunal provinces (solid lines) in the Recent western Atlantic (modified from Petuch, 2004).

Harasewych and Chapman (2001) analyzed the bathymetric and geographic distributions of 946 taxa of gastropod molluscs inhabiting depths greater than 100 m in the tropical and warm temperate western Atlantic (North Carolina to Brazil), based largely on literature records. Their preliminary analyses show that gastropod taxa could be divided into continental slope, abyssal plain, and hadal communities. For this deepwater fauna, the greatest similarities occurred between sub-regions of the warm temperate North Atlantic and northern Brazil, and between the faunas of the sub-regions of Cuba and the Lesser Antilles. Deepwater faunas of the sub-regions on the Caribbean Tectonic Plate were more heterogeneous than the other sub-regions discussed above. The results of this analysis are preliminary and it is not clear how these sub-regions may fit into or reconcile with the molluscan provinces presented by Petuch (1988, 2004).

## MATERIALS AND METHODS

### Gastropod Data for the Bahamas

The gastropod mollusc data used here were obtained from the Academy of Natural Science's (ANS) Western Atlantic Gastropod Database (Rosenberg, 1993a; 1993b). The total holdings of the database presently include 4,666 species of gastropod molluscs that extend from Greenland to Antarctica. The database is the largest of its kind and includes information by species on latitudinal and longitudinal ranges (with the computed size of the geographic ranges by latitude and longitude), maximum body size of each species, and depth ranges. The information is based on over 2,500 references in the literature. Nine

hundred and sixty species are catalogued in the ANS database that have geographic ranges that extend into the Bahamas, as a result of a search by Dr. Gary Rosenberg at the ANS.

All of the taxa in the previous two chapters collected from Lee Stocking Island that were identified to species level are included in the ANS data set and analysis in this chapter. Where the occurrence of certain species of gastropods were reported in Chapter 2 as new depth records for the Bahamas, they are based on the most recent available information, and do not include minimum or maximum depth records for localities outside of the Bahamas.

The data used in this analysis were obtained from the ANS in an Excel spreadsheet by genus and species with northern and southern latitudinal limits and east and west longitudinal limits. Additional parameters included minimum and maximum depth and maximum body size. Depth ranges were computed by subtracting the minimum depth from maximum depth in Excel. Sizes of geographic ranges were computed from the latitudinal and longitudinal ranges, according the method described by Reaka (1980) using the formula:

$$\sqrt{{}^{\circ}\text{latitude}^2 + {}^{\circ}\text{longitude}^2}$$

This formula provides a comparable unit, referred to hereon as a Geographic Range Index, by which geographic ranges of different shapes (long and thin vs. square, or greatest length along latitudinal vs. longitudinal axes) can be compared. The species of gastropods used in the present analysis from the ANS data set are presented in their entirety in Appendix 1,

along with their corresponding depth ranges, maximum sizes, and Geographic Range Index.

### Hypotheses and Objectives

The purpose of this chapter is to describe biogeographic patterns of species of gastropod molluscs that occur in the Bahamas in the context of the past and present geological and oceanographic conditions of the region. This chapter particularly emphasizes the relationship of the present-day distribution of species of gastropod molluscs to the three main biogeographical provinces as described by Petuch (2004). In addition to the geographic affinities of the species of gastropods, the relationships among their maximal body size, their reported depth ranges, and the sizes of their geographic ranges is explored with the ANS data set. Specific hypotheses include:

- ▶ *Minimum and maximum reported depths of species of gastropods that occur in the Bahamas are related to the sizes of their respective geographic ranges;*
- ▶ *Maximum body sizes of species of gastropods that occur in the Bahamas are related to their reported depths; and,*
- ▶ *Maximum body sizes of species of gastropods that occur in the Bahamas are related to the sizes of their respective geographic ranges; and,*
- ▶ *Species of gastropods that occur in the Bahamas show greater affinities among the Carolinian and Caribbean biogeographic provinces than with the Brazilian, East Pacific, and East Atlantic biogeographic provinces.*

## Quantitative and Descriptive Analyses

Scatter plots and simple regression tests were performed with SAS JMP to explore relationships between seven parameters: maximum body size, minimum depth, maximum depth, depth range, latitudinal range, longitudinal range, and geographic range index. Seventeen combinations that were seen as relevant to the central hypotheses were run as bivariate fits (y by x). Where two parameters showed a significant relationship, individual scatter plots of the bivariate fit (y by x) were provided in the following section along with fitted regression lines. Where either the y or x variable appeared highly skewed in a scatter plot, the data were transformed according to Sokal and Rohlf (1987) to achieve a more uniform distribution. Maximum body sizes, minimum depth, maximum depth, and depth range were natural (base) log transformed. By default, a 95% bivariate normal density ellipse was imposed on each scatter plot. The variables were seen as bivariate normally distributed, as the ellipses enclosed approximately 95% of the data points, which is a function to test bivariate normal distributions in the JMP SAS program. Transformed data were plotted in all figures using the log of the values, rather than the actual values plotted on a log scale. This approach was used to accommodate zeroes in the data, by adding a "1" to each parameter that was transformed, e.g.,  $\log [\text{maximum body size} + 1]$ . To further interpret the data on body size and depth, histograms were run to see the spread of values in size classes of the gastropods and their depth ranges.

### *Estimating Geographic Distributions*

The resolution of the ANS data in latitudinal and longitudinal spans precluded the precise separation of species in the data set between the Caribbean and Carolinian

provinces because of the irregular shapes of those two provinces. It was possible however, to determine the number of species whose ranges crossed into the Eastern Pacific, Western Atlantic (Caribbean/Carolinian and north; Brazilian and south), and Eastern Atlantic. To do this, a series of latitudinal/longitudinal “boxes” were constructed by sorting within a spreadsheet of the data in SAS JMP. The Eastern Pacific included species with ranges  $< 15^{\circ}\text{N}$  and  $> 90^{\circ}\text{W}$  and those with ranges  $< 7.2^{\circ}\text{N}$  and  $> 80^{\circ}\text{W}$  and  $< 90^{\circ}\text{W}$ ; the Eastern Atlantic included species with ranges  $< 20^{\circ}\text{W}$ ; and, the Western Atlantic included species with ranges  $> 2.5^{\circ}\text{N}$ .

Highest densities of latitudinal and longitudinal spans from all species in the data set were estimated visually on a plot of lat/long “crosshairs” of all 960 species in the data set. Four centers of highest density were apparent, which were enclosed by hand-drawn boxes. From these boxes, the latitudinal and longitudinal spans were determined and then superimposed on the map of the three provinces to ascertain the distribution of the centers of highest densities of the molluscs among the provinces.

#### *Principal Components Analysis*

Because of the limitations of the ANS latitudinal and longitudinal range data for showing precise provincial affinities, PCA was used as an alternate method to explore the geographic tendencies of the species’ ranges by reducing the spread of the north, south, east, and west latitudinal and longitudinal components for each species in the ANS data set to only two dimensions. The PCA allowed visualization of the relative positioning of species geographically among the provinces. This approach is based on PCA applications as described by McGarigal et al. (2000).

Raw data (absolute values of north and south latitudes and east and west longitudes) were explored by simple plotting to see if the data appeared to be co-linear. Each possible combination of the data was plotted: north by south, east by west, north by east, and north by west. Because the spread of the data points in the plots appeared to show some co-linearity, data reduction and ordination was performed with a PCA. The data on the four directional components (north, south, east, west), by species, were reduced using the PCA to the minimum number of dimensions (two) to see if any geographic patterns emerged. Code was written in MATLAB 6.1 ([www.mathworks.com](http://www.mathworks.com)) with the assistance of Dr. Bernhard Riegl of Nova Southeastern University. The principal components were calculated by taking the linear combination of an eigenvector of the correlation matrix with the original variables. Co-variance values were used for all parameters to determine how each related to each other. Data were not standardized because all data for latitudinal and longitudinal ranges were in the same units (degrees). The PCA plot of non-standardized co-variance values produced a wider spread of values for easier interpretation. Eigenvalues were used to determine the proportion of total variance explained by the principal components. Eigenvalue loadings (eigenvectors) were used to interpret the directional trends of the principal components. Principal component scores associated with each record in the original spreadsheet of the data were used to conduct several post-hoc tests to evaluate any apparent relationships between clustering seen in the PCA plot (representing geographic distribution of the species of gastropods) and other parameters in the original dataset.



## RESULTS

### Relationships of Gastropod Body Size, Depth, and Geographic Range

#### *Maximum body size*

Maximum body sizes for the species of gastropods from the ANS data set that occur in the Bahamas ranged from 0.2 mm to 420 mm. When these species were binned into 30 size classes in a histogram, 54% were less than 15 mm, and 74% were less than 30 mm (Figure 3.3). The relationship between maximum body size of the gastropod species and minimum depth or maximum depth was not significant ( $p < 0.821$  and  $p < 0.288$ , respectively) (Table 3.2). Maximum body size was significantly and positively correlated with depth range ( $p < 0.045$ ), latitudinal range ( $p < 0.001$ ), longitudinal range ( $p < 0.001$ ), and geographic range index ( $p < 0.001$ ) (Figure 3.4), i.e., larger gastropod species had larger ranges overall.

#### *Depth*

The minimum depth at which gastropod species occurred was significantly correlated with depth range ( $p < 0.001$ ), latitudinal range ( $p < 0.001$ ), longitudinal range ( $p < 0.001$ ), and geographic range index ( $p < 0.001$ ) (Table 3.2). Species that have shallow minimum depths have small depth ranges, while those that have deeper minimum depths have broader depth ranges (Figure 3.5). However, species that have shallow minimum depths have large geographic ranges (latitude, longitude, Geographic Range Index), while those that have deeper minimum depths have smaller geographic ranges (latitude, longitude, Geographic Range Index). There also appears to be a grouping of very shallow-dwelling, broadly distributed species (i.e., shallow specialists).

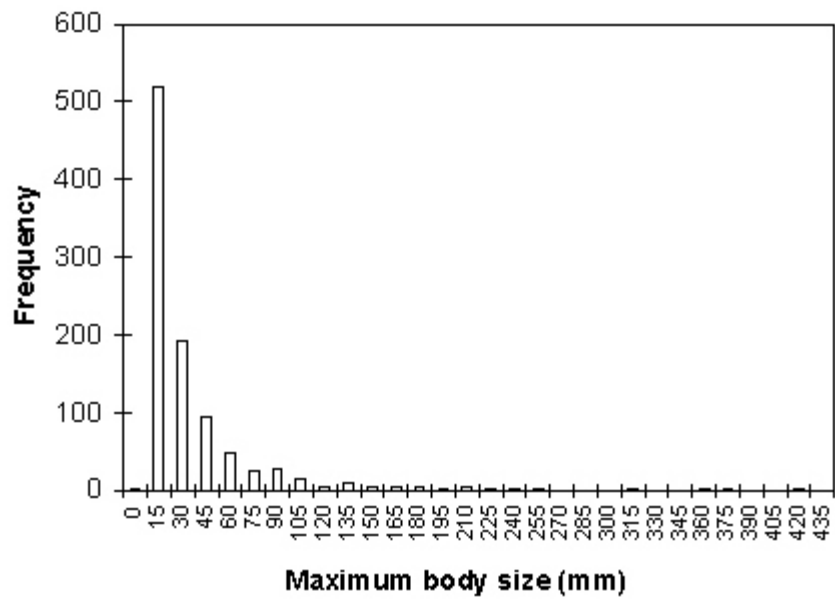


Figure 3.3. Histogram of maximum body size (mm) for 959 species of gastropod molluscs that occur in the Bahamas. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

Table 3.2. Results of bivariate fit (Y by X) regression analysis for various combinations of seven parameters for species of gastropod molluscs that occur in the Bahamas: maximum body size (mm), minimum depth (m), maximum depth (m), depth range (m), latitudinal range (degrees), longitudinal range (degrees), and geographic range index.\* Data from the Academy of Natural Sciences Western Atlantic Gastropod Database.

| Bivariate fit (“Y” by “X”) | Test Result | p**       |
|----------------------------|-------------|-----------|
| Maximum body size vs.      |             |           |
| Minimum depth              | ns          | p < 0.821 |
| Maximum depth              | ns          | p < 0.288 |
| Depth range                | s           | p < 0.045 |
| Latitudinal range          | s           | p < 0.001 |
| Longitudinal range         | s           | p < 0.001 |
| Geographic range index     | s           | p < 0.001 |
| Minimum depth vs.          |             |           |
| Depth range                | s           | p < 0.001 |
| Latitudinal range          | s           | p < 0.001 |
| Longitudinal range         | s           | p < 0.001 |
| Geographic range index     | s           | p < 0.001 |
| Maximum depth vs.          |             |           |
| Depth range                | s           | p < 0.001 |
| Latitudinal range          | s           | p < 0.001 |
| Longitudinal range         | s           | p < 0.002 |
| Geographic range index     | s           | p < 0.001 |
| Depth range vs.            |             |           |
| Latitudinal range          | s           | p < 0.001 |
| Longitudinal range         | s           | p < 0.001 |
| Geographic range index     | s           | p < 0.001 |

\*Geographic range index computed from latitudinal and longitudinal ranges as:

$$\sqrt{^{\circ}\text{latitude}^2 + ^{\circ}\text{longitude}^2}$$

\*\*The probability of obtaining, by chance alone, a correlation with greater absolute value than the computed value if no linear relationship exists between the X and Y variables.

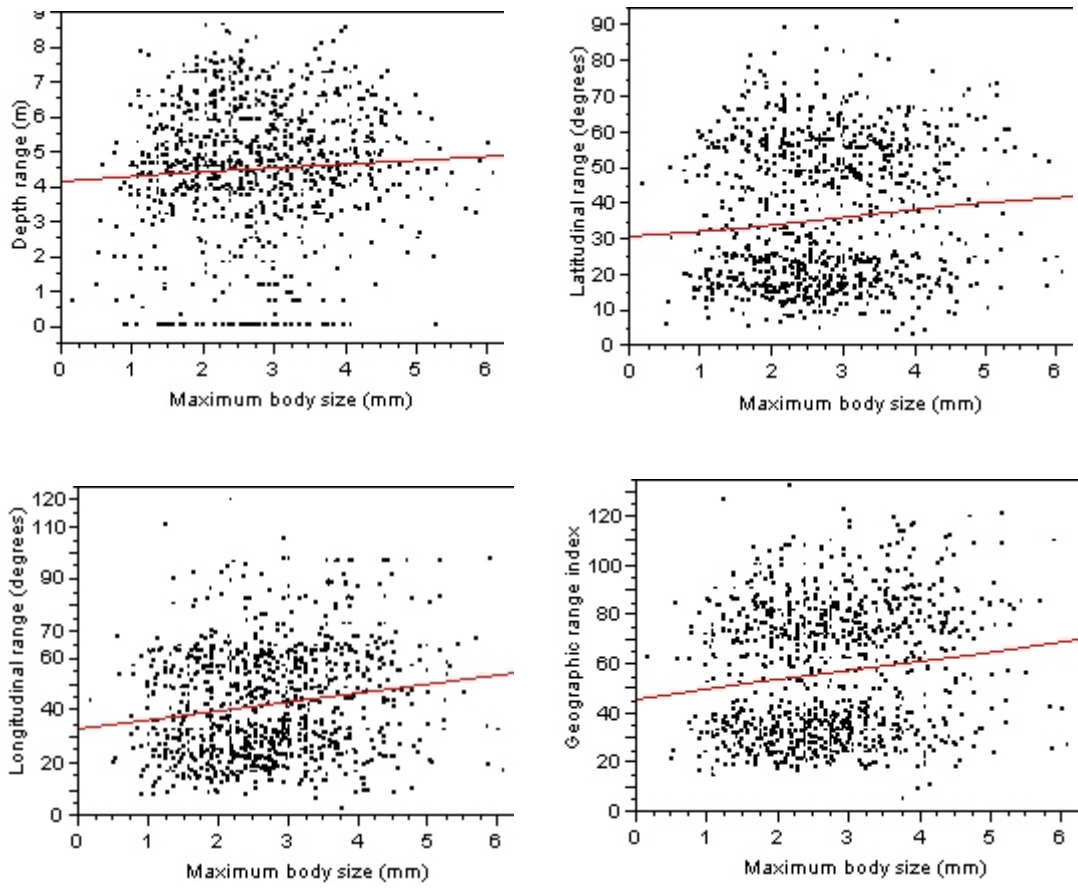


Figure 3.4. Scatter plots for maximum body size (mm) by: depth range (m), latitudinal range (degrees), longitudinal range (degrees), and geographic range index for species of gastropod molluscs that occur in the Bahamas. Data for maximum body size and depth range were log transformed. Solid lines show linear fits for simple regression. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

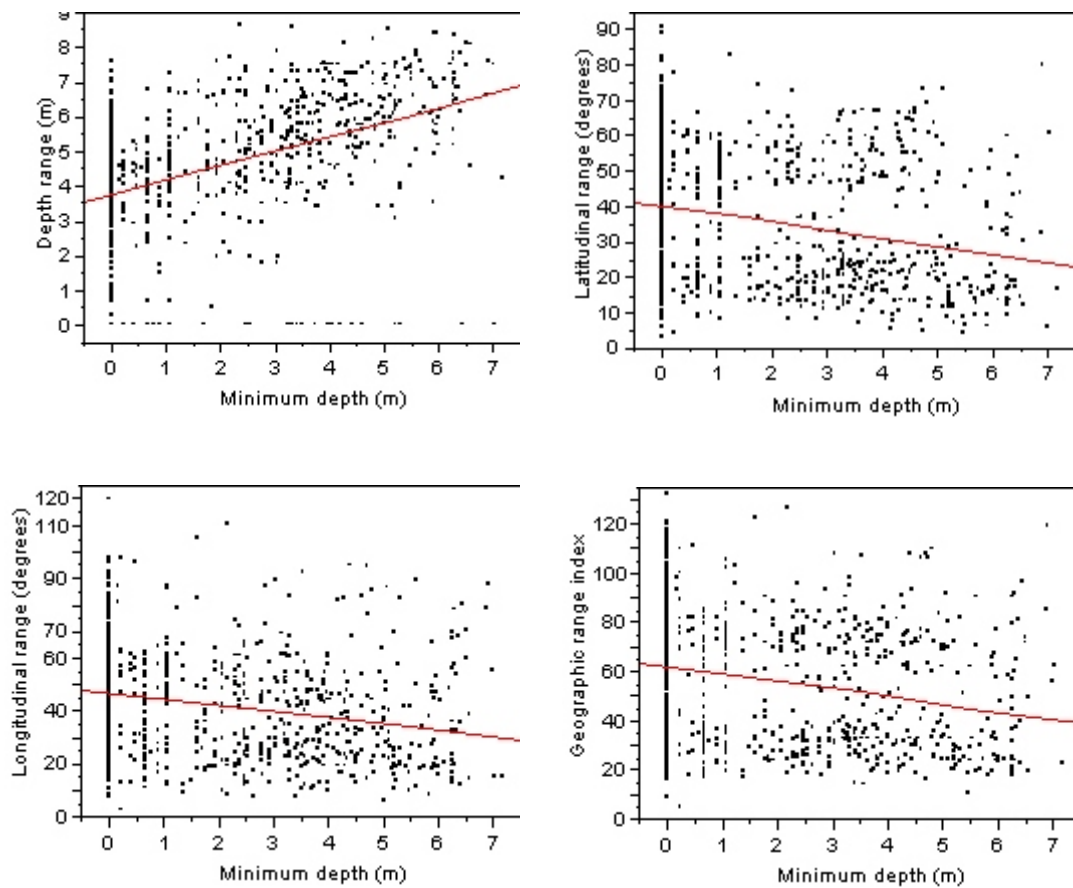


Figure 3.5. Scatter plots for minimum depth (m) by: depth range (m), latitudinal range (degrees), longitudinal range (degrees), and geographic range index for species of gastropod molluscs that occur in the Bahamas. Data for minimum depth and depth range were log transformed. Solid lines show linear fits for simple regression. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

The maximum depth that gastropod species occurred was significantly and positively correlated with depth range ( $p < 0.001$ ), latitudinal range ( $p < 0.001$ ), longitudinal range ( $p < 0.002$ ), and geographic range index ( $p < 0.001$ ) (Table 3.2, Figure 3.6). Species that occurred at greater maximal depths had broader depth ranges, and occurred over broader geographic ranges (latitude, longitude, Geographic Range Index).

Depth ranges for the species of gastropods from the ANS data set that occur in the Bahamas ranged from zero (i.e., species that were reported from only one depth or from the intertidal zone) to 5,124 m. Because either minimum or maximum depth was not available was not available for 20 of the species in the data set out of the total of 960, determination of depth range was possible only for 940 of the total number of species. When these species were binned into 30 depth range classes in a histogram, 65% (616 species) had ranges less than or equal to 183 m (Figure 3.7). The modal depth range was 0 since many of the species were intertidal or were reported from only one depth.

The depth range of gastropod species was significantly and positively correlated with latitudinal range ( $p < 0.001$ ), longitudinal range ( $p < 0.001$ ), and geographic range index ( $p < 0.001$ , Table 3.2); i.e., gastropods that occur over increasingly broad depth ranges have increasingly broad geographic distributions (Figure 3.8).

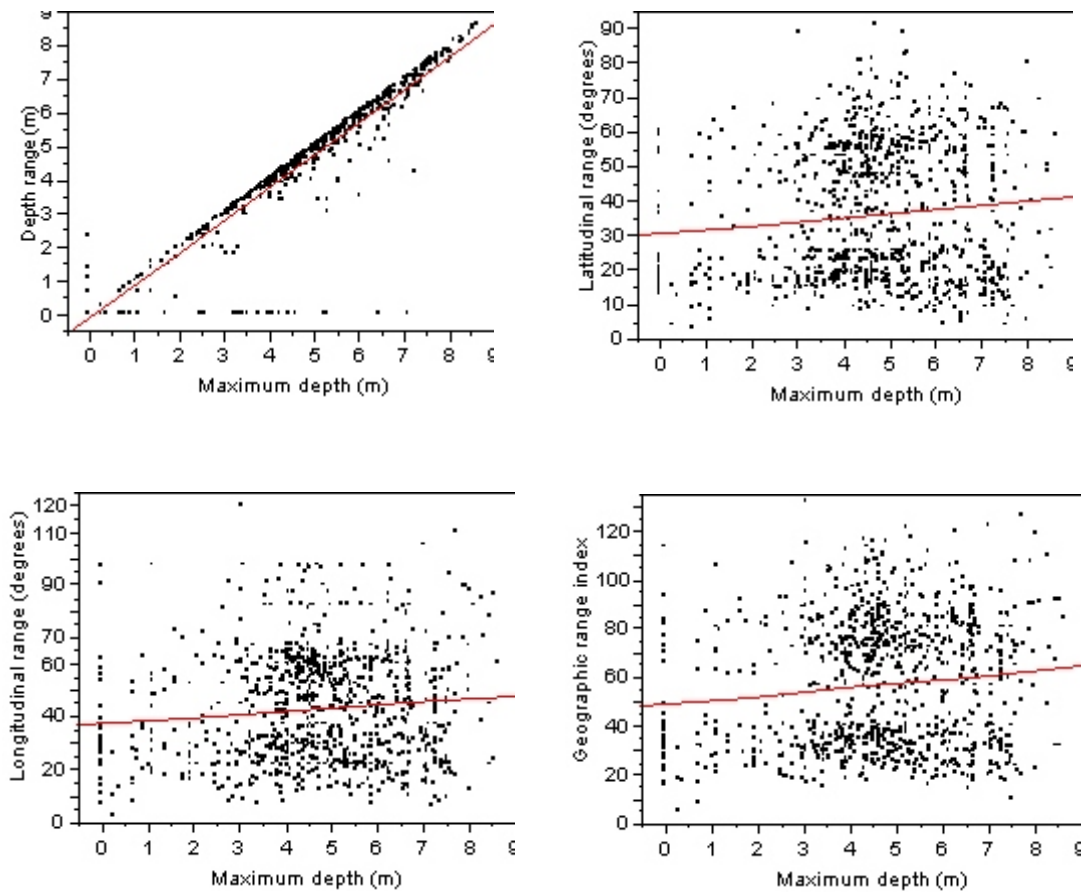


Figure 3.6. Scatter plots for maximum depth (m) by: depth range (m), latitudinal range (degrees), longitudinal range (degrees), and geographic range index for species of gastropod molluscs that occur in the Bahamas. Data for maximum depth and depth range were log transformed. Solid lines shows linear fits for simple regression. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

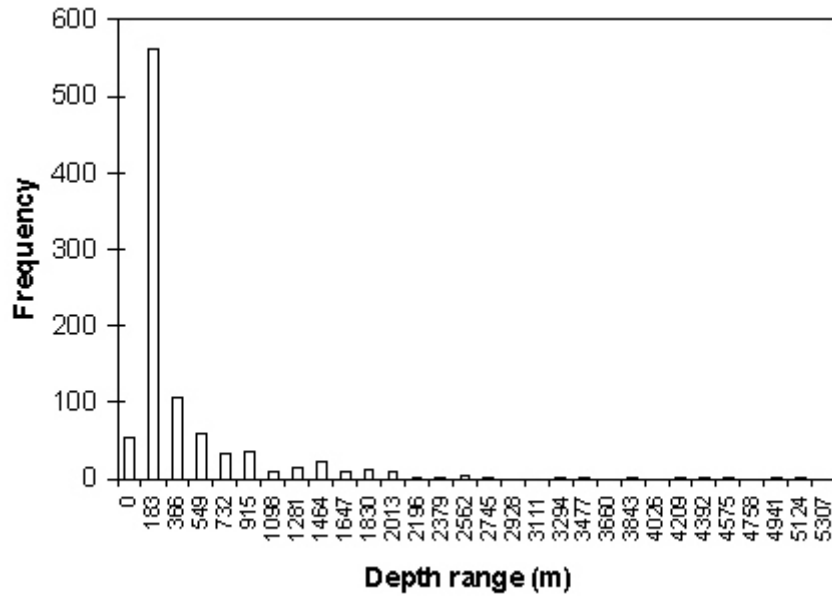


Figure 3.7. Histogram of depth range (m) for 940 species of gastropod molluscs that occur in the Bahamas. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.



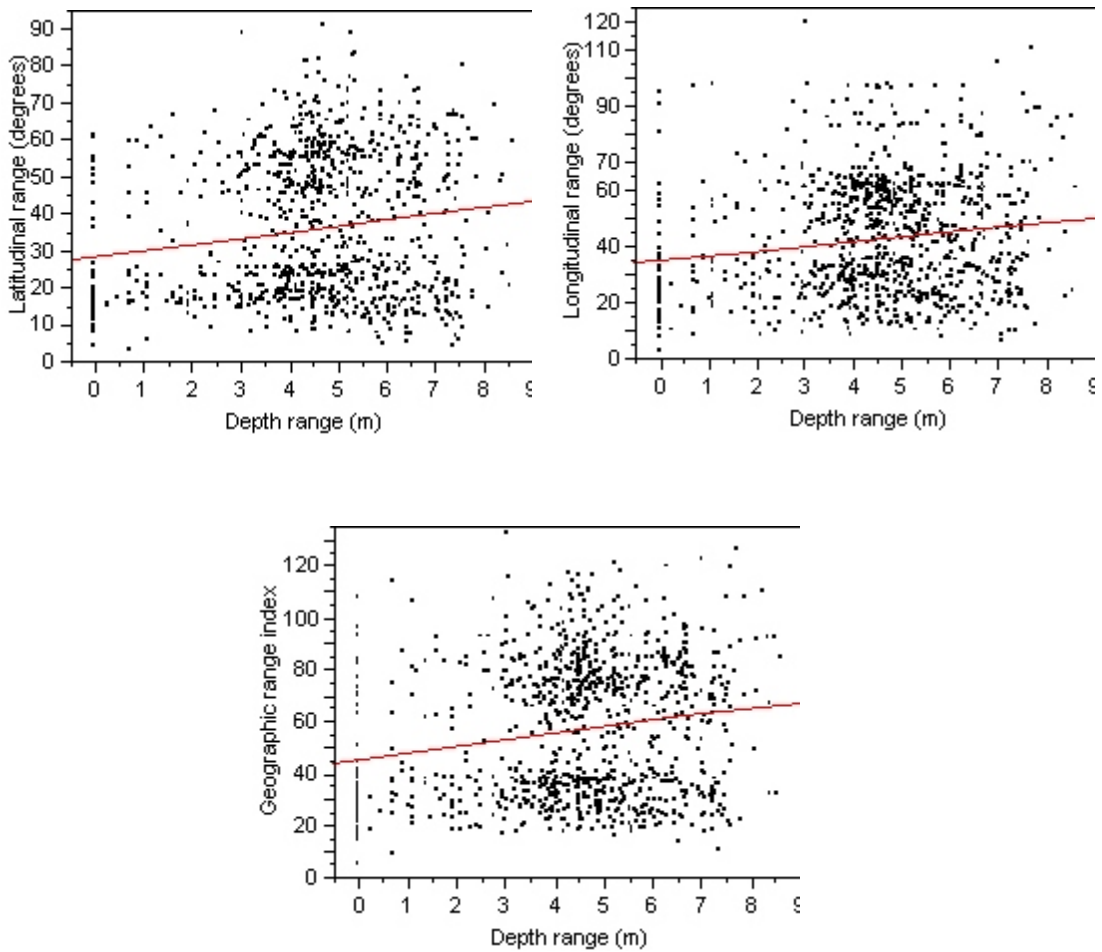


Figure 3.8. Scatter plots for depth range (m) by: latitudinal range (degrees), longitudinal range (degrees), and geographic range index for species of gastropod molluscs that occur in the Bahamas. Data for depth range were log transformed. Solid lines shows linear fits for simple regression. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

### Geographic Affinities of Gastropod Species

Numbers of species whose ranges extended into the Eastern Pacific (350 species, 36.5% of total) and Brazilian province (480 species, 50% of total) were relatively high, considering that all of these species were present in the Bahamas, and that the Eastern Pacific is separated by the physical barrier of the Isthmus of Panama, and that the Brazilian province is relatively distant from the Caribbean (Table 3.3).

All of the species that occur in the Bahamas are found in the Caribbean province. Presently, there are no published data on the number of Recent species of gastropod molluscs that are endemic to the Bahamas. The Bahamas are designated as a sub-province according to the 30% endemism rule (for a sub-province) by Petuch (2004) (Table 3.1), based on unpublished data on Bahamian endemics, notably cone shells (E. Petuch, pers. comm.). In the ANS data set, only one species of gastropod, *Conus jucundus*, was determined to be endemic to the Bahamas based on the limits of the geographic range data for that species.

The high number of Bahamian species of gastropods whose ranges extend into the East Pacific (37%) and especially into the Brazilian (50%) provinces likely reflects the broad common distribution of ancestral Tethyan assemblages before the rise of the Isthmus and ensuing separation of the Brazilian populations by the South Atlantic gyre. The low number of species (83 species, 8.6% of total) shared with the Eastern Atlantic probably reflects the distance barrier between the eastern and western Atlantic ocean and historical factors such as divergence and extinction.

Table 3.3. Distribution of the maximum reported ranges of 960 species of gastropod molluscs that occur in the Bahamas and extend into the Eastern Pacific, Western Atlantic, and Eastern Atlantic regions. Percentages are based on the number of species out the total of 960 (all of which occur in the Caribbean Province in which the Bahamas are included as a sub-province). Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

| Region/province                  | Number of Species | Percent of Total |
|----------------------------------|-------------------|------------------|
| Eastern Pacific                  | 350               | 37               |
| Western Atlantic                 |                   |                  |
| Caribbean/Carolinian (and north) | 960               | 100              |
| Brazilian (and south)            | 480               | 50               |
| Eastern Atlantic                 | 83                | 9                |

A plot of the values for principal component 1 vs. principal component 2 revealed four apparent large clusters (Figure 3.9). From analysis of the eigenvalues, most of the variation was seen in the principal components 1 and 2, 77% and 15%, respectively (Table 3.5). The eigenvalue loadings with a high first principal component score indicated a south-east tendency in a positive direction and a slight tendency to the northwest from the lower negative scores. Eigenvalue loadings with a second principal component score indicated a positive tendency towards the south and a negative tendency towards the east. When the first principal component scores were sorted and compared with the actual latitudinal and longitudinal ranges, clusters 3 and 4 in Figure 3.9 generally were oriented to the south-east and clusters 1 and 2 showed a tendency towards the higher latitudes. Examination of “cross hairs” generated by the latitudinal and longitudinal ranges clearly shows a northern latitudinal boundary for most of the species that is approximately aligned with Cape Hatteras, NC. While all the species have ranges that occur in the Bahamas, there is a strong tendency, or spread of the latitudinal ranges, towards the south.

The regions in Table 3.4 reflect the approximate centers of density of the north, south, east, and west spans of the ranges of the species of gastropods in the ANS data set. When the four clusters in Figure 3.9 were visually compared with bivariate densities (from SAS JMP analysis) for the latitudinal and longitudinal spans of the ANS species data, it could be seen that the clusters were generally consistent with the approximate regions of the four groupings of the data in Table 3.4.

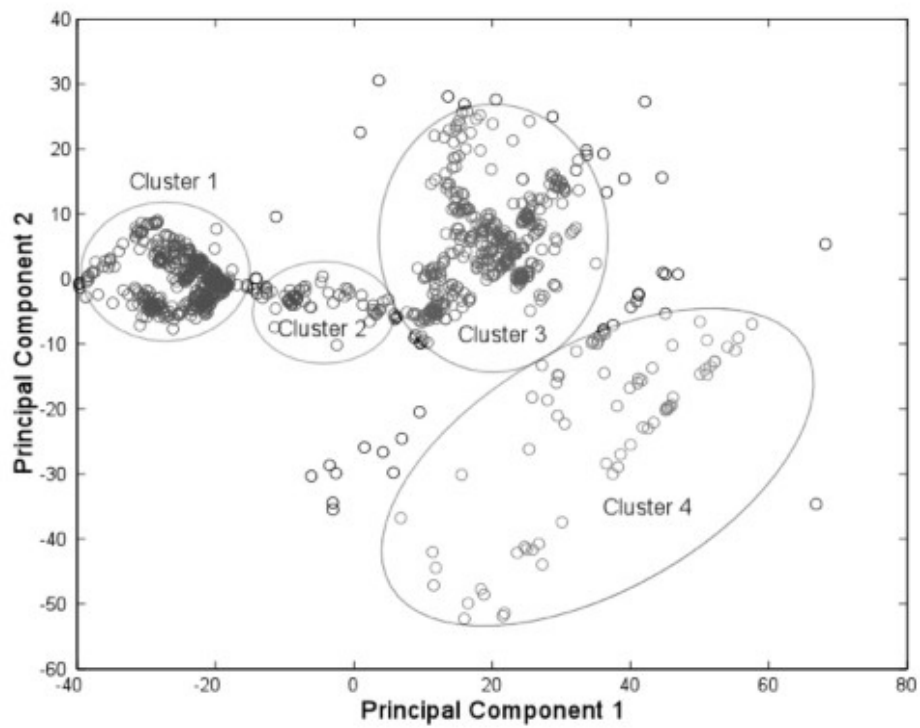


Figure 3.9. Two-dimensional Principal Components plot of the distribution of 960 species of gastropod molluscs that occur in the Bahamas. Ovals (“clusters” 1, 2, 3, and 4) are intended to guide the reader, and were drawn as interpreted by the author. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

Table 3.4. Highest densities of latitudinal and longitudinal spans from an analysis of 960 species of gastropod molluscs that occur in the Bahamas. Regions\* are approximate centers of highest densities as interpreted visually by the author and do not reflect precise provincial boundaries for Western Atlantic gastropods. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

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|            | Latitudinal Span | Longitudinal Span | Region*              |
|------------|------------------|-------------------|----------------------|
| Cluster 1: | 34.5°N to 10.9°N | 61.5°W to 89.7°W  | Caribbean/Carolinian |
| Cluster 2: | 26.3°N to 10.9°N | 35.1°W to 97.1°W  | Caribbean            |
| Cluster 3: | 34.5°N to 22.1°S | 63.6°W to 82.2°W  | Caribbean/Brazilian  |
| Cluster 4: | 27.5°N to 22.1°S | 35.1°W to 91.0°W  | Caribbean/Brazilian  |

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Table 3.5. Eigenvalues for principal components analysis on north, south, west, and east directional components for 960 species of gastropods that occur in the Bahamas. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

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| Eigenvalue | Percent | Cumulative Percent |  |  |
|------------|---------|--------------------|--|--|
| 583.0383   | 76.984  | 76.984             |  |  |
| 109.5580   | 14.466  | 91.451             |  |  |
| 43.0197    | 5.680   | 97.131             |  |  |
| 21.7291    | 2.869   | 100.000            |  |  |

Eigenvectors:

|       | PC1      | PC2      | PC3     | PC4      |
|-------|----------|----------|---------|----------|
| North | -0.04174 | 0.08958  | 0.53253 | 0.84062  |
| South | 0.67915  | 0.72823  | 0.05114 | -0.07628 |
| West  | -0.05338 | -0.06500 | 0.84369 | -0.53020 |
| East  | 0.73086  | -0.67634 | 0.04451 | 0.08016  |

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### *Post-hoc Analyses*

As a means of further exploring the data set for patterns and relationships between the geographic distributions of the gastropod species in a post hoc manner, it was possible to see how principal component scores related to selected records of the ANS data set. The four “clusters” of the first principal component scores were divided into three more or less distinct classes (a, b, and c) as a categorical variable and tested against the above parameters in a series of one-way ANOVAs in SAS JMP. Because of the overlap seen in clusters 3 and 4 (Figure 3.9), it was not possible to further divide the principal component scores as they related to their actual latitudinal and longitudinal distributions of the gastropod species. Thus, clusters 3 and 4 were combined for post hoc analyses.

The purpose of these analyses was to see if any significant differences existed between class I (Carolinian/Caribbean cluster 1), class II (Caribbean cluster 2), class III (Caribbean/Brazilian clusters) and minimum depth, maximum depth, depth range, maximum size, and the size of the geographic range as computed in the Geographic Range Index. In other words, these post hoc tests with principal components provided a means to see if there were any significant relationships between the ANS parameters above and the three clusters, which provided additional insight into the findings in the previous set of regression analyses.

Minimum depth was significantly deeper in classes I and II than class III, while maximum depth was significantly shallower in class I than classes II and III (Table 3.6). Depth range was significantly smaller in class I than classes II and III. Maximum body size



Table 3.6. Results of one-way analysis of variance (mean  $\pm$  standard error) as post-hoc tests of the relationship between geographic distribution of gastropod species as seen in principal components analysis scores and selected life history characteristics of 960 species of gastropods that occur in the Bahamas. Data from the Academy of Natural Sciences, Western Atlantic Gastropod Database.

| PC1 category           | I                           | II                          | III                         | p        |
|------------------------|-----------------------------|-----------------------------|-----------------------------|----------|
| Minimum depth (m)      | 2.1 <sup>a</sup> $\pm$ 0.1  | 2.0 <sup>a</sup> $\pm$ 0.2  | 1.4 <sup>b</sup> $\pm$ 0.1  | <0 .0001 |
| Maximum depth (m)      | 4.4 <sup>a</sup> $\pm$ 0.1  | 5.0 <sup>b</sup> $\pm$ 0.2  | 5.0 <sup>b</sup> $\pm$ 0.1  | <0 .0001 |
| Depth range (m)        | 4.1 <sup>a</sup> $\pm$ 0.1  | 4.7 <sup>b</sup> $\pm$ 0.2  | 4.8 <sup>b</sup> $\pm$ 0.1  | <0 .0001 |
| Maximum body size (mm) | 2.6 <sup>a</sup> $\pm$ 0.1  | 3.0 <sup>b</sup> $\pm$ 0.1  | 3.0 <sup>b</sup> $\pm$ 0.1  | <0 .0002 |
| Geographic Range Index | 30.2 <sup>a</sup> $\pm$ 0.5 | 53.5 <sup>b</sup> $\pm$ 1.1 | 81.7 <sup>c</sup> $\pm$ 0.5 | < 0.0001 |

(<sup>abc</sup>Means with same superscript are not significantly different.)

in class I was significantly smaller than classes II and III. Finally, Geographic Range Index was significantly (and progressively) higher between classes I, II, and III. Given that class I (PC1) represents a Carolinian/Caribbean orientation, class II (PC2) represents a Caribbean orientation, and class III (PC3) represents a Caribbean/Brazilian orientation, the results of the ANOVAs imply that 1) minimum depth of gastropod species is shallowest in the Caribbean/Brazilian class, 2) maximum depth of gastropod species tends to be shallowest in the Carolinian/Caribbean class, 3) gastropod species have narrowest depth ranges in the Carolinian/Caribbean class, 4) maximum body sizes of gastropod species are smallest in the Carolinian/Caribbean classes, and 5) gastropod species have increasingly wider geographic ranges from the Carolinian/Caribbean class to the Caribbean class to the Caribbean/Brazilian class.

## DISCUSSION

### *Maximum Body Size vs. Depth and Geographic Range*

The ANS data set, while somewhat limited in the coarse-scale presentation of the latitudinal and longitudinal range data, offered insight into the distributional patterns of species of gastropods in the Western Atlantic region. One of the most interesting findings was the positive relationship ( $p < 0.0001$ ) between the size of species of gastropods and their geographic ranges (geographic range index). This finding is consistent with other studies such as Reaka's (1980) study on coral-dwelling mantis shrimps. Having a broad geographic range, which was shown with species of gastropods of larger size, is a hedge against extinction due to local environmental changes (Reaka, 1980). This life history

characteristic held true for the relationship between not only larger body size and the overall size of the geographic range, but also for larger body size and latitudinal and longitudinal ranges ( $p < 0.001$  and  $p < 0.001$ , respectively). Maximum body size was also positively correlated with depth range ( $p < 0.045$ ), indicating that larger species of gastropods occur over a broader range of depths. Occurrence over a broader depth range would tend to increase the potential for larval dispersal, particularly in areas with stronger ocean circulation.

The finding that nearly three-quarters of the gastropod species in the ANS data set were less than 30 mm provided additional insight into the limitation that the size of the openings of the artificial benthic collectors used in my study at Lee Stocking Island had on the ability of gastropods to colonize the collectors. Since the size of the openings in the benthic collectors used in my Lee Stocking Island collections were 3 cm (30 mm), the vast majority of species of gastropods that occur in the Bahamas could have fit into the collectors, even at their maximum size. This finding is interesting, in that it quantitatively shows that the majority of species of gastropods that occur in the Bahamas, and likely in the greater Caribbean Province, are relatively small in body size. While it is perhaps a topic of future exploration with the ANS data, it is possible that Cope's Rule, the tendency for lineages to evolve to larger body sizes could be tested across depth, temperature, and latitude. Although the status of Cope's Rule has been a subject of some controversy (Jablonski, 1997), nonetheless, the ANS data set offers additional possibilities for further analysis on the topic, though beyond the scope of the present study.

### *Relationship of Depth and Geographic Range*

Minimum depth was positively correlated with depth range ( $p < 0.0001$ ), indicating that species that have deeper minimum depths were more likely to have broader depth ranges. Conversely, minimum depth was negatively correlated with latitudinal range ( $p < 0.001$ ), longitudinal range ( $p < 0.001$ ), and geographic range index ( $p < 0.001$ ). Thus, those species with the shallowest minimum depths have the broadest geographic ranges and the narrowest depth range. Gastropods with deeper minimum depths had broader depth ranges but narrower geographic distributions. There appear to be a guild of exclusively shallow water dispersers with broad geographic ranges, as is the case in stomatopod crustaceans (Reaka, 1980).

The strong (near-linear) positive relationship of maximum depth with depth range ( $p < 0.001$ ) suggested that deeper-occurring species were more likely to have broader depth ranges. The positive correlation of maximum depth with latitudinal range ( $p < 0.001$ ), longitudinal range ( $p < 0.002$ ), and geographic range index ( $p < 0.001$ ), all suggested that the deeper-dwelling species of gastropods were more widely distributed geographically. Depth range was positively correlated with latitudinal range ( $p < 0.001$ ), longitudinal range ( $p < 0.001$ ), and geographic range index ( $p < 0.001$ ). Thus, species of gastropods with broad depth distributions were also broadly distributed geographically. Over half of the species of gastropods in the ANS data set had depth ranges greater than 100 m (ranging from 100 - 5,490 m). These wide ranges of reported depths for these species and their correlation with geographic range suggest that depth range may be one of the more important life history characteristics to help explain the relatively wide

geographic distribution of gastropods in the Caribbean and adjacent regions. A wider depth range implies that habitat requirements are less specialized, there is probably wide dispersal, and thus there is little tendency towards endemism.

Gastropods with surface-dwelling larvae, however, would seem to be more likely to have a wide dispersal and range of occurrence. This view is consistent with the mapping of dispersal routes of fish larvae in the Caribbean by Roberts (1997) and is seen in a subset of the gastropod species that have the shallowest minimum depths, the narrowest depth ranges, and the broadest geographic distributions (above) For the Atlantic continental shelf, Epifanio and Garvine (2001) described three principal forcing agents affecting larval transport: wind stress, tides, and density differences in water masses. Thus, it is important to consider passive larval transport in molluscan biogeography of the Western Atlantic in the context of more than just surface currents. Some gastropod species, such as Queen Conch, *Strombus gigas*, have pelagic stages that last only 2-3 weeks (Smith and Pitts, 2004). Scheltema (1995) noted that laboratory and field data have shown that many Caribbean molluscs have larval life spans that enable long-distance dispersal, that larval advection follows major ocean currents in the Caribbean, but that some species lacking long planktonic larval stages nevertheless have wide geographic ranges.

#### *Geographic Affinities*

While the results of the collections at Lee Stocking Island that I examined did not include any species of gastropod molluscs that were endemic to the Bahamian sub-province, their geographic ranges opened up a number of questions that were addressed

with the larger Academy of Natural Sciences (ANS) data set for Western Atlantic species of gastropod species. One of the more obvious and interesting features of the geographic ranges are the northern limits, around 35°N, that clearly reflects the northern oceanographic boundary off Cape Hatteras in the Carolinian province. This northern latitudinal boundary predominates in nearly all the species of gastropods in the Lee Stocking Island collection as well as the species in the ANS data set.

Only approximately 26% of the estimated numbers of species of global molluscs have been described. Around 70,000 species have been described and an estimated 200,000 or so species remain to be discovered (Systematic Agenda 2000, 1994). There is even little agreement as to how many species of molluscs have actually been discovered (G. Rosenberg, pers. comm.). Interestingly, a number of molluscan paleontologists until around the late 1940's concluded that Western Atlantic molluscs were *already* thoroughly understood (Allmon et al., 1996). However, more recent investigations have revealed that systematic knowledge of these molluscs is still far from complete, both on geologic time scales and for recent distributions throughout the Western Atlantic region, particularly with respect to deeper water species assemblages. Discoveries of new species are continually being reported, particularly in deeper water that is now more accessible due to technological advances and more innovative collecting techniques.

The Recent western Atlantic molluscan fauna has traditionally been regarded as less diverse than that of the eastern Pacific (Allmon et. al, 1996). The data in the present study refer only to the western Atlantic fauna that extends into the eastern Pacific, and do not represent the whole eastern Pacific molluscan fauna. Until fairly recently, the western

Atlantic was believed to have declined from approximate parity in molluscan diversity with the east Pacific before the closure of the Isthmus of Panama to a “depauperate” condition. For example, Stanley and Campbell (1981) demonstrated that Pliocene molluscan faunas in the Western Atlantic experienced as much as 70 to 80% extinction, compared to only 30% extinction in Pliocene faunas from California.

Some authors such as Olsson (1968) and Campbell et al. (1975) reported that the Florida Pinecrest Sandstone beds of the early and late Pliocene may have had up to 1,000 species of molluscs, which they believed to be similar in number to the entire Recent Caribbean molluscan fauna. The obvious problem with these estimates is that the number of species of molluscs in the Caribbean region is becoming larger with the increased sampling efforts of various researchers in the region. Redfern (2001) reported nearly 1,000 species of molluscs from Abaco Island alone in the Bahamas, with most of his collections focused on readily accessible shallow-water habitats.

Compilations such as Abbott’s *American Seashells* (1974) and Redfern’s *Bahamian Seashells* (2001) are currently viewed as subsets of the likely far higher total number of species in the western Atlantic and Bahamas, respectively. No one has yet compiled or published a complete list of known Recent molluscan species for the whole of the tropical and subtropical western Atlantic that includes the Caribbean Basin, Florida, Bahamas, and Bermuda. To address this problem for gastropods, the full database assembled by Dr. Gary Rosenberg at the ANS lists all known gastropods of the Western Atlantic from Cape Hatteras to Rio de Janeiro, including Bermuda. The database is based on literature reports such as Abbott (1974), Turgeon et al. (1988) and over 2,500 other

works. The total database (which presently contains nearly 5,000 species of shelled gastropods) has 1,200 species from a *single* collection location (Bimini, Bahamas). The increasing number of molluscan species reported is reflected in publications in the literature such as the second edition of Turgeon et al. (1998), and the number of species encountered in the field continues to rise with nearly every new exploratory effort.

The molluscan faunas of deeper reef environments are poorly understood, relative to shallow water reef environments. This is typical for other taxa as well. For example, Pyle (2000) reported unexpectedly high fish biodiversity on deep coral reefs from 60 - 150 m on several Pacific Islands. Since his findings that new species assemblages on deep reefs show comparatively low distributional overlap, suggesting higher endemism than for shallow water reef fish assemblages, the analog may exist for deep-slope molluscs in the Caribbean region in general, including the Bahamas. Pyle (2000) estimated that as many as 2,000 or more coral reef fish species are undiscovered on deep reefs throughout the Indo-Pacific region. From submersible observations along deep water transects in Exuma Sound, Bahamas, G. Dennis (pers. comm.) reported 34 families of fishes with a total of 103 species. Thus, if an analog with molluscs exists at similar depths in the Bahamas, it is conceivable that a rich molluscan fauna with a high degree of endemism may be present in the deep-slope depth range, assuming suitable conditions (i.e., substrate type, available food source, angle of slope, etc.). However, the results of the present study – showing a high proportion of broadly distributed species with wide depth ranges – does not support this hypothesis for the Bahamas.



It has been a paradigm of biogeography and evolutionary biology that isolation favors speciation and faunal endemism (Brown et al., 1998). The three biogeographic provinces (i.e., Carolinian, Caribbean, and Brazilian) described by Petuch (2004) follow a generally accepted configuration for various taxa in the western Atlantic. Petuch's sub-provincial divisions reflect extensive analysis of patterns in the fossil record, and offer an excellent framework to compare information on distributions of other taxa such as fishes and corals in the western Atlantic. From the perspective of larval dispersal, circulation patterns for the Caribbean Basin appear consistent with Petuch's (2004) designation of the Caribbean as a separate province from the Carolinian, as larval transport as shown by Roberts (1997) follows roughly the contour of the Loop Current in the Gulf of Mexico, the Florida Current and ultimately the Gulf Stream, which veers away from Florida after it passes through the Straights of Florida. The Brazilian Province is presently separated from the Caribbean Province not only by barriers such as distance and coastal freshwater outflows, but by the Brazilian current that flows in a southerly direction, away from the Caribbean.

On a worldwide scale, Valentine (1973) and Briggs (1995) have shown that provinces of marine organisms such as echinoderms, corals, and fishes align basically with the geographical limits of molluscan faunal provinces. The modern northern boundary of the Carolinian province is the position of the Gulf Stream, which is counter-balanced by cooler circulation from the mid-Atlantic. These currents converge approximately off Cape Hatteras, and offer a rather distinct temperature and circulation northern boundary that warm-water (non-migratory) species tend to be restricted to. For molluscs, the boundaries

of the Carolinian province are delineated by the entire family Busyconidae (Petuch, 2004) and a number of other endemic molluscan genera and species. In the southernmost western Atlantic province, the Brazilian, cone shells show a high rate of endemism (E. Petuch, pers. comm.), and cone shells also exhibit a high rate of endemism in the Caribbean province, as do other endemic molluscs that account for the provincial status determined by the 50% endemism rule (though Petuch's data on species for these provincial arrangements are not yet published). The Brazilian province, formerly considered part of the Caribbean province, was recently recognized by Petuch (1988, 2004) as having full provincial status. For molluscs, the Brazilian fauna resembles the recent Panamic province even more than the Caribbean, and contains many Pleistocene relicts, according to Petuch (2004).

Present-day Caribbean circulation likely contributes to the relative homogeneity of the fishes, corals, molluscs, and other taxa in the region through larval advection. The main influence for this generally northward advection along the Antillean Island arc is the Caribbean current. Deepwater currents in the basin are influenced by bathymetry and thermohaline (density-driven) circulation, relatively little movement of the middle layer, and wind-driven surface currents. Very little is known of the deeper molluscan assemblages or of the influence of deepwater oceanographic processes that regulate distributions of deepwater molluscan species in the region.

The numbers of species of gastropods in the ANS data set whose ranges extended into the Eastern Pacific region and Brazilian province were unexpectedly high, considering that all of these species are present in the Bahamas, that the Eastern Pacific is

separated by the physical barrier of the Isthmus of Panama, and the relative distance, geographically, of the Brazilian province from the Caribbean. The commonality of the species reported from either side of the Isthmus of Panama likely reflects the unrestricted ranges of species that were present before the rise of the Isthmus. The relatively high number of species that have overlapping ranges in the Brazilian and Caribbean provinces probably reflects historical Tethyan connectivity. However, the Brazilian Province has long been recognized for the distinctiveness of its marine biota because of the lack of coral reefs in a vast stretch of coastline along the northeastern coast of South America beginning around the Orinoco River delta and extending to the northern coast of Brazil. Thus, while the Brazilian Province indeed has a large endemic component according to Petuch (2004), the results of the present study also indicate a relatively large proportion of species of gastropods that occur in the Caribbean and Bahamas have ranges that extend to the Brazilian Province.

The low number of species in the Eastern Atlantic reflects divergence and extinction and the present-day distance barrier. The faunal affinities between the eastern and western Atlantic ocean are very slight (Ekman, 1953); with a sparse west African fauna (with not much to send), and the distance between the two coasts is so great that the time it would take larvae to cross by drifting with the currents is longer than the pelagic stages of the molluscs. Even without the great distances involved, tropical circulation between the two continents would not tend to transport larvae from west to east. These findings are reasonably consistent with Briggs's (1995) description of the barriers and circulation patterns of the Western Atlantic region.

As collections increase with species of gastropods and other molluscan species from the Western Atlantic, the understanding of biogeographic affinities will undoubtedly improve, as will the understanding of patterns in life histories. The ANS data set has offered an excellent tool for exploring patterns in a large number of species, and with its continued expansion, the patterns seen in Western Atlantic gastropods will offer researchers insight into patterns of other taxa and lead to a far better understanding of the underlying processes that regulate tropical ecosystems.

Appendix 1. Species of gastropod molluscs used in the analysis with depth range (m), maximum size (mm), and geographic range index. Data courtesy of Dr. Gary Rosenberg, Academy of Natural Sciences, Philadelphia, PA. Asterisk = no data.

| Taxa                               | Depth Range<br>(m) | Maximum Size<br>(mm) | Geographic Range<br>Index |
|------------------------------------|--------------------|----------------------|---------------------------|
| <i>Acanthotrophon striatoides</i>  | 0 - 55             | 24.8                 | 63.23                     |
| <i>Acteocina inconspicua</i>       | 0 - 16             | 2.7                  | 35.09                     |
| <i>Acteocina recta</i>             | 2 - 128            | 2.5                  | 73.41                     |
| <i>Acteocina bullata</i>           | 11 - 100           | 10                   | 77.32                     |
| <i>Acteocina bidentata</i>         | 0 - 366            | 4                    | 92.85                     |
| <i>Acteocina candei</i>            | 0 - 51             | 4.5                  | 95.92                     |
| <i>Acteocina lepta</i>             | 2 - 457            | 5.3                  | 53.41                     |
| <i>Acteocina canaliculata</i>      | 0 - 49             | 5.5                  | 57.87                     |
| <i>Acteon delicatus</i>            | 135 - 567          | 10                   | 29.42                     |
| <i>Acteon finlayi</i>              | 0 - 366            | 12                   | 27.27                     |
| <i>Acteon danaida</i>              | 370 - 620          | 11                   | 63.00                     |
| <i>Acteon incisus</i>              | 31 - 1170          | 10                   | 31.64                     |
| <i>Acteon candens</i>              | 0 - 124            | 10                   | 74.83                     |
| <i>Acteon melampoides</i>          | 402 - 4707         | 9.6                  | 32.06                     |
| <i>Adelphotectonica uruguayana</i> | 96 - 250           | 25                   | 71.55                     |
| <i>Aesopus stearnsii</i>           | 7 - 51             | 6                    | 69.35                     |
| <i>Agathotoma castellata</i>       | 3 - 21             | 6.5                  | 17.07                     |
| <i>Agathotoma candidissima</i>     | 0 - 103            | 10                   | 85.26                     |
| <i>Agatrix agassizii</i>           | 33 - 91            | 13.5                 | 24.87                     |
| <i>Alaba incerta</i>               | 0 - 40             | 10                   | 99.96                     |
| <i>Alvania auberiana</i>           | 0 - 101            | 1.8                  | 85.50                     |
| <i>Amaea mitchelli</i>             | 0 - 55             | 60                   | 46.65                     |
| <i>Amaea retifera</i>              | 15 - 219           | 30                   | 56.55                     |
| <i>Amphithalamus valleii</i>       | 0 - 15             | 1.25                 | 72.70                     |
| <i>Anatoma alta</i>                | 20 - 823           | 2.1                  | 53.76                     |
| <i>Anatoma crispata</i>            | 8 - 2221           | 2.5                  | 126.45                    |
| <i>Ancistrobasis costulata</i>     | 1170 - 1170        | 3.6                  | 62.82                     |
| <i>Angiola lineata</i>             | 0 - 48             | 7                    | 106.07                    |
| <i>Anticlimax athleenae</i>        | *                  | 2.6                  | 18.39                     |
| <i>Anticlimax pilsbryi</i>         | 0 - 152            | 3.6                  | 31.62                     |
| <i>Antillophos beauii</i>          | 10 - 150           | 39                   | 25.02                     |
| <i>Antillophos candeanus</i>       | 2 - 183            | 30                   | 73.90                     |
| <i>Architectonica nobilis</i>      | 0 - 73             | 51                   | 116.75                    |
| <i>Arene microforis</i>            | 80 - 311           | 5.4                  | 76.21                     |
| <i>Arene miniata</i>               | 0 - 27             | 2.5                  | 27.54                     |
| <i>Arene riisei</i>                | 0 - 36             | 8                    | 69.58                     |
| <i>Arene venustula</i>             | 16 - 80            | 8.2                  | 17.44                     |

Appendix 1. (Continued).

|                                    |            |      |        |
|------------------------------------|------------|------|--------|
| <i>Arene cruentata</i>             | 0 - 115    | 16.3 | 37.57  |
| <i>Arene briareus</i>              | 33 - 878   | 9    | 52.85  |
| <i>Arene tricarinata</i>           | 0 - 183    | 3.6  | 54.89  |
| <i>Arene variabilis</i>            | 26 - 494   | 6    | 74.96  |
| <i>Arene bairdii</i>               | 27 - 1472  | 6    | 94.80  |
| <i>Aspella castor</i>              | 53 - 53    | 13.4 | 65.39  |
| <i>Assimineea succinea</i>         | 0 - 4      | 2.9  | 86.38  |
| <i>Astraliium phoebium</i>         | 0 - 91     | 76   | 72.55  |
| <i>Astyris verrilli</i>            | 567 - 1472 | 9    | 65.02  |
| <i>Astyris raveneli</i>            | 9 - 227    | 9.5  | 20.27  |
| <i>Astyris profundi</i>            | 196 - 1472 | 8    | 58.54  |
| <i>Astyris lunatus</i>             | 0 - 115    | 5.8  | 98.53  |
| <i>Attiliosa aldridgei</i>         | 0.3 - 20   | 31.5 | 29.96  |
| <i>Atys riiseanus</i>              | 2 - 93     | 13   | 77.33  |
| <i>Atys macandrewii</i>            | 11 - 75    | 7.3  | 75.39  |
| <i>Atys caribaeus</i>              | 0 - 183    | 11   | 70.29  |
| <i>Atys sandersoni</i>             | 30 - 1472  | 8    | 80.46  |
| <i>Axelella smithii</i>            | 20 - 99    | 17   | 38.56  |
| <i>Babelomurex mansfieldi</i>      | 0.6 - 177  | 31   | 76.58  |
| <i>Babelomurex dalli</i>           | 51 - 1606  | 55   | 86.18  |
| <i>Bactrocythara asarca</i>        | 46 - 101   | 6    | 32.60  |
| <i>Bailya intricata</i>            | 0 - 91     | 18   | 35.85  |
| <i>Bailya parva</i>                | 0.6 - 51   | 20   | 33.94  |
| <i>Barleeia tinctoria</i>          | 0 - 8      | 2.8  | 24.42  |
| <i>Bathynnerita naticoidea</i>     | 541 - 1135 | 16   | 36.07  |
| <i>Bathytoma viabrunnea</i>        | 183 - 653  | 70   | 29.29  |
| <i>Batillaria minima</i>           | 0 - 0      | 21   | 76.94  |
| <i>Bellaspira pentagonalis</i>     | 13 - 366   | 10.1 | 21.19  |
| <i>Belomitra pourtalesii</i>       | 454 - 1620 | 30   | 24.21  |
| <i>Benthobia tryonii</i>           | 686 - 4038 | 13   | 71.71  |
| <i>Benthomangelia antonia</i>      | 124 - 3834 | 15   | 109.66 |
| <i>Benthonella tenella</i>         | 10 - 5500  | 9    | 84.74  |
| <i>Benthonellania acuticostata</i> | 59 - 1249  | 3.7  | 40.25  |
| <i>Benthonellania colombiana</i>   | 45 - 221   | 1.3  | 32.38  |
| <i>Bittiolium varium</i>           | 0 - 11     | 6.1  | 92.61  |
| <i>Boonea jadisi</i>               | 0 - 2.2    | 3.5  | 79.20  |
| <i>Boonea somersi</i>              | 18 - 80    | 2.6  | 35.56  |
| <i>Boonea impressa</i>             | 0.3 - 30   | 6.7  | 81.30  |
| <i>Boonea seminuda</i>             | 0 - 101    | 6.9  | 102.66 |
| <i>Bostrycapulus aculeatus</i>     | 0 - 80     | 32   | 107.23 |
| <i>Brachycythara barbarae</i>      | 0 - 103    | 3.5  | 52.43  |
| <i>Brachycythara biconica</i>      | 0 - 90     | 6    | 67.80  |
| <i>Bufo</i>                        | 0 - 100    | 60   | 64.35  |

Appendix 1. (Continued).

|                                |            |      |        |
|--------------------------------|------------|------|--------|
| <i>Bulla solida</i>            | 0 - 25     | 52   | 30.69  |
| <i>Bulla pinguicula</i>        | 538 - 1170 | 12.8 | 56.28  |
| <i>Bulla striata</i>           | 0 - 81     | 44   | 113.47 |
| <i>Bursa grayana</i>           | 0 - 93     | 55   | 60.83  |
| <i>Bursa ranelloides</i>       | 30 - 250   | 75   | 65.45  |
| <i>Bursa natalensis</i>        | 40 - 780   | 85   | 72.22  |
| <i>Bursa corrugata</i>         | 2 - 137    | 75   | 102.03 |
| <i>Bursa rhodostoma</i>        | 0 - 250    | 35   | 103.82 |
| <i>Bursa granularis</i>        | 0 - 60     | 65   | 78.25  |
| <i>Busycon sinistrum</i>       | 0 - 73     | 450  | 26.75  |
| <i>Caecum antillarum</i>       | 5 - 100    | 1.7  | 71.95  |
| <i>Caecum brasilicum</i>       | 2 - 24     | 4    | 74.04  |
| <i>Caecum breve</i>            | 0 - 6      | 1.2  | 61.40  |
| <i>Caecum gurgulio</i>         | 0 - 0      | 2    | 17.03  |
| <i>Caecum regulare</i>         | 10 - 58    | 2.5  | 33.31  |
| <i>Caecum subvolutum</i>       | 12 - 296   | 3.6  | 25.80  |
| <i>Caecum circumvolutum</i>    | 1.5 - 40   | 3.3  | 73.33  |
| <i>Caecum strigosum</i>        | 0 - 40     | 2.1  | 70.57  |
| <i>Caecum condylum</i>         | 12 - 30    | 3.36 | 31.03  |
| <i>Caecum insularum</i>        | 1.5 - 1.5  | 3.4  | 21.91  |
| <i>Caecum ryssotitum</i>       | 0 - 101    | 2.3  | 83.62  |
| <i>Caecum textile</i>          | 0 - 6      | 2.2  | 38.94  |
| <i>Caecum clava</i>            | 0 - 101    | 3.6  | 40.49  |
| <i>Caecum imbricatum</i>       | 0 - 183    | 4.5  | 84.12  |
| <i>Caecum plicatum</i>         | 2 - 101    | 4    | 74.38  |
| <i>Caecum cycloferum</i>       | 0 - 101    | 6    | 84.94  |
| <i>Caecum floridanum</i>       | 0 - 60     | 5.6  | 79.48  |
| <i>Caecum heladum</i>          | 2 - 46     | 4.2  | 73.93  |
| <i>Caecum cooperi</i>          | 0 - 73     | 6.1  | 32.39  |
| <i>Caecum johnsoni</i>         | 0 - 75     | 4.5  | 68.88  |
| <i>Caecum pulchellum</i>       | 0.3 - 101  | 4.5  | 100.20 |
| <i>Caelatura rustica</i>       | 2 - 805    | 3.3  | 68.39  |
| <i>Calliostoma javanicum</i>   | 1 - 97     | 35   | 74.01  |
| <i>Calliostoma sarcodum</i>    | 6 - 12     | 11   | 27.25  |
| <i>Calliostoma brunneum</i>    | 27 - 1767  | 32   | 26.01  |
| <i>Calliostoma echinatum</i>   | 37 - 220   | 10   | 71.39  |
| <i>Calliostoma orion</i>       | 20 - 146   | 20.2 | 31.45  |
| <i>Calliostoma sapidum</i>     | 121 - 1472 | 6    | 59.46  |
| <i>Calliostoma stirophorum</i> | 713 - 805  | 7.6  | 18.76  |
| <i>Calliostoma euglyptum</i>   | 0 - 91     | 26   | 41.69  |
| <i>Calliostoma jujubinum</i>   | 0 - 192    | 34   | 84.75  |
| <i>Calliostoma pulchrum</i>    | 1 - 366    | 16   | 38.62  |
| <i>Calliostoma yucatecanum</i> | 8 - 1170   | 16   | 23.76  |

Appendix 1. (Continued).

|                                 |            |      |        |
|---------------------------------|------------|------|--------|
| <i>Calliostoma roseolum</i>     | 13 - 146   | 14   | 21.30  |
| <i>Calliotropis aeglees</i>     | 366 - 713  | 7.6  | 18.76  |
| <i>Calliotropis actinophora</i> | 220 - 2276 | 10   | 50.48  |
| <i>Calliotropis lissocona</i>   | 415 - 587  | 6.3  | 22.89  |
| <i>Calliotropis rhina</i>       | 558 - 1719 | 10   | 59.73  |
| <i>Calliotropis calatha</i>     | 247 - 1620 | 10   | 29.16  |
| <i>Calyptraea centralis</i>     | 0 - 183    | 15   | 92.39  |
| <i>Cancellaria adela</i>        | *          | 53   | 17.64  |
| <i>Cancellaria reticulata</i>   | 0 - 73     | 55   | 80.17  |
| <i>Capulus incurvus</i>         | 0 - 538    | 17   | 83.63  |
| <i>Capulus ungaricus</i>        | 1 - 838    | 50   | 56.71  |
| <i>Careliopsis styliformis</i>  | 0 - 95     | 4.1  | 23.66  |
| <i>Carenzia carinata</i>        | 988 - 1706 | 4.4  | 85.42  |
| <i>Carenzia trispinosa</i>      | 684 - 2360 | 4.8  | 73.80  |
| <i>Casmaria atlantica</i>       | 7 - 30     | 45   | 67.60  |
| <i>Cassis flammea</i>           | 1 - 12     | 154  | 41.16  |
| <i>Cassis madagascariensis</i>  | 5 - 183    | 409  | 40.62  |
| <i>Cassis tuberosa</i>          | 0 - 27     | 301  | 85.43  |
| <i>Cataegis meroglypta</i>      | 576 - 1236 | 19   | 37.23  |
| <i>Cataegis finkli</i>          | 384 - 1281 | 25   | 35.23  |
| <i>Cenchritis muricata</i>      | -9 - 0     | 30   | 37.82  |
| <i>Cerithidea pliculosa</i>     | 0 - 2      | 33   | 36.56  |
| <i>Cerithidea costata</i>       | 0 - 402    | 20.3 | 41.76  |
| <i>Cerithidea scalariformis</i> | 0 - 0      | 33   | 34.89  |
| <i>Cerithiopsis flava</i>       | 11 - 101   | 3.8  | 34.04  |
| <i>Cerithiopsis albovittata</i> | 11 - 101   | 5    | 35.96  |
| <i>Cerithiopsis gemmulosa</i>   | 0 - 91     | 5.3  | 70.06  |
| <i>Cerithiopsis io</i>          | 5.4 - 6    | 2.3  | 24.81  |
| <i>Cerithiopsis ara</i>         | 24 - 55    | 3.2  | 35.51  |
| <i>Cerithiopsis fusiformis</i>  | 0 - 165    | 3.3  | 36.91  |
| <i>Cerithiopsis iota</i>        | 7 - 115    | 5    | 37.24  |
| <i>Cerithiopsis lata</i>        | 0 - 44     | 3.3  | 38.45  |
| <i>Cerithiopsis greenii</i>     | 0 - 75     | 4.6  | 102.31 |
| <i>Cerithium guinaicum</i>      | 0 - 20     | 45   | 89.91  |
| <i>Cerithium eburneum</i>       | 0 - 18     | 43   | 76.06  |
| <i>Cerithium lutosum</i>        | 0 - 8      | 20   | 44.86  |
| <i>Cerithium litteratum</i>     | 0 - 88     | 34   | 87.38  |
| <i>Cerithium atratum</i>        | 0 - 91     | 50   | 116.21 |
| <i>Cerodrillia thea</i>         | 0 - 203    | 15   | 77.38  |
| <i>Cerodrillia carminura</i>    | 183 - 203  | 11.5 | 29.94  |
| <i>Cerodrillia perryae</i>      | 2 - 95     | 12.9 | 79.29  |
| <i>Cerodrillia simpsoni</i>     | 9 - 82     | 8    | 43.84  |
| <i>Charonia variegata</i>       | 0.3 - 110  | 374  | 110.02 |



Appendix 1. (Continued).

|                                    |            |      |       |
|------------------------------------|------------|------|-------|
| <i>Cheilea equestris</i>           | 0 - 780    | 40   | 97.14 |
| <i>Chicoreus brevifrons</i>        | 0 - 83     | 155  | 55.50 |
| <i>Chicoreus mergus</i>            | 6 - 91     | 49   | 33.84 |
| <i>Chicoreus florifer</i>          | 1 - 196    | 84   | 29.84 |
| <i>Chrysallida toroensis</i>       | 0 - 238    | 2.8  | 58.75 |
| <i>Chrysallida gemmulosa</i>       | 1.2 - 1.2  | 3.9  | 30.95 |
| <i>Chrysallida cancellata</i>      | 26 - 101   | 2.6  | 37.58 |
| <i>Circulus semisculptus</i>       | 0 - 0      | 3.2  | 21.76 |
| <i>Cirsotrema pilsbryi</i>         | 137 - 165  | 29   | 38.26 |
| <i>Cirsotrema dalli</i>            | 9 - 227    | 41   | 74.34 |
| <i>Cittarium pica</i>              | 0 - 7      | 136  | 33.15 |
| <i>Clathrodrillia albicoma</i>     | 154 - 1470 | 34   | 68.44 |
| <i>Cocculina rathbuni</i>          | 124 - 1127 | 12   | 33.36 |
| <i>Cochlespira elegans</i>         | 55 - 1472  | 60   | 18.52 |
| <i>Cochlespira radiata</i>         | 24 - 1170  | 32   | 40.79 |
| <i>Cochliolepis adamsii</i>        | *          | 8.5  | 24.87 |
| <i>Cochliolepis parasitica</i>     | 0 - 48     | 4.2  | 39.80 |
| <i>Colubraria testacea</i>         | 2.5 - 780  | 49   | 95.99 |
| <i>Columbella mercatoria</i>       | 0 - 81     | 24   | 85.17 |
| <i>Columbellopsis fusiformis</i>   | 1.5 - 5    | 7    | 22.63 |
| <i>Columbellopsis nycteis</i>      | 1.5 - 50   | 8.1  | 32.25 |
| <i>Compsodrillia acestra</i>       | 58 - 732   | 19   | 67.00 |
| <i>Compsodrillia haliostrephis</i> | 48 - 154   | 19.5 | 65.37 |
| <i>Compsodrillia eucosmia</i>      | 18 - 311   | 24   | 31.31 |
| <i>Compsodrillia disticha</i>      | 238 - 329  | 26.6 | 18.30 |
| <i>Compsodrillia tristicha</i>     | 164 - 384  | 23   | 69.53 |
| <i>Compsodrillia canna</i>         | 91 - 311   | 15.3 | 29.94 |
| <i>Conella ovulata</i>             | 0 - 0.3    | 20   | 30.06 |
| <i>Conus granulatus</i>            | 1.5 - 30   | 64.1 | 36.40 |
| <i>Conus puncticulatus</i>         | 0 - 15     | 29.9 | 23.33 |
| <i>Conus attenuatus</i>            | 10 - 30    | 28   | 25.77 |
| <i>Conus jucundus</i>              | 0.3 - 0.3  | 43   | 4.72  |
| <i>Conus regius</i>                | 0 - 95     | 75   | 73.43 |
| <i>Conus caribbaeus</i>            | *          | 35   | 17.68 |
| <i>Conus ermineus</i>              | 11 - 101   | 103  | 55.08 |
| <i>Conus spurius</i>               | 0 - 64     | 80   | 35.17 |
| <i>Conus mazei</i>                 | 152 - 549  | 59   | 41.56 |
| <i>Conus cancellatus</i>           | 26 - 110   | 80   | 48.66 |
| <i>Conus armiger</i>               | 35 - 227   | 40   | 46.39 |
| <i>Conus villepini</i>             | 25 - 475   | 93   | 90.47 |
| <i>Conus delessertii</i>           | 15 - 198   | 100  | 29.16 |
| <i>Conus mus</i>                   | 0 - 18     | 43.5 | 45.16 |
| <i>Conus amphiurgus</i>            | 9 - 61     | 54   | 32.03 |

Appendix 1. (Continued).

|                                    |            |      |        |
|------------------------------------|------------|------|--------|
| <i>Conus daucus</i>                | 0 - 120    | 66   | 74.87  |
| <i>Conus mindanus</i>              | 0 - 210    | 50   | 72.74  |
| <i>Coralliophila aedonia</i>       | 85 - 250   | 18.8 | 93.33  |
| <i>Coralliophila aberrans</i>      | 0 - 525    | 23   | 83.59  |
| <i>Coralliophila galea</i>         | 0 - 23     | 41   | 83.75  |
| <i>Coralliophila caribaea</i>      | 0 - 116    | 35   | 90.48  |
| <i>Coralliophila scalariformis</i> | 0.3 - 139  | 33   | 26.16  |
| <i>Corinnaeturris leucomata</i>    | 100 - 1719 | 19   | 76.80  |
| <i>Cornisepta acuminata</i>        | 291 - 713  | 5    | 29.49  |
| <i>Cosmioconcha calliglypta</i>    | 7 - 200    | 14.2 | 71.61  |
| <i>Cosmioconcha nitens</i>         | 0 - 183    | 14.5 | 49.99  |
| <i>Cosmotriphora arnoldoi</i>      | 20 - 55    | 6    | 30.47  |
| <i>Cosmotriphora ornata</i>        | 0 - 90     | 10   | 83.40  |
| <i>Cosmotriphora melanura</i>      | 0.6 - 91   | 8.5  | 111.19 |
| <i>Costaclis egregia</i>           | 250 - 1436 | 13   | 61.53  |
| <i>Costaclis hyalina</i>           | 2 - 848    | 10.7 | 60.39  |
| <i>Costoanachis hotessieriana</i>  | 0 - 73     | 7.7  | 39.63  |
| <i>Costoanachis catenata</i>       | 1.5 - 34   | 10   | 77.18  |
| <i>Costoanachis sparsa</i>         | 0.5 - 80   | 12   | 82.32  |
| <i>Costoanachis sertulariarum</i>  | 0 - 20     | 13   | 99.77  |
| <i>Costoanachis avara</i>          | 0 - 46     | 14.5 | 35.29  |
| <i>Costoanachis lafresnayi</i>     | 0 - 152    | 18   | 44.82  |
| <i>Cranopsis agger</i>             | 249 - 1966 | 6    | 23.78  |
| <i>Cranopsis granulata</i>         | 150 - 1966 | 8    | 70.00  |
| <i>Cranopsis asturiana</i>         | 183 - 2017 | 21   | 72.03  |
| <i>Crassispira rhythmica</i>       | 200 - 200  | 15   | 23.57  |
| <i>Crassispira cubana</i>          | 1 - 91     | 27   | 45.71  |
| <i>Crassispira fuscescens</i>      | 0.6 - 90   | 24   | 81.10  |
| <i>Crenilabium exile</i>           | 274 - 2654 | 8    | 90.61  |
| <i>Crepidula convexa</i>           | 0 - 70     | 20   | 39.59  |
| <i>Crepidula plana</i>             | 0 - 110    | 43   | 110.59 |
| <i>Crockerella toreumata</i>       | 402 - 715  | 10.2 | 23.81  |
| <i>Crucibulum auricula</i>         | 1 - 115    | 29   | 72.42  |
| <i>Crucibulum striatum</i>         | 0 - 422    | 34   | 53.01  |
| <i>Cryoturris quadrilineata</i>    | 15 - 20    | 10   | 30.93  |
| <i>Cryoturris fargoi</i>           | 11 - 80    | 18   | 25.72  |
| <i>Cyclodostomia didyma</i>        | 0 - 101    | 2.7  | 35.65  |
| <i>Cyclostrema tortuganum</i>      | 29 - 82    | 10   | 67.20  |
| <i>Cyclostrema cancellatum</i>     | 0 - 2012   | 12   | 65.06  |
| <i>Cyclostrema amabile</i>         | 27 - 146   | 6.2  | 37.28  |
| <i>Cyclostremella humilis</i>      | 0 - 29     | 2    | 29.75  |
| <i>Cyclostremiscus cubanus</i>     | 1 - 137    | 1.2  | 35.84  |
| <i>Cyclostremiscus jeannae</i>     | 0 - 128    | 2.3  | 32.65  |

Appendix 1. (Continued).

|                                   |           |      |        |
|-----------------------------------|-----------|------|--------|
| <i>Cyclostremiscus beauii</i>     | 0 - 46    | 12.5 | 75.08  |
| <i>Cyclostremiscus pentagonus</i> | 0 - 538   | 3.5  | 39.74  |
| <i>Cylichna verrillii</i>         | 91 - 805  | 7.5  | 72.89  |
| <i>Cylindriscala andrewsii</i>    | 165 - 914 | 8    | 79.96  |
| <i>Cylindrobulla beauii</i>       | 0 - 40    | 13.6 | 67.37  |
| <i>Cylindrobulla gigas</i>        | 0.5 - 18  | 17.5 | 26.61  |
| <i>Cymatium raderi</i>            | 21 - 27   | 196  | 56.85  |
| <i>Cymatium vespaceum</i>         | 4.5 - 4.5 | 41   | 28.83  |
| <i>Cymatium martinianum</i>       | *         | 80   | 27.62  |
| <i>Cymatium tranquebaricum</i>    | *         | 35   | 98.08  |
| <i>Cymatium rehderi</i>           | 30 - 366  | 92   | 26.35  |
| <i>Cymatium occidentale</i>       | 0 - 128   | 40   | 85.91  |
| <i>Cymatium pfeifferianum</i>     | 0 - 46    | 46   | 60.14  |
| <i>Cymatium femorale</i>          | 0.6 - 150 | 212  | 82.02  |
| <i>Cymatium muricinum</i>         | 0 - 27    | 75   | 76.16  |
| <i>Cymatium nicobaricum</i>       | 0 - 36    | 90   | 104.22 |
| <i>Cymatium pharcida</i>          | 85 - 220  | 45   | 24.38  |
| <i>Cymatium aquatile</i>          | 0 - 18    | 95   | 88.87  |
| <i>Cymatium cynocephalum</i>      | 0 - 137   | 84   | 79.93  |
| <i>Cymatium labiosum</i>          | 0.2 - 91  | 30   | 93.72  |
| <i>Cymatium krebsii</i>           | 2 - 146   | 92   | 53.40  |
| <i>Cymatium parthenopeum</i>      | 0 - 75    | 180  | 108.56 |
| <i>Cymatium comptum</i>           | 2 - 214   | 34   | 85.20  |
| <i>Cymatium cingulatum</i>        | 0 - 382   | 75   | 94.37  |
| <i>Cymbovula acicularis</i>       | 0.3 - 27  | 17   | 43.84  |
| <i>Cyphoma signatum</i>           | 0.3 - 90  | 45   | 77.64  |
| <i>Cyphoma gibbosum</i>           | 0 - 29    | 38   | 73.35  |
| <i>Cyphoma mcgintyi</i>           | 0.8 - 90  | 39.5 | 34.75  |
| <i>Cypraecassis testiculus</i>    | 0 - 50    | 85   | 111.76 |
| <i>Daphnella lymneiformis</i>     | 0 - 46    | 19   | 61.85  |
| <i>Daphnella margaretae</i>       | 15 - 94   | 14   | 69.94  |
| <i>Daphnella reticulosa</i>       | 2 - 139   | 11.5 | 36.54  |
| <i>Daphnella corbicula</i>        | 46 - 238  | 11.2 | 72.73  |
| <i>Daphnella retifera</i>         | 37 - 124  | 7.2  | 79.19  |
| <i>Dendropoma corrodens</i>       | 0 - 0     | 10   | 38.54  |
| <i>Dendropoma irregulare</i>      | 0 - 7     | 36   | 81.97  |
| <i>Dendropoma exsertum</i>        | 57 - 1832 | 11   | 40.46  |
| <i>Dentimargo reductus</i>        | 1 - 50    | 3    | 18.20  |
| <i>Dentimargo aureocinctus</i>    | 0 - 165   | 4.7  | 63.65  |
| <i>Dentimargo eburneolus</i>      | 0 - 1097  | 9    | 40.70  |
| <i>Dentistyla asperrima</i>       | 66 - 402  | 8.5  | 24.13  |
| <i>Dentistyla dentifera</i>       | 146 - 311 | 8    | 39.28  |
| <i>Depressiscala nitidella</i>    | 12 - 165  | 20   | 82.27  |

Appendix 1. (Continued).

|                                    |            |      |        |
|------------------------------------|------------|------|--------|
| <i>Depressiscula nautlae</i>       | 6 - 121    | 22   | 78.73  |
| <i>Dermomurex abyssicola</i>       | 45 - 500   | 11   | 24.87  |
| <i>Dermomurex elizabethae</i>      | 2 - 3      | 20   | 28.88  |
| <i>Dermomurex pauperculus</i>      | 0 - 30     | 30   | 66.21  |
| <i>Dillwynella modesta</i>         | 413 - 805  | 4    | 25.26  |
| <i>Diodora variegata</i>           | 0 - 6      | 15   | 26.81  |
| <i>Diodora wetmorei</i>            | 91 - 212   | 24   | 18.38  |
| <i>Diodora minuta</i>              | 0 - 132    | 16   | 32.30  |
| <i>Diodora arcuata</i>             | 0 - 183    | 12   | 40.94  |
| <i>Diodora viridula</i>            | 0 - 208    | 32   | 28.35  |
| <i>Diodora jaumei</i>              | 0 - 402    | 22   | 49.59  |
| <i>Diodora meta</i>                | 0 - 110    | 16   | 84.71  |
| <i>Diodora aguayoi</i>             | 50 - 823   | 17   | 30.70  |
| <i>Diodora dysoni</i>              | 0 - 40     | 22   | 80.14  |
| <i>Diodora listeri</i>             | 0 - 44     | 45   | 76.43  |
| <i>Diodora sayi</i>                | 0 - 402    | 30   | 84.36  |
| <i>Diodora fluviana</i>            | 38 - 1472  | 12   | 66.12  |
| <i>Diodora tanneri</i>             | 190 - 730  | 58   | 28.99  |
| <i>Diodora cayenensis</i>          | 0 - 100    | 51   | 106.36 |
| <i>Discopsis omalos</i>            | 6 - 538    | 1.7  | 23.69  |
| <i>Discotectonica discus</i>       | 80 - 329   | 17.5 | 35.80  |
| <i>Distorsio perdistorta</i>       | 100 - 282  | 82   | 106.23 |
| <i>Distorsio constricta</i>        | 25 - 274   | 65   | 85.43  |
| <i>Distorsio clathrata</i>         | 0 - 300    | 79   | 111.52 |
| <i>Dolicholaturus pauli</i>        | 40 - 366   | 30   | 19.34  |
| <i>Douglassia bealiana</i>         | 26 - 91    | 12   | 67.44  |
| <i>Drillia cydia</i>               | 0 - 183    | 23   | 41.01  |
| <i>Drilliola loprestiana</i>       | 48 - 1829  | 8.1  | 80.80  |
| <i>Eccliseogyra nitida</i>         | 549 - 4693 | 10   | 92.08  |
| <i>Echinolittorina angustior</i>   | 0 - 0      | 16   | 31.73  |
| <i>Echinolittorina dilatata</i>    | 0 - 0      | 10   | 28.47  |
| <i>Echinolittorina meleagris</i>   | 0 - 0      | 9.8  | 93.35  |
| <i>Echinolittorina mespillum</i>   | -2 - 0     | 10   | 30.49  |
| <i>Echinolittorina ziczac</i>      | -3 - 0     | 23   | 37.82  |
| <i>Echinophoria coronadoi</i>      | 33 - 234   | 121  | 25.67  |
| <i>Elachisina floridana</i>        | 0 - 101    | 2.4  | 83.72  |
| <i>Emarginula tuberculosa</i>      | 10 - 1170  | 18   | 95.45  |
| <i>Emarginula pumila</i>           | 0 - 525    | 12   | 87.03  |
| <i>Emarginula phrixodes</i>        | 0 - 1966   | 7    | 44.38  |
| <i>Engina turbinella</i>           | 0 - 63     | 15   | 82.81  |
| <i>Entemnotrochus adansonianus</i> | 107 - 482  | 190  | 44.29  |
| <i>Eosipho canetae</i>             | 420 - 896  | 85.4 | 47.89  |
| <i>Episcynia inornata</i>          | 0 - 128    | 3.4  | 85.66  |

Appendix 1. (Continued).

|                                  |            |      |        |
|----------------------------------|------------|------|--------|
| <i>Epitonium phymanthi</i>       | 0 - 2      | 16.9 | 23.09  |
| <i>Epitonium unifasciatum</i>    | 0 - 9      | 18   | 70.27  |
| <i>Epitonium xenicima</i>        | 0 - 25     | 23   | 57.29  |
| <i>Epitonium worsfoldi</i>       | 1 - 1      | 25.3 | 16.58  |
| <i>Epitonium denticulatum</i>    | 0 - 1472   | 17   | 68.31  |
| <i>Epitonium foliaceicosta</i>   | 0 - 219    | 25   | 74.64  |
| <i>Epitonium sericifila</i>      | 0 - 7      | 10   | 29.07  |
| <i>Epitonium occidentale</i>     | 3 - 270    | 28   | 68.06  |
| <i>Epitonium albidum</i>         | 0 - 366    | 28   | 93.20  |
| <i>Epitonium echinaticosta</i>   | 0 - 366    | 15   | 79.70  |
| <i>Epitonium lamellosum</i>      | 0 - 60     | 34   | 93.41  |
| <i>Epitonium babylonia</i>       | 152 - 1337 | 30   | 24.36  |
| <i>Epitonium candeanum</i>       | 0 - 805    | 22   | 89.39  |
| <i>Epitonium krebsii</i>         | 0 - 294    | 19   | 80.32  |
| <i>Epitonium frielei</i>         | 91 - 250   | 16   | 71.70  |
| <i>Epitonium apiculatum</i>      | 1 - 90     | 11   | 38.41  |
| <i>Epitonium novangliae</i>      | 0 - 457    | 20   | 85.56  |
| <i>Epitonium celesti</i>         | 146 - 640  | 22   | 68.99  |
| <i>Epitonium dallianum</i>       | 115 - 478  | 13   | 105.88 |
| <i>Epitonium angulatum</i>       | 0 - 219    | 25   | 98.14  |
| <i>Epitonium rupicola</i>        | 0 - 65     | 25   | 39.18  |
| <i>Epitonium humphreysii</i>     | 0 - 95     | 24   | 83.19  |
| <i>Epitonium multistriatum</i>   | 2.5 - 219  | 15.5 | 103.12 |
| <i>Eratoidea hematita</i>        | 2 - 165    | 9    | 73.09  |
| <i>Erosaria acicularis</i>       | 0 - 780    | 31   | 89.64  |
| <i>Eubela limacina</i>           | 155 - 1472 | 11   | 69.95  |
| <i>Euchelus guttarosea</i>       | 34 - 823   | 6    | 32.99  |
| <i>Eucyclotoma cingulata</i>     | 26 - 80    | 15.5 | 35.15  |
| <i>Eucyclotoma stegeri</i>       | 25 - 150   | 23   | 70.58  |
| <i>Eudolium crosseanum</i>       | 17 - 914   | 81   | 77.87  |
| <i>Eudolium bairdii</i>          | 17 - 823   | 76   | 93.05  |
| <i>Eulima bifasciata</i>         | 0 - 84     | 10.6 | 85.56  |
| <i>Eulima patula</i>             | 4 - 805    | 6    | 31.95  |
| <i>Eulima auricincta</i>         | 0 - 183    | 4.9  | 100.15 |
| <i>Eulima fulvocincta</i>        | 0 - 115    | 6.6  | 33.85  |
| <i>Eulimastoma canaliculatum</i> | 0 - 60     | 3    | 86.24  |
| <i>Eulimastoma surinamense</i>   | 0 - 0      | 3.8  | 44.27  |
| <i>Eulimastoma teres</i>         | 11 - 360   | 6    | 27.59  |
| <i>Eulimella smithii</i>         | 35 - 267   | 8.2  | 35.12  |
| <i>Eulimostraca subcarinata</i>  | 0 - 192    | 5.4  | 93.86  |
| <i>Eulithidium adamsi</i>        | 0 - 30     | 3.8  | 35.52  |
| <i>Eulithidium affine</i>        | 0 - 63     | 7.9  | 87.86  |
| <i>Eulithidium bellum</i>        | 0 - 137    | 5.2  | 76.42  |

Appendix 1. (Continued).

|                                 |            |      |       |
|---------------------------------|------------|------|-------|
| <i>Eulithidium thalassicola</i> | 2 - 214    | 7.1  | 70.17 |
| <i>Euspira radiata</i>          | 538 - 1536 | 10.7 | 49.08 |
| <i>Eutriphora bermudensis</i>   | 4 - 56     | 6.1  | 26.80 |
| <i>Famelica scipio</i>          | 227 - 1796 | 14   | 25.42 |
| <i>Fargoa bushiana</i>          | 1 - 91     | 3.7  | 82.20 |
| <i>Fasciolaria tulipa</i>       | 0 - 73     | 250  | 55.65 |
| <i>Fastigiella carinata</i>     | 0 - 1      | 53   | 8.54  |
| <i>Favartia nucea</i>           | 44 - 73    | 27.8 | 73.41 |
| <i>Favartia minirosea</i>       | 18 - 110   | 7.7  | 22.37 |
| <i>Favartia alveata</i>         | 1 - 20     | 22   | 79.45 |
| <i>Favartia cellulosa</i>       | 0 - 310    | 29   | 84.52 |
| <i>Fenimorea pagodula</i>       | 30 - 282   | 18   | 62.94 |
| <i>Fenimorea halidorema</i>     | 0 - 110    | 25.5 | 67.10 |
| <i>Fenimorea janetae</i>        | 0 - 128    | 37.8 | 29.17 |
| <i>Fenimorea sunderlandi</i>    | 61 - 150   | 40   | 29.83 |
| <i>Fenimorea fucata</i>         | 6 - 45     | 27   | 69.20 |
| <i>Ficus howelli</i>            | 73 - 823   | 51   | 62.35 |
| <i>Ficus communis</i>           | 0 - 176    | 130  | 33.46 |
| <i>Finella adamsi</i>           | 2 - 30     | 4    | 35.28 |
| <i>Finella dubia</i>            | 0 - 805    | 4.5  | 86.66 |
| <i>Fissurella angusta</i>       | 0 - 6      | 31   | 34.73 |
| <i>Fissurella nodosa</i>        | 0 - 1      | 40   | 31.79 |
| <i>Fissurella barbouri</i>      | 0 - 0      | 19   | 27.31 |
| <i>Fissurella fascicularis</i>  | 0 - 0      | 32   | 28.41 |
| <i>Fissurella rosea</i>         | 0 - 40     | 30   | 80.32 |
| <i>Fissurella barbadensis</i>   | 0 - 8      | 41   | 47.33 |
| <i>Fissurella punctata</i>      | 0 - 1      | 27   | 24.08 |
| <i>Fissurisepta oxia</i>        | 538 - 805  | 4    | 19.07 |
| <i>Fluxinella discula</i>       | 305 - 1796 | 6.5  | 35.68 |
| <i>Folinia bermudezi</i>        | 25 - 73    | 5.2  | 58.70 |
| <i>Fossarus orbigny</i>         | 0 - 40     | 3.5  | 79.81 |
| <i>Fossarus compactus</i>       | 18 - 154   | 2.3  | 25.05 |
| <i>Fusinus blakensis</i>        | 366 - 400  | 89.7 | 65.94 |
| <i>Fusinus halistreptus</i>     | 180 - 618  | 99   | 19.80 |
| <i>Fusinus timessus</i>         | 37 - 465   | 158  | 23.00 |
| <i>Gaza watsoni</i>             | 66 - 1170  | 15   | 52.84 |
| <i>Gaza fischeri</i>            | 604 - 1061 | 30   | 39.04 |
| <i>Gaza superba</i>             | 260 - 1006 | 40   | 32.78 |
| <i>Gemmula periscelida</i>      | 150 - 475  | 40.5 | 33.63 |
| <i>Gibberula lavalleana</i>     | 0 - 73     | 4    | 68.99 |
| <i>Glyphostoma gratulum</i>     | 55 - 1472  | 17.5 | 32.68 |
| <i>Glyphostoma elsae</i>        | 67 - 67    | 14.3 | 18.80 |
| <i>Glyphostoma herminea</i>     | 37 - 165   | 21   | 68.57 |

Appendix 1. (Continued).

|                               |            |      |        |
|-------------------------------|------------|------|--------|
| <i>Glyphostoma gabbii</i>     | 55 - 780   | 17.5 | 77.95  |
| <i>Glyphoturris rugirima</i>  | 2 - 366    | 8    | 76.79  |
| <i>Glyphoturris quadrata</i>  | 0 - 93     | 6.8  | 41.53  |
| <i>Graphis underwoodae</i>    | 0 - 305    | 3.2  | 72.72  |
| <i>Gymnobela edgariana</i>    | 380 - 512  | 64   | 25.66  |
| <i>Gymnobela blakeana</i>     | 620 - 3082 | 12   | 22.39  |
| <i>Gymnobela agassizii</i>    | 71 - 3383  | 47   | 91.15  |
| <i>Hadroconus altus</i>       | 503 - 2276 | 8.2  | 58.27  |
| <i>Haliotnella patinaria</i>  | 24 - 80    | 14   | 32.76  |
| <i>Haliotis pourtalesii</i>   | 36 - 366   | 25   | 36.26  |
| <i>Haminoea petiti</i>        | 1 - 23     | 11.5 | 55.56  |
| <i>Haminoea antillarum</i>    | 0 - 2      | 18   | 106.49 |
| <i>Haminoea elegans</i>       | 0 - 34     | 23.5 | 103.14 |
| <i>Haminoea succinea</i>      | 0 - 55     | 12   | 44.76  |
| <i>Haplocochlias swifti</i>   | 5 - 45     | 3.9  | 24.52  |
| <i>Hastula maryleeae</i>      | 0 - 0      | 25   | 40.71  |
| <i>Hastula cinerea</i>        | 0 - 27     | 68   | 83.93  |
| <i>Hastula hastata</i>        | 0 - 75     | 37   | 80.14  |
| <i>Hastula salleana</i>       | 0 - 0      | 40   | 82.29  |
| <i>Haustellum tryoni</i>      | 33 - 366   | 50   | 39.62  |
| <i>Haustellum cabritii</i>    | 13 - 140   | 78   | 37.44  |
| <i>Haustellum rubidum</i>     | 0 - 105    | 50   | 64.33  |
| <i>Heliacus perrieri</i>      | 0 - 8      | 17   | 84.38  |
| <i>Heliacus cylindricus</i>   | 0 - 46     | 14   | 80.72  |
| <i>Heliacus bisulcatus</i>    | 0 - 366    | 12   | 93.13  |
| <i>Hemitoma emarginata</i>    | 0 - 152    | 25.5 | 37.21  |
| <i>Hemitoma octoradiata</i>   | 0 - 23     | 40   | 73.69  |
| <i>Henrya morrisoni</i>       | 0 - 0      | 1.5  | 21.26  |
| <i>Henrya goldmani</i>        | 0 - 4      | 2.2  | 62.17  |
| <i>Hespererato maugeriae</i>  | 1.5 - 115  | 6    | 82.11  |
| <i>Hindsiclava macilenta</i>  | 174 - 203  | 37   | 32.92  |
| <i>Hipponix benthophila</i>   | 91 - 682   | 8    | 59.08  |
| <i>Hipponix antiquatus</i>    | 0 - 525    | 20   | 99.09  |
| <i>Hipponix subrufus</i>      | 0 - 780    | 13   | 81.52  |
| <i>Homalopoma linnei</i>      | 80 - 1472  | 5.5  | 62.31  |
| <i>Homalopoma albidum</i>     | 64 - 1832  | 8    | 31.30  |
| <i>Homalopoma indutum</i>     | 27 - 5130  | 6.9  | 31.50  |
| <i>Horologica pupa</i>        | 0 - 101    | 4.3  | 37.16  |
| <i>Hyalina pallida</i>        | 0 - 11     | 15.3 | 33.15  |
| <i>Hyalorisia galea</i>       | 342 - 768  | 18.5 | 40.50  |
| <i>Hydatina vesicaria</i>     | 0.2 - 64   | 45   | 98.09  |
| <i>Iniforis turristhoniae</i> | 0 - 101    | 9    | 75.72  |
| <i>Inodrillia pharcida</i>    | 183 - 1832 | 11.8 | 27.41  |

Appendix 1. (Continued).

|                                  |            |      |        |
|----------------------------------|------------|------|--------|
| <i>Inodrillia acloneta</i>       | 311 - 805  | 12   | 24.52  |
| <i>Inodrillia aepynota</i>       | 46 - 227   | 15.6 | 21.50  |
| <i>Iselica globosa</i>           | 0 - 550    | 5.1  | 84.49  |
| <i>Ithycythara cymella</i>       | 128 - 402  | 20   | 35.69  |
| <i>Ithycythara auberiana</i>     | 1 - 100    | 8    | 37.29  |
| <i>Ithycythara rubricata</i>     | 55 - 152   | 6    | 22.20  |
| <i>Ithycythara parkeri</i>       | 1 - 55     | 6    | 31.27  |
| <i>Ithycythara lanceolata</i>    | 0 - 100    | 12   | 87.21  |
| <i>Ithycythara psila</i>         | 88 - 465   | 7.1  | 29.85  |
| <i>Japonactaeon pusillus</i>     | 201 - 823  | 11   | 82.30  |
| <i>Jaspidella blanesi</i>        | 9 - 50     | 10   | 26.38  |
| <i>Jaspidella jaspidea</i>       | 1 - 13     | 23   | 78.98  |
| <i>Kurtziella dorvilliae</i>     | 0 - 50     | 10.5 | 66.53  |
| <i>Kurtziella serga</i>          | 6 - 1966   | 10   | 88.09  |
| <i>Kurtziella citronella</i>     | 26 - 421   | 10.5 | 33.57  |
| <i>Kurtziella atrostyla</i>      | 0 - 88     | 9    | 27.98  |
| <i>Kurtziella cerina</i>         | 1 - 55     | 10   | 33.82  |
| <i>Laevinesta atlantica</i>      | 55 - 238   | 9.5  | 78.55  |
| <i>Lamellaria leucosphaera</i>   | 1 - 11     | 16   | 19.75  |
| <i>Lamellaria perspicua</i>      | 0 - 211    | 20   | 117.08 |
| <i>Lamellitrochus pourtalesi</i> | 293 - 2276 | 10.3 | 20.12  |
| <i>Lamellitrochus inceratus</i>  | 86 - 1472  | 8.2  | 29.41  |
| <i>Lamellitrochus carinatus</i>  | 100 - 366  | 2.9  | 77.08  |
| <i>Lamellitrochus lamellosus</i> | 25 - 250   | 4.2  | 35.11  |
| <i>Latitromitra cryptodon</i>    | 589 - 1500 | 55   | 80.29  |
| <i>Latirus infundibulum</i>      | 2 - 55     | 80   | 76.27  |
| <i>Latirus carinifer</i>         | 0 - 183    | 73   | 80.21  |
| <i>Latirus angulatus</i>         | 0 - 72     | 76.5 | 74.86  |
| <i>Latirus ceramidus</i>         | 95 - 412   | 47   | 32.66  |
| <i>Latitriphora albida</i>       | 0 - 29     | 15   | 20.62  |
| <i>Lepeta caeca</i>              | 4 - 1097   | 18   | 122.64 |
| <i>Leptadrillia cookei</i>       | 0 - 421    | 9.5  | 52.70  |
| <i>Leucosyrinx tenoceras</i>     | 402 - 1324 | 60   | 76.84  |
| <i>Leucosyrinx verrillii</i>     | 274 - 2910 | 36   | 70.44  |
| <i>Leucozonia leucozonalis</i>   | 0 - 0      | 53.7 | 26.51  |
| <i>Leucozonia ocellata</i>       | 0 - 23     | 37.7 | 75.04  |
| <i>Leucozonia nassa</i>          | 0 - 70     | 68.2 | 91.69  |
| <i>Lioglyphostoma oenoa</i>      | 110 - 293  | 9.1  | 16.27  |
| <i>Lioglyphostoma hendersoni</i> | 77 - 421   | 12.4 | 75.58  |
| <i>Lithopoma tuber</i>           | 0 - 30     | 75   | 28.30  |
| <i>Lithopoma caelatum</i>        | 0 - 44     | 100  | 38.88  |
| <i>Lithopoma americanum</i>      | 0 - 33     | 40   | 40.77  |
| <i>Litiopa melanostoma</i>       | 0 - 805    | 6    | 85.66  |



Appendix 1. (Continued).

|                                   |          |      |        |
|-----------------------------------|----------|------|--------|
| <i>Littoraria tessellata</i>      | 0 - 0    | 23   | 26.63  |
| <i>Littoraria nebulosa</i>        | -1 - 0   | 28   | 49.42  |
| <i>Littoraria angulifera</i>      | -1 - 0   | 41   | 113.86 |
| <i>Littoridinops monroensis</i>   | 0 - 0.3  | 4.5  | 18.12  |
| <i>Lodderena pulchella</i>        | 1 - 100  | 0.84 | 60.98  |
| <i>Lodderena ornata</i>           | 0 - 18   | 0.8  | 84.21  |
| <i>Lottia leucopleura</i>         | -1 - 3   | 19   | 33.36  |
| <i>Lucapina sowerbii</i>          | 0 - 45   | 30   | 82.16  |
| <i>Lucapina philippiana</i>       | 0 - 110  | 18   | 77.01  |
| <i>Lucapina aegis</i>             | 0 - 55   | 36   | 83.80  |
| <i>Lucapina suffusa</i>           | 0 - 24   | 36   | 83.02  |
| <i>Lucapinella limatula</i>       | 0 - 146  | 18   | 104.02 |
| <i>Luria cinerea</i>              | 0 - 1472 | 45   | 85.62  |
| <i>Macrocypraea cervus</i>        | 0 - 35   | 190  | 35.74  |
| <i>Macrocypraea zebra</i>         | 0 - 37   | 133  | 86.25  |
| <i>Macromphalina floridana</i>    | 1 - 34.5 | 3.1  | 26.38  |
| <i>Macromphalina palmalitoris</i> | 11 - 161 | 2.9  | 34.34  |
| <i>Mancinella deltoidea</i>       | 0 - 12   | 52   | 86.08  |
| <i>Manzonina caribaea</i>         | *        | 3    | 67.53  |
| <i>Marshallora modesta</i>        | 1 - 20   | 5.7  | 21.84  |
| <i>Marshallora nigrocincta</i>    | 0 - 70   | 8    | 88.61  |
| <i>Mathilda hendersoni</i>        | 46 - 100 | 10   | 36.40  |
| <i>Mathilda barbadensis</i>       | 2 - 183  | 8    | 37.35  |
| <i>Mathilda scitula</i>           | 18 - 150 | 8    | 78.88  |
| <i>Megalomphalus troudei</i>      | 0 - 34   | 2.8  | 55.37  |
| <i>Megalomphalus pilsbryi</i>     | 0 - 50   | 3    | 31.27  |
| <i>Megalomphalus oxychone</i>     | 0 - 26   | 4    | 75.55  |
| <i>Meioceras cornucopiae</i>      | 0 - 37   | 2.5  | 73.75  |
| <i>Meioceras nitidum</i>          | 0 - 24   | 3.1  | 90.63  |
| <i>Meioceras cubitatum</i>        | 0 - 183  | 2    | 75.31  |
| <i>Melanella eulimoides</i>       | 0.6 - 94 | 16   | 70.36  |
| <i>Melanella hypsela</i>          | 15 - 525 | 8    | 84.41  |
| <i>Melanella conoidea</i>         | 0 - 538  | 10   | 94.04  |
| <i>Melanella gracilis</i>         | *        | 6.1  | 33.80  |
| <i>Melanella jamaicensis</i>      | 0 - 366  | 12.5 | 89.27  |
| <i>Melanella perversa</i>         | 0 - 210  | 4.5  | 33.72  |
| <i>Melanella oleacea</i>          | 7 - 17   | 6.3  | 30.99  |
| <i>Metaxia excelsa</i>            | 6 - 101  | 6.2  | 80.64  |
| <i>Metaxia rugulosa</i>           | 0 - 128  | 6.1  | 37.90  |
| <i>Metaxia abrupta</i>            | 22 - 183 | 6.3  | 73.80  |
| <i>Metaxia metaxa</i>             | 4 - 366  | 5.5  | 84.13  |
| <i>Metula agassizi</i>            | 50 - 594 | 37.3 | 80.28  |
| <i>Metulella columbellata</i>     | 24 - 227 | 15   | 61.59  |

Appendix 1. (Continued).

|                                  |           |      |        |
|----------------------------------|-----------|------|--------|
| <i>Microgaza rotella</i>         | 45 - 1472 | 6.8  | 37.96  |
| <i>Micromelo undatus</i>         | 0 - 5     | 17   | 82.96  |
| <i>Mirachelus clinocnemus</i>    | 40 - 250  | 4.5  | 76.76  |
| <i>Mirachelus corbis</i>         | 75 - 1426 | 5    | 31.49  |
| <i>Miralda havanensis</i>        | 0 - 0     | 1.95 | 66.49  |
| <i>Miralda abbotti</i>           | 0 - 101   | 2.6  | 31.77  |
| <i>Mitra pallida</i>             | *         | 39   | 24.74  |
| <i>Mitra barbadensis</i>         | 0 - 82    | 44   | 90.43  |
| <i>Mitra straminea</i>           | 4 - 329   | 31   | 74.97  |
| <i>Mitra antillensis</i>         | 55 - 780  | 80   | 79.37  |
| <i>Mitra nodulosa</i>            | 0 - 55    | 50   | 79.58  |
| <i>Mitrella antares</i>          | 10 - 90   | 3.6  | 67.90  |
| <i>Mitrella dichroa</i>          | 0 - 8     | 8.5  | 81.42  |
| <i>Mitrella ocellata</i>         | 0 - 15    | 13   | 106.98 |
| <i>Mitrolumna biplicata</i>      | 10 - 805  | 8    | 77.15  |
| <i>Mitromica foveata</i>         | 0 - 34    | 8.3  | 27.55  |
| <i>Modulus carchedonius</i>      | 0 - 29    | 17   | 68.23  |
| <i>Modulus modulus</i>           | 0 - 105   | 16.5 | 89.81  |
| <i>Moelleriopsis sincera</i>     | 538 - 805 | 3.3  | 44.99  |
| <i>Monostiolum tessellatum</i>   | 1 - 42    | 18   | 49.94  |
| <i>Morum lamarckii</i>           | 12 - 12   | 28   | 28.27  |
| <i>Morum oniscus</i>             | 0 - 72    | 25   | 79.62  |
| <i>Morum dennisoni</i>           | 30 - 370  | 54   | 76.54  |
| <i>Murchisonella bermudensis</i> | 0 - 73    | 3.8  | 72.01  |
| <i>Murexiella glypta</i>         | 7 - 52    | 25.3 | 75.27  |
| <i>Murexiella macgintyi</i>      | 0 - 183   | 40   | 70.55  |
| <i>Murexiella hidalgoi</i>       | 75 - 780  | 38   | 85.79  |
| <i>Muricopsis oxytata</i>        | 1 - 64    | 40   | 37.67  |
| <i>Mysouffa cumingii</i>         | 10 - 366  | 20   | 70.69  |
| <i>Nannodiella vespuciana</i>    | 0 - 93    | 6    | 46.80  |
| <i>Nannodiella oxia</i>          | 0 - 91    | 5    | 25.99  |
| <i>Nanobalcis worsfoldi</i>      | 0 - 73    | 2.3  | 19.53  |
| <i>Nassarina metabrunnea</i>     | 80 - 600  | 8    | 60.10  |
| <i>Nassarina bushiae</i>         | 27 - 278  | 9.15 | 25.61  |
| <i>Nassarina glypta</i>          | 7 - 805   | 5.8  | 27.39  |
| <i>Nassarius antillarum</i>      | 57 - 57   | 12   | 50.34  |
| <i>Nassarius polygonatus</i>     | 0 - 0     | 16   | 39.26  |
| <i>Nassarius candidissimus</i>   | *         | 11.4 | 27.04  |
| <i>Nassarius albus</i>           | 0 - 58    | 12   | 86.66  |
| <i>Nassarius consensus</i>       | 6 - 80    | 14.6 | 35.16  |
| <i>Nassarius hotessierianus</i>  | 64 - 164  | 5.5  | 30.61  |
| <i>Nassarius acutus</i>          | 2 - 110   | 15   | 30.44  |
| <i>Nassarius vibex</i>           | 0 - 31    | 20   | 93.23  |

Appendix 1. (Continued).

|                              |             |      |        |
|------------------------------|-------------|------|--------|
| <i>Natica perlineata</i>     | 128 - 419   | 18.5 | 24.95  |
| <i>Natica tedbayeri</i>      | 0 - 50      | 22   | 56.97  |
| <i>Natica menkeana</i>       | 9 - 256     | 18   | 73.17  |
| <i>Natica marochiensis</i>   | 0 - 94      | 40   | 108.07 |
| <i>Natica guesti</i>         | 165 - 421   | 33   | 36.93  |
| <i>Natica livida</i>         | 0 - 20      | 21   | 94.80  |
| <i>Naticarius canrena</i>    | 0 - 101     | 65   | 89.47  |
| <i>Nerita fulgurans</i>      | 0 - 0       | 32   | 72.88  |
| <i>Nerita peloronta</i>      | 0 - 0       | 47   | 39.68  |
| <i>Nerita tessellata</i>     | 0 - 3       | 25   | 61.21  |
| <i>Nerita versicolor</i>     | -1 - 0      | 26   | 37.82  |
| <i>Neritina clenchi</i>      | 0 - 0       | 20.1 | 33.67  |
| <i>Neritina virginea</i>     | 0 - 1.5     | 25   | 86.30  |
| <i>Neritina usnea</i>        | 0 - 1.5     | 24   | 44.14  |
| <i>Neverita duplicata</i>    | 0 - 58      | 82   | 35.88  |
| <i>Niso hendersoni</i>       | 27 - 203    | 27.8 | 32.93  |
| <i>Niso aeglees</i>          | 0 - 260     | 21   | 92.34  |
| <i>Nitidella nitida</i>      | 0 - 2       | 16   | 70.48  |
| <i>Nototriphora decorata</i> | 0 - 104     | 12   | 94.27  |
| <i>Oceanida graduata</i>     | 0 - 122     | 3    | 95.79  |
| <i>Odostomia laevigata</i>   | 0 - 40      | 5    | 96.07  |
| <i>Odostomia unidentata</i>  | 115 - 640   | 4    | 63.11  |
| <i>Oliva scripta</i>         | 8 - 66      | 47   | 61.59  |
| <i>Oliva formosa</i>         | 0.5 - 200   | 62.5 | 58.22  |
| <i>Oliva reticularis</i>     | 0 - 40      | 45   | 36.72  |
| <i>Oliva sayana</i>          | 0 - 130     | 91   | 27.32  |
| <i>Olivella rotunda</i>      | 11 - 1472   | 25   | 32.37  |
| <i>Olivella acteocina</i>    | 25 - 25     | 4    | 32.12  |
| <i>Olivella dealbata</i>     | 0 - 15      | 14   | 38.63  |
| <i>Olivella minuta</i>       | 0 - 13      | 15   | 79.08  |
| <i>Olivella rosolina</i>     | *           | 8.2  | 29.41  |
| <i>Olivella bullula</i>      | 30 - 538    | 11   | 36.16  |
| <i>Olivella lactea</i>       | 0 - 40      | 13   | 29.14  |
| <i>Olivella perplexa</i>     | 1 - 58      | 5    | 31.85  |
| <i>Olivella watermani</i>    | 22 - 525    | 13.5 | 84.63  |
| <i>Olivella nivea</i>        | 0 - 60      | 34   | 84.78  |
| <i>Olivella floralia</i>     | 0 - 70      | 15   | 80.61  |
| <i>Olivella mutica</i>       | 0 - 156     | 17.2 | 50.21  |
| <i>Oocorys clerica</i>       | 346 - 1554  | 92   | 17.42  |
| <i>Oocorys barbouri</i>      | 238 - 1829  | 65   | 9.86   |
| <i>Oocorys cancellata</i>    | 1125 - 2926 | 47   | 55.71  |
| <i>Oocorys sulcata</i>       | 161 - 5073  | 55   | 91.66  |
| <i>Opalia abbotti</i>        | 64 - 704    | 4.5  | 81.54  |

Appendix 1. (Continued).

|                                   |            |      |        |
|-----------------------------------|------------|------|--------|
| <i>Opalia crenata</i>             | 0.3 - 82   | 22   | 68.46  |
| <i>Opalia eolis</i>               | 77 - 238   | 13   | 25.98  |
| <i>Opalia hotessieriana</i>       | 0 - 165    | 14   | 73.34  |
| <i>Opalia burryi</i>              | 30 - 168   | 15.2 | 27.68  |
| <i>Opalia morchiana</i>           | 12 - 183   | 12   | 38.89  |
| <i>Opalia pumilio</i>             | 0 - 183    | 15   | 74.54  |
| <i>Opalia aurifila</i>            | 91 - 311   | 11   | 30.26  |
| <i>Opaliopsis atlantis</i>        | 115 - 485  | 14   | 76.34  |
| <i>Opaliopsis opalina</i>         | 538 - 1256 | 25   | 23.43  |
| <i>Orbitestella bermudezi</i>     | 8 - 15     | 0.74 | 24.36  |
| <i>Ovulactaeon meekii</i>         | 366 - 823  | 5.5  | 62.36  |
| <i>Palazzia planorbis</i>         | 538 - 2966 | 2.2  | 90.04  |
| <i>Parvanachis obesa</i>          | 0 - 68     | 6    | 94.69  |
| <i>Parviphos adelus</i>           | 36 - 80    | 16.5 | 27.41  |
| <i>Parviturbo weberi</i>          | 1 - 52     | 1.7  | 67.79  |
| <i>Parviturbo rehderi</i>         | 0 - 40     | 1.7  | 59.15  |
| <i>Parviturboides interruptus</i> | 0 - 91     | 1.9  | 84.86  |
| <i>Patelloida pustulata</i>       | 0 - 51     | 25   | 44.06  |
| <i>Paziella hystricina</i>        | 165 - 552  | 21   | 24.69  |
| <i>Pazinotus stimpsonii</i>       | 52 - 1832  | 12   | 67.65  |
| <i>Pedicularia decussata</i>      | 49 - 1170  | 13   | 44.24  |
| <i>Peristichia agria</i>          | 0 - 115    | 6    | 80.44  |
| <i>Perotrochus lucaya</i>         | 275 - 427  | 59   | 19.39  |
| <i>Perotrochus amabilis</i>       | 100 - 411  | 93   | 74.11  |
| <i>Persicula catenata</i>         | 0 - 168    | 7    | 61.06  |
| <i>Persicula pulcherrima</i>      | 0 - 80     | 9    | 61.00  |
| <i>Petaloconchus mcgintyi</i>     | 2 - 61     | 35   | 62.54  |
| <i>Petaloconchus nigricans</i>    | 0 - 0      | 60   | 22.87  |
| <i>Petaloconchus floridanus</i>   | 0 - 73     | 31   | 27.22  |
| <i>Petaloconchus erectus</i>      | 2 - 1400   | 40   | 69.89  |
| <i>Petaloconchus varians</i>      | 0 - 0      | 200  | 83.67  |
| <i>Petitilla crosseana</i>        | 0 - 0      | 3    | 21.64  |
| <i>Phenacovolva piragua</i>       | 42 - 70    | 23   | 19.99  |
| <i>Philine infundibulum</i>       | 68 - 724   | 12   | 45.27  |
| <i>Philine alba</i>               | 46 - 300   | 23   | 63.70  |
| <i>Philine sagra</i>              | 2 - 86     | 6    | 66.55  |
| <i>Phyllonotus oculatus</i>       | 1 - 10     | 80   | 65.06  |
| <i>Phyllonotus pomum</i>          | 0 - 73     | 133  | 74.21  |
| <i>Pilsbryspira albocincta</i>    | 0 - 11     | 14   | 27.67  |
| <i>Pilsbryspira albomaculata</i>  | 0 - 42     | 11   | 34.58  |
| <i>Pilsbryspira jayana</i>        | 42 - 42    | 12.7 | 28.53  |
| <i>Pilsbryspira leucocyma</i>     | 0 - 20     | 14   | 79.49  |
| <i>Pisania pusio</i>              | 0 - 63     | 48   | 103.09 |

Appendix 1. (Continued).

|                                     |            |      |        |
|-------------------------------------|------------|------|--------|
| <i>Platycythara elata</i>           | 11 - 73    | 4.8  | 21.99  |
| <i>Plesiothyreus rushii</i>         | 0 - 55     | 10   | 30.36  |
| <i>Plesiothyreus hamillei</i>       | 0 - 3      | 8    | 83.05  |
| <i>Pleuromalaxis balesi</i>         | 0 - 100    | 1.8  | 35.30  |
| <i>Pleurotomella ipara</i>          | 72 - 1170  | 7    | 71.59  |
| <i>Plicopurpura patula</i>          | 0 - 2      | 85   | 41.33  |
| <i>Poirieria actinophora</i>        | 100 - 714  | 24   | 39.82  |
| <i>Polinices hepaticus</i>          | 0 - 55     | 51   | 83.62  |
| <i>Polinices leptaleus</i>          | 538 - 1170 | 8.9  | 20.49  |
| <i>Polinices lacteus</i>            | 0 - 120    | 40   | 115.94 |
| <i>Polinices porcellanus</i>        | 27 - 183   | 25   | 97.67  |
| <i>Pollia karinae</i>               | 9 - 63     | 23   | 73.87  |
| <i>Pollia auritula</i>              | 0 - 29     | 35   | 84.43  |
| <i>Pollia tinctoria</i>             | 0 - 80     | 32   | 66.26  |
| <i>Polygireulima amblytera</i>      | *          | 5.5  | 26.61  |
| <i>Polystira vibex</i>              | 73 - 366   | 60   | 21.52  |
| <i>Polystira albida</i>             | 15 - 229   | 116  | 53.59  |
| <i>Polystira florencae</i>          | 1 - 219    | 25   | 28.63  |
| <i>Profundisepta circularis</i>     | 538 - 1609 | 7    | 30.91  |
| <i>Profundisepta sportella</i>      | 183 - 1097 | 4.5  | 20.13  |
| <i>Profundisepta profundi</i>       | 538 - 2652 | 6    | 79.18  |
| <i>Propilidium reticulatum</i>      | 128 - 538  | 2.6  | 26.12  |
| <i>Propustularia surinamensis</i>   | 7 - 780    | 48   | 74.29  |
| <i>Prunum carneum</i>               | 0 - 40     | 18   | 33.77  |
| <i>Prunum torticulum</i>            | 69 - 538   | 11.5 | 20.77  |
| <i>Prunum amabile</i>               | 0 - 229    | 25   | 63.41  |
| <i>Prunum apicinum</i>              | 0 - 25     | 14   | 36.05  |
| <i>Pseudocyphoma intermedium</i>    | 0 - 128    | 50   | 86.56  |
| <i>Pseudomalaxis zancleus</i>       | 128 - 234  | 11.6 | 72.70  |
| <i>Pseudorotella parvicallum</i>    | 0 - 91     | 2    | 38.30  |
| <i>Pseudorotella goniogyrus</i>     | 11 - 101   | 2    | 31.49  |
| <i>Pseudorotella incerta</i>        | 11 - 55    | 2    | 68.35  |
| <i>Pseudorotella coccolitoris</i>   | 18 - 122   | 3    | 68.47  |
| <i>Pseudoscilla decorata</i>        | 0 - 91     | 2    | 36.96  |
| <i>Pseudoscilla babylonia</i>       | 0 - 123    | 2.5  | 77.29  |
| <i>Pseudosimnia vanhyningi</i>      | 46 - 183   | 14   | 74.34  |
| <i>Pseudostomatella erythrocoma</i> | 99 - 99    | 6.5  | 27.91  |
| <i>Pseudotorinia bullisi</i>        | 82 - 137   | 10.2 | 32.49  |
| <i>Pseudotorinia architae</i>       | 82 - 82    | 10   | 107.59 |
| <i>Psilaxis krebsii</i>             | 9 - 116    | 10.5 | 87.95  |
| <i>Pterotyphis pinnatus</i>         | 2 - 50     | 34   | 22.41  |
| <i>Pugnus serrei</i>                | 0 - 6      | 1.5  | 28.80  |
| <i>Puncturella plecta</i>           | 538 - 713  | 6.4  | 19.07  |

Appendix 1. (Continued).

|                                     |            |      |        |
|-------------------------------------|------------|------|--------|
| <i>Puperita pupa</i>                | 0 - 0      | 10.6 | 35.33  |
| <i>Pyramidella dolabrata</i>        | 0 - 57     | 36   | 97.05  |
| <i>Pyramidella suturalis</i>        | 0 - 49     | 14   | 40.31  |
| <i>Pyramidella candida</i>          | 0 - 350    | 14   | 59.51  |
| <i>Pyrgocythara filosa</i>          | 8 - 15     | 6.5  | 18.34  |
| <i>Pyrgocythara caribaea</i>        | 0 - 2      | 5.6  | 80.69  |
| <i>Pyrgocythara plicosa</i>         | 0 - 22     | 13.2 | 41.70  |
| <i>Pyrgophorus parvulus</i>         | 0 - 1.8    | 3.5  | 27.66  |
| <i>Pyrgospira ostrearum</i>         | 0 - 165    | 23   | 76.06  |
| <i>Pyrgospira tampaensis</i>        | 0 - 165    | 32   | 55.47  |
| <i>Pyrunculus caelatus</i>          | 5 - 155    | 4.2  | 90.04  |
| <i>Pyrunculus ovatus</i>            | 640 - 640  | 3    | 96.52  |
| <i>Rapana venosa</i>                | 10 - 60    | 161  | 75.26  |
| <i>Retilaskya bicolor</i>           | 0 - 65     | 20   | 87.60  |
| <i>Retusa sulcata</i>               | 5 - 174    | 3    | 43.77  |
| <i>Rhombinella laevigata</i>        | 0 - 23     | 20   | 37.82  |
| <i>Rictaxis punctostriatus</i>      | 0 - 110    | 7.5  | 48.91  |
| <i>Rimosodaphnella morra</i>        | 9 - 823    | 8    | 82.12  |
| <i>Rimula pycnonema</i>             | 15 - 265   | 4.3  | 26.37  |
| <i>Rimula aequisculpta</i>          | 22 - 243   | 7.4  | 39.53  |
| <i>Rimula frenulata</i>             | 0 - 400    | 8    | 53.67  |
| <i>Ringicula semistriata</i>        | 42 - 465   | 3    | 38.04  |
| <i>Ringicula nitida</i>             | 110 - 1966 | 7.5  | 107.95 |
| <i>Risomurex caribbaeus</i>         | 0 - 219    | 15.2 | 31.92  |
| <i>Risomurex roseus</i>             | 1 - 18     | 15   | 28.26  |
| <i>Rissoella caribaea</i>           | 0 - 12     | 1.8  | 51.96  |
| <i>Rissoella galba</i>              | 0 - 2      | 0.7  | 20.74  |
| <i>Rissoina sagraiana</i>           | *          | 5.7  | 39.50  |
| <i>Rissoina striosa</i>             | 0 - 1      | 8    | 62.63  |
| <i>Rissoina elegantissima</i>       | 0 - 128    | 3.6  | 41.23  |
| <i>Rissoina multicostata</i>        | 0 - 525    | 5.2  | 82.96  |
| <i>Rissoina cancellata</i>          | 0.5 - 106  | 8    | 76.30  |
| <i>Rissoina dyscrita</i>            | *          | 6    | 23.22  |
| <i>Rissoina decussata</i>           | 0 - 106    | 9.7  | 75.45  |
| <i>Rissopsetia hummelincki</i>      | 0 - 1.2    | 1.8  | 30.96  |
| <i>Rubellatoma rubella</i>          | 11 - 146   | 11   | 76.26  |
| <i>Runcina divae</i>                | 1 - 2      | 0.2  | 62.86  |
| <i>Sabinella troglodytes</i>        | 1 - 46     | 4.1  | 22.50  |
| <i>Saccharoturris monocingulata</i> | 183 - 402  | 6.8  | 23.85  |
| <i>Sansonia tuberculata</i>         | 5 - 713    | 2.5  | 35.97  |
| <i>Satondella tabulata</i>          | 35 - 713   | 2.1  | 14.00  |
| <i>Sayella fusca</i>                | 0 - 25     | 6    | 41.10  |
| <i>Scalenostoma subulatum</i>       | 0 - 58     | 22   | 76.47  |

Appendix 1. (Continued).

|                                   |             |      |        |
|-----------------------------------|-------------|------|--------|
| <i>Scaphander darius</i>          | 18 - 374    | 23   | 67.50  |
| <i>Scaphander watsoni</i>         | 44 - 649    | 42.5 | 42.11  |
| <i>Scaphander bathymophila</i>    | 713 - 3964  | 39   | 48.77  |
| <i>Scaphander nobilis</i>         | 1000 - 3012 | 38   | 118.75 |
| <i>Scaphander punctostriatus</i>  | 20 - 2683   | 36   | 107.26 |
| <i>Schwartziella vanpeli</i>      | 10 - 82     | 3.8  | 62.55  |
| <i>Schwartziella bryerea</i>      | 2 - 34      | 5.8  | 105.03 |
| <i>Schwartziella catesbyana</i>   | 0 - 40      | 4.6  | 87.67  |
| <i>Schwartziella chesnelii</i>    | 4 - 57      | 6    | 41.16  |
| <i>Schwartziella fischeri</i>     | 0 - 55      | 4.5  | 83.96  |
| <i>Sconsia striata</i>            | 27 - 640    | 67   | 73.29  |
| <i>Seguenzia hapala</i>           | 80 - 150    | 2.1  | 63.63  |
| <i>Seila adamsii</i>              | 0 - 80      | 13   | 98.83  |
| <i>Semicassis cicatricosa</i>     | 0 - 6       | 60   | 64.48  |
| <i>Semicassis granulata</i>       | 0 - 97      | 121  | 108.73 |
| <i>Serpulorbis decussatus</i>     | 0 - 80      | 90   | 82.24  |
| <i>Sigatica semisulcata</i>       | 0 - 60      | 15   | 29.18  |
| <i>Similiphora intermedia</i>     | 0 - 102     | 7.8  | 91.74  |
| <i>Simnialena uniplicata</i>      | 1 - 116     | 21   | 74.06  |
| <i>Sinezona confusa</i>           | 0 - 56      | 1.5  | 80.22  |
| <i>Sinum maculatum</i>            | 0.3 - 70    | 34   | 88.64  |
| <i>Sinum perspectivum</i>         | 0 - 70      | 51   | 91.35  |
| <i>Siphonochelus riosi</i>        | 75 - 722    | 12   | 70.77  |
| <i>Siratus articulatus</i>        | 16 - 400    | 93   | 51.03  |
| <i>Siratus cailleti</i>           | 46 - 400    | 67   | 24.19  |
| <i>Siratus formosus</i>           | 12 - 213    | 80   | 57.49  |
| <i>Siratus consuela</i>           | 14 - 250    | 79   | 80.04  |
| <i>Siratus beauui</i>             | 24 - 463    | 121  | 79.58  |
| <i>Smaragdia viridis</i>          | 0 - 20      | 8    | 132.55 |
| <i>Solariella multirestis</i>     | 201 - 251   | 11.8 | 22.79  |
| <i>Solariella cristata</i>        | 201 - 256   | 9.5  | 27.98  |
| <i>Solariella lubrica</i>         | 73 - 1472   | 4    | 74.56  |
| <i>Solariella tiara</i>           | 558 - 1966  | 5.6  | 23.76  |
| <i>Solariella lacunella</i>       | 18 - 1472   | 8.7  | 31.56  |
| <i>Solariorbis infracarinatus</i> | 0 - 66      | 2    | 71.69  |
| <i>Solariorbis mooreanus</i>      | 0 - 20      | 2.8  | 72.95  |
| <i>Solariorbis bartschi</i>       | *           | 2    | 73.32  |
| <i>Solariorbis multistriatus</i>  | 5 - 260     | 4.5  | 47.48  |
| <i>Solatisonax borealis</i>       | 183 - 805   | 12   | 29.75  |
| <i>Spirolaxis centrifuga</i>      | 34 - 550    | 4.3  | 107.19 |
| <i>Spirotropis stirophora</i>     | 85 - 640    | 7.6  | 71.17  |
| <i>Splendrillia lissotropis</i>   | 30 - 453    | 7    | 65.55  |
| <i>Splendrillia woodringi</i>     | 37 - 188    | 18.2 | 49.24  |

Appendix 1. (Continued).

|                                 |            |       |        |
|---------------------------------|------------|-------|--------|
| <i>Splendrillia moseri</i>      | 5 - 90     | 30    | 60.69  |
| <i>Steironepion moniliferum</i> | 0 - 82     | 5.1   | 36.09  |
| <i>Steironepion minus</i>       | 0 - 219    | 6     | 72.44  |
| <i>Stellatoma stellata</i>      | 2 - 2      | 8.9   | 71.09  |
| <i>Stenodrillia horrenda</i>    | 396 - 640  | 62    | 57.50  |
| <i>Sthenorytis pernobilis</i>   | 91 - 1472  | 43    | 31.32  |
| <i>Stigmaulax cancellatus</i>   | 35 - 70    | 24    | 74.10  |
| <i>Stigmaulax sulcatus</i>      | 0 - 44     | 38    | 34.58  |
| <i>Stosicia aberrans</i>        | 0 - 93     | 6     | 78.44  |
| <i>Stramonita rustica</i>       | 0 - 4      | 50    | 91.50  |
| <i>Stramonita haemastoma</i>    | 0 - 538    | 112.5 | 119.78 |
| <i>Strictispira solida</i>      | 2 - 2      | 17.3  | 28.16  |
| <i>Strobiligera bigemma</i>     | 538 - 1170 | 15.2  | 24.29  |
| <i>Strobiligera inflata</i>     | 538 - 1170 | 11    | 24.91  |
| <i>Strombus pugilis</i>         | 0 - 55     | 110   | 72.91  |
| <i>Strombus gallus</i>          | 0.3 - 82   | 197   | 75.68  |
| <i>Strombus gigas</i>           | 0.3 - 25   | 352   | 41.37  |
| <i>Strombus raninus</i>         | 0.3 - 55   | 121   | 69.66  |
| <i>Strombus costatus</i>        | 2 - 55     | 231   | 85.17  |
| <i>Supplanaxis nucleus</i>      | 0 - 3      | 13    | 35.71  |
| <i>Suturoglypta pretrii</i>     | 15 - 33    | 10.5  | 32.65  |
| <i>Synaptocochlea picta</i>     | 0 - 525    | 7     | 99.21  |
| <i>Tectarius antonii</i>        | -2 - 0     | 21    | 26.58  |
| <i>Tectonatica pusilla</i>      | 0 - 130    | 8     | 88.86  |
| <i>Tectura antillarum</i>       | 0 - 0      | 25    | 39.13  |
| <i>Tegula gruneri</i>           | *          | 10    | 23.01  |
| <i>Tegula excavata</i>          | 0 - 1      | 18    | 36.14  |
| <i>Tegula hotessieriana</i>     | 0 - 10     | 12.7  | 36.10  |
| <i>Tegula lividomaculata</i>    | 0 - 2      | 20    | 37.80  |
| <i>Tegula fasciata</i>          | 0 - 90     | 20    | 80.53  |
| <i>Teinostoma clavium</i>       | 0 - 18     | 2.3   | 30.64  |
| <i>Teinostoma biscaynense</i>   | 0 - 500    | 2.2   | 36.71  |
| <i>Teinostoma lerema</i>        | 0 - 48     | 1.4   | 38.12  |
| <i>Teinostoma megastoma</i>     | 0 - 123    | 2.5   | 79.21  |
| <i>Teinostoma umbilicatum</i>   | 18 - 305   | 2.5   | 36.35  |
| <i>Tenagodus modestus</i>       | 37 - 1463  | 100   | 75.91  |
| <i>Tenagodus squamatus</i>      | 11 - 732   | 150   | 84.48  |
| <i>Tenaturris inepta</i>        | 0 - 823    | 15    | 80.60  |
| <i>Terebra acrior</i>           | 183 - 183  | 8     | 25.50  |
| <i>Terebra alba</i>             | *          | 15    | 37.79  |
| <i>Terebra glossema</i>         | 2 - 13     | 28    | 19.40  |
| <i>Terebra taurina</i>          | 1 - 80     | 178   | 84.77  |
| <i>Terebra nassula</i>          | 153 - 1170 | 68    | 34.13  |



Appendix 1. (Continued).

|                                   |            |      |        |
|-----------------------------------|------------|------|--------|
| <i>Terebra protexta</i>           | 1 - 106    | 28   | 84.36  |
| <i>Terebra concava</i>            | 7 - 113    | 25   | 72.73  |
| <i>Terebra dislocata</i>          | 0 - 146    | 64   | 74.40  |
| <i>Terelatirus cayohuesonicus</i> | 0 - 5      | 19   | 23.73  |
| <i>Thaleia nisonis</i>            | 50 - 1930  | 9    | 74.37  |
| <i>Thelecythara floridana</i>     | 20 - 25    | 9    | 38.38  |
| <i>Thelecythara mucronata</i>     | 0 - 50     | 8.6  | 57.81  |
| <i>Theta chariessa</i>            | 384 - 4791 | 52   | 67.37  |
| <i>Tomura bicaudata</i>           | 0 - 0      | 1.5  | 16.46  |
| <i>Tonna pennata</i>              | 0 - 13     | 158  | 92.81  |
| <i>Tonna galea</i>                | 0 - 185    | 180  | 121.36 |
| <i>Torcula acropora</i>           | 5.5 - 755  | 42   | 22.61  |
| <i>Torcula exoleta</i>            | 2 - 183    | 75   | 87.72  |
| <i>Trachypollia sclera</i>        | 15 - 46    | 16.3 | 29.21  |
| <i>Trachypollia nodulosa</i>      | 0 - 21     | 20   | 114.82 |
| <i>Trachypollia turricula</i>     | 0 - 525    | 15   | 86.95  |
| <i>Trichotropis migrans</i>       | 65 - 366   | 10   | 43.05  |
| <i>Trigonostoma rugosum</i>       | 0 - 25     | 25   | 17.36  |
| <i>Triphora pompona</i>           | 150 - 805  | 20   | 61.79  |
| <i>Triphora longissima</i>        | 73 - 1040  | 26   | 69.84  |
| <i>Triphora triserialis</i>       | 55 - 1472  | 11   | 34.25  |
| <i>Triptychus niveus</i>          | 0 - 46     | 9.5  | 36.79  |
| <i>Tritonoharpa lanceolata</i>    | 0 - 178    | 38   | 86.77  |
| <i>Trivia leucosphaera</i>        | 0 - 0      | 6    | 41.62  |
| <i>Trivia suffusa</i>             | 0 - 525    | 12   | 85.98  |
| <i>Trivia quadripunctata</i>      | 0 - 51     | 10   | 35.18  |
| <i>Trivia nix</i>                 | 15 - 116   | 11.5 | 57.31  |
| <i>Trivia antillarum</i>          | 9 - 549    | 6    | 82.27  |
| <i>Trivia candidula</i>           | 3 - 780    | 7.9  | 87.11  |
| <i>Trivia maltbiana</i>           | 2 - 91     | 13   | 75.22  |
| <i>Trivia pediculus</i>           | 0 - 129    | 15.8 | 83.09  |
| <i>Trophon lacunellus</i>         | 366 - 1406 | 41   | 33.21  |
| <i>Truncadaphne chrysoleuca</i>   | 18 - 274   | 7.5  | 20.28  |
| <i>Truncatella caribaeensis</i>   | 0 - 1.5    | 9    | 41.08  |
| <i>Truncatella pulchella</i>      | 0 - 0      | 6.5  | 70.26  |
| <i>Turbinella angulata</i>        | 0 - 45     | 360  | 25.23  |
| <i>Turbo cailletii</i>            | 4 - 35     | 37   | 32.77  |
| <i>Turbo canaliculatus</i>        | 2 - 300    | 98   | 70.36  |
| <i>Turbo haraldi</i>              | 50 - 100   | 25   | 25.84  |
| <i>Turbo castanea</i>             | 0 - 141    | 55   | 67.67  |
| <i>Turbonilla riisei</i>          | 11 - 11    | 4.5  | 21.43  |
| <i>Turbonilla belothea</i>        | 37 - 183   | 14   | 32.65  |
| <i>Turbonilla elegans</i>         | 0 - 4      | 3.5  | 39.09  |

Appendix 1. (Continued).

|                               |           |      |        |
|-------------------------------|-----------|------|--------|
| <i>Turbonilla penistoni</i>   | 3 - 12    | 7    | 18.86  |
| <i>Turbonilla pupoides</i>    | 4 - 51    | 5.5  | 33.39  |
| <i>Turbonilla stimpsoni</i>   | *         | 5.4  | 26.93  |
| <i>Turbonilla coomansi</i>    | 0 - 538   | 3.4  | 69.66  |
| <i>Turbonilla curta</i>       | 0 - 1170  | 8.3  | 30.69  |
| <i>Turbonilla dalli</i>       | 0 - 6     | 12   | 22.63  |
| <i>Turbonilla exilis</i>      | 5 - 115   | 4.2  | 24.25  |
| <i>Turbonilla levis</i>       | 27 - 196  | 4.6  | 28.67  |
| <i>Turbonilla peilei</i>      | 2 - 115   | 6    | 26.52  |
| <i>Turbonilla puncta</i>      | 0 - 52    | 5.6  | 25.01  |
| <i>Turbonilla textilis</i>    | 3.5 - 26  | 3.6  | 28.67  |
| <i>Turbonilla virga</i>       | 0 - 27    | 9    | 26.93  |
| <i>Turbonilla unilirata</i>   | 29 - 29   | 5    | 34.58  |
| <i>Turbonilla reticulata</i>  | 33 - 33   | 3.2  | 29.91  |
| <i>Turbonilla interrupta</i>  | 0 - 196   | 8    | 107.48 |
| <i>Turritella variegata</i>   | 0 - 53    | 120  | 47.85  |
| <i>Typhinellus sowerbii</i>   | 51 - 110  | 31   | 49.24  |
| <i>Typhis expansus</i>        | 4 - 73    | 39   | 59.58  |
| <i>Varicopeza crystallina</i> | 11 - 1605 | 19   | 35.72  |
| <i>Vasum muricatum</i>        | 0 - 15    | 125  | 30.87  |
| <i>Vermicularia spirata</i>   | 3 - 80    | 90   | 73.02  |
| <i>Vermicularia knorrii</i>   | 2 - 110   | 80   | 35.92  |
| <i>Vetulonia jeffreysi</i>    | 538 - 805 | 0    | 17.42  |
| <i>Vexillum dermestinum</i>   | 0 - 24    | 17   | 33.23  |
| <i>Vexillum albocinctum</i>   | 1.5 - 6   | 7    | 29.47  |
| <i>Vexillum catenatum</i>     | 12 - 18   | 15   | 18.38  |
| <i>Vexillum exiguum</i>       | 0 - 128   | 6.9  | 73.69  |
| <i>Vexillum trophonium</i>    | 27 - 311  | 19.3 | 56.59  |
| <i>Vexillum histrio</i>       | 0 - 275   | 19   | 76.96  |
| <i>Vexillum pulchellum</i>    | 21 - 94   | 21   | 68.68  |
| <i>Vexillum laterculatum</i>  | 0 - 92    | 18   | 24.68  |
| <i>Vexillum sykesi</i>        | 2 - 73    | 13   | 34.76  |
| <i>Vexillum styria</i>        | 46 - 609  | 19   | 36.09  |
| <i>Vexillum hendersoni</i>    | 9 - 805   | 20   | 72.26  |
| <i>Vexillum puella</i>        | 0 - 40    | 12   | 37.09  |
| <i>Vexillum wandoense</i>     | 11 - 805  | 8.8  | 69.05  |
| <i>Vitreolina arcuata</i>     | 0 - 166   | 4.2  | 93.14  |
| <i>Vitricythara metria</i>    | 0 - 55    | 7.5  | 38.80  |
| <i>Vitrinella hemphilli</i>   | 0.6 - 73  | 2.5  | 27.08  |
| <i>Vitrinella filifera</i>    | 0 - 1     | 1.3  | 74.60  |
| <i>Vitrinella floridana</i>   | 0 - 46    | 2.1  | 29.76  |
| <i>Vitrinella helicoidea</i>  | 0 - 42    | 3    | 41.14  |
| <i>Vitrinella pusilla</i>     | 27 - 27   | 1.6  | 31.18  |

Appendix 1. (Continued)

|                                 |             |      |        |
|---------------------------------|-------------|------|--------|
| <i>Vitrinella tryoni</i>        | 29 - 29     | 2    | 14.28  |
| <i>Volvarina fauna</i>          | *           | 12   | 17.69  |
| <i>Volvarina subtriplicata</i>  | 9 - 203     | 8    | 25.11  |
| <i>Volvarina abbreviata</i>     | 0 - 51      | 9    | 67.43  |
| <i>Volvarina albolineata</i>    | 0 - 50      | 12.3 | 70.56  |
| <i>Volvarina avena</i>          | 0 - 80      | 17   | 82.17  |
| <i>Volvulella texasiana</i>     | 0 - 139     | 5.1  | 28.82  |
| <i>Volvulella paupercula</i>    | 33 - 713    | 4    | 78.23  |
| <i>Volvulella minuta</i>        | 0 - 305     | 4.6  | 83.19  |
| <i>Volvulella persimilis</i>    | 0 - 805     | 6    | 96.12  |
| <i>Xanthodaphne pompholyx</i>   | 188 - 2066  | 12.5 | 21.60  |
| <i>Xanthodaphne sofia</i>       | 1337 - 1406 | 8.5  | 22.26  |
| <i>Xenophora caribaea</i>       | 30 - 640    | 100  | 82.09  |
| <i>Xenophora conchyliophora</i> | 0 - 635     | 72   | 101.17 |
| <i>Xenophora longleyi</i>       | 139 - 823   | 150  | 83.86  |
| <i>Zafrona dicomata</i>         | 0.5 - 0.5   | 9    | 17.96  |
| <i>Zafrona idalina</i>          | 1 - 21      | 9    | 69.53  |
| <i>Zafrona pulchella</i>        | 0.6 - 9     | 12   | 38.54  |
| <i>Zebina laevigata</i>         | *           | 5    | 29.95  |
| <i>Zebina browniana</i>         | 0 - 51      | 5.1  | 76.38  |

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## CURRICULUM VITAE

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### Education:

Ph.D. Candidate, University of Maryland, Marine and Estuarine Environmental Sciences

M.S. University of Puerto Rico, Marine Sciences, 1979

B.S. St. Mary's College of Maryland, Biology, 1973.

### Professional Experience:

- 1990 - *Oceanographer (GS-1360-14), NOAA, National Ocean Service, Center for Sponsored Coastal Ocean Research.* I serve as Program Manager to develop and implement major coral reef ecosystem research projects. I currently oversee six programs: the National Coral Reef Institute, the Hawaii Coral Reef Initiative, the Caribbean Coral Reef Institute, Coral Reef Research for Puerto Rico, and long-term coral reef ecosystem studies in the Caribbean and Micronesia. Since 1990, I have provided oversight for over \$40M in coastal ocean ecosystem research around the U. S., covering the east and west coasts, Gulf of Mexico, Caribbean and Bering Seas. I also am periodically responsible for leading various planning and research activities such as the interagency scientific assessment of hypoxia in the Gulf of Mexico for the White House Committee on Environment and Natural Resources and developing an interagency research policy on coral reefs for the U. S. Coral Reef Task Force.
- 1989-90 *Oceanographer (GM-1360-13), NOAA, Office of the Chief Scientist.* I served as NOAA's Regional Coordinator for the Gulf of Mexico. I helped plan and coordinate marine and estuarine research activities concerning the region's coastal resources.
- 1981-89 *Oceanographer (GS-1360-12), NOAA, National Environmental Satellite, Data, and Information Service.* I served as Project Manager to lead multi-disciplinary teams of scientists to produce a series of assessments on the effects of weather and oceanography on aquatic-related economic resources in selected coastal regions around the U.S. (Chesapeake Bay, Southeast States, Gulf of Mexico, and San Francisco Bay).
- 1980-81 *Oceanographer (GS-1360-9), NOAA, Environmental Data and Information Service.* As part of a multi-disciplinary team of scientists, I helped develop a prototype computerized inventory of global oceanographic research.
- 1979 *Marine Biologist, the Arctic Company, Ltd.* I helped develop study plans on the impacts of petroleum-related development on the U. S. east coast outer continental shelf and the potential environmental effects of a sea-level canal in Panama.
- 1975-79 *Research Assistant, University of Puerto Rico, Department of Marine Sciences.* I collected oceanic and inshore reef fishes from the tropical Atlantic and Caribbean for studies of parasites and diseases. I developed new collection methods and collected fishes and parasites that established new records for Puerto Rico.

### Awards and Achievements:

- Oyster restoration volunteer diver, Magothy River Association
- NOAA Scientific Diver and NAUI Certifications; underwater habitat and submersible experience
- NOAA Bronze Medal Award for development of an interagency research policy on coral reefs
- NOAA Administrator's Award for Special Achievement for documenting the oceanographic effects of 1993 Mississippi River flooding
- Twenty-seven performance awards with NOAA from 1980-present
- NOAA long-term training assignment, University of Maryland, 1991-94
- *Homalometron dowgialloi* sp. n. named for contributions to helminthology
- Basic Grant, University of Puerto Rico, 1975-79
- Senatorial Scholarship, 1972-73
- Dean's List, Prince Georges Community College, 1970

### Publications:

Dowgiallo, M. J. (editor) 1994. *Coastal Oceanographic Effects of Summer 1993 Mississippi River Flooding*. Special NOAA Report, Coastal Ocean Office/National Weather Service, Silver Spring, MD. 76 pp.

Dowgiallo, M. J. 1989. *Chesapeake Bay Surface Salinities, 1951-88*. NOAA Technical Report AISC 15.

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