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Episodic rainfall influences the distribution and abundance of the regular sea urchin Lytechinus variegatus in Saint Andrew Bay, northern Gulf of Mexico

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Episodic Rainfall Influences the Distribution and Abundance of the Regular Sea Urchin *Lytechinus variegatus* in Saint Andrew Bay, Northern Gulf of Mexico

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The distribution and abundance of *Lytechinus variegatus* (Lamarck) were determined at three shallow-water stations in Saint Andrew Bay, FL, in the northern Gulf of Mexico. Populations were monitored at 4-mo intervals from Aug. 1997 to Aug. 1999 along 2- × 10-m transects, with four transects at each station. In Aug. 1997 individuals ranged in size from 15- to 63-mm diameter (mean = 38 mm; density = 1.4 individuals (ind.) m^{-2}) at Station 1 (Stations 2 and 3 were not sampled on that date). By Oct. 1997 individuals at Station 1 ranged in size from 26 to 62 mm (mean = 48 mm; density = 0.6 ind. m^{-2}), suggesting the growth of individuals within the population. At Station 2, individuals ranged between 50 and 70 mm (mean = 59 mm; densities = 1.0 ind. m^{-2}) and at Station 3 between 30 and 79 mm (mean = 51 mm; densities = 1.4 ind. m^{-2}) in Oct. 1997, indicating a population with no recent recruits. A mass mortality event was observed in April 1998 and was attributed to reduced salinities resulting from above-average rainfall in the previous month. Sea urchins were absent at Stations 1 and 2, whereas at Station 3 postdisturbance recruits were smaller (mean = 28 mm) and densities lower. Sea urchin tests were also observed at beach stations proximate to Stations 1 and 2. By July 1998 the populations had partially recovered at Stations 2 and 3 (densities = 0.6 and 1.1 m^{-2}, respectively), but test diameters were small at both stations. Test diameters had increased in Dec. 1998 at Station 3 when compared with those of July, but individuals at Station 2 showed overall smaller test diameters (mean = 28 mm), and densities had decreased again, presumably after another mass mortality caused by another major rainfall in Sep. In April 1999 test diameters had decreased further at Stations 2 and 3, indicating emigration or death of larger animals. We suggest that the shallow-water Saint Andrew Bay population of *L. variegatus* is reduced for several years at a time by episodic heavy rainfalls. This observation emphasizes the importance of density-independent processes controlling the distribution and abundance of marine organisms.

Regular sea urchins are important members of epibenthic communities regulating macrophytic (Lawrence, 1975a; Ebert, 1977; De Ridder and Lawrence, 1982; Lawrence and Sammarco, 1982; Harrold and Pearse, 1987) and faunal production and diversity (Paine and Vadas, 1969). Substantial increases in sea urchin populations can have pronounced effects on community structure (Moore and McPherson, 1965; Camp et al., 1973; Mann, 1977; Whitman et al., 1982; Valentine and Heck, 1991; Macia and Lirman, 1999). Similarly, decreases in sea urchin populations, such as those observed during mass mortality events, can result in equally marked changes in community structure (Lang and Mann, 1976; Ebeling et al., 1985; Scheibling, 1986; Lessios, 1988, 1995). Mass mortalities in regular sea urchins have been related to a variety of different biotic and abiotic factors (for review see Lawrence, 1996), including disease (Pearse et al., 1977; Lessios et al., 1984; Scheibling and Stephenson, 1984; Hagen, 1992), desiccation through aerial exposure (Glynn, 1968; Yamaguchi, 1975; Junqueira et al., 1997), extreme temperature changes (Crisp, 1964; Ziegelmeier, 1964; Glynn, 1968; Rivera, 1978; Imafku and Imaoka, 1983; Beukema, 1985; Beddingfield and McClintock, 1994; Junqueira et al., 1997), and low salinities (Goodbody, 1961; Allain, 1975, 1977; Lawrence, 1975b; Greenway, 1977; Irlandi et al., 1997).

The regular sea urchin *Lytechinus variegatus* ranges from North Carolina to Brazil, occurring in a variety of shallow-water habitats (Serafy, 1979). In Saint Andrew Bay and in some of the neighboring bays in the northern Gulf of Mexico, *L. variegatus* often occurs in seagrass beds of *Thalassia testudinum* and on sand bottom habitats that are not vegetated (Beddingfield and McClintock, 2000). In these nearshore habitats, physical factors may have a

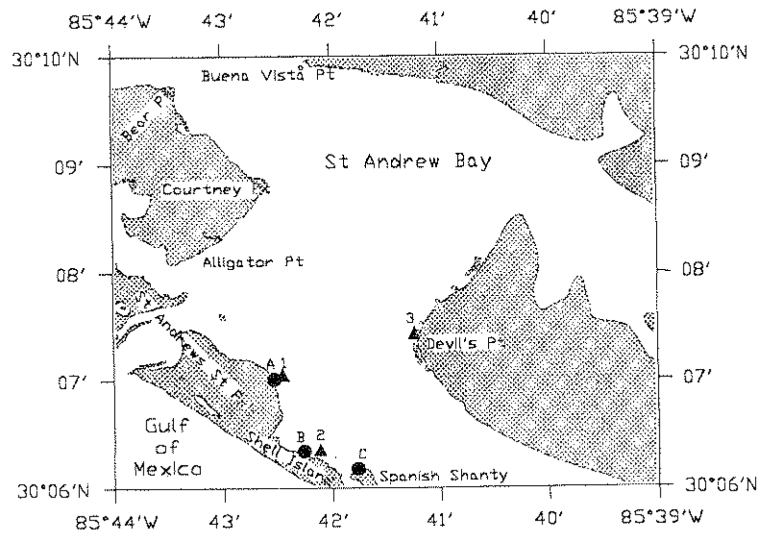


Fig. 1. Location of the study sites in Saint Andrew Bay, FL, showing the sea stations (1–3) used to examine the sea urchin population within the bay and displaying the beach stations (A–C) used to determine the effects of mortality in April 1998.

greater impact on the abundance of *L. variegatus* than on those living in deep-water habitats (Watts et al., 2001). The initial objective of this study was to document the population structure of *L. variegatus* at several sites in Saint Andrew Bay over a period of 2 yr. During this period several above-average rainfalls occurred, thereby reducing salinities and resulting presumably in two mass mortality events. Thus, we were able to observe the population decline and recovery that followed these catastrophic mortalities.

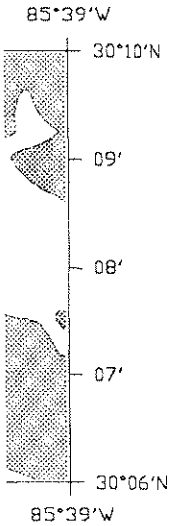
Materials and Methods

Site descriptions.—Saint Andrew Bay is located along the northern boundary of the Gulf of Mexico and includes a variety of different habitats. Three shallow-water stations (1- to 1.7-m depth, Fig. 1) were selected on the basis of their differences in vegetation and proximity within the bay (Table 1). Three beach stations adjacent to shallow-water stations were chosen to document the occurrence of sea urchin tests after the mortality events.

Population analysis.—Sampling was conducted between Aug. 1997 and Aug. 1999. Densities and test diameters (measured at the ambitus) of *L. variegatus* were recorded at each station three times per year for 2 yr along four 2- × 10-m transects. Transects were perpendicular to the shoreline. Stations 1 and 2 were ca. 50 m offshore, whereas Station 3 was ca. 10 m from the shoreline. Densities were recorded as individuals (ind.) m^{-2}. Size frequencies were calculated and recorded as the percentage of the total population at a particular station. Small individuals with a test diameter below 20 mm were considered to be recruits (Junqueira et al., 1997). In April 1998 a mass mortality occurred in the bay, resulting in the disappearance of *L. variegatus* from all stations except Station 3. At this point, two beach stations proximate to Stations 1 and 2, respectively (Fig. 1), were chosen. At Station 3 the beach

Table 1. Vegetation structure of three stations used for determination of the population size frequency and density of *Lytechinus variegatus* in Saint Andrew Bay, FL. Stations were selected for their location, vegetation, and presence of *L. variegatus* at no more than 3-m depth.

Station	Vegetation
Station 1	Sand patches mixed with beds of *Thalassia testudinum*
Station 2	Sand patches mixed with beds of *T. testudinum* and *Syringodium filiforme*
Station 3	Thick beds of *T. testudinum*



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station was located on the property of a government military installation (Tyndall Air Force Base) and could not be investigated (request for access was denied). Size frequencies and densities of empty tests were determined along four 2- × 10-m transects at beach sites B and C, parallel to the tidemark.

Water salinity (ppt) and temperature (C) were measured at each shallow-water station on each sampling date. Additional seawater temperature and rainfall recordings for Saint Andrew Bay were obtained from the National Climate Data Center (Saint Andrew Bay Station # 86842).

Statistical analyses.—Preceding all statistical analyses were assessments of the assumptions of normality (Kolmogorov–Smirnov test) and homoscedasticity (Spearman–Rank correlation). Size-frequency distributions were compared using a contingency table followed by Student's t-test analyses. Sea urchin densities were analyzed using a two-way ANOVA on ranks followed by a Tukey test for pairwise multiple comparisons to examine variations through time and among stations (Zar, 1996). Statistical significance was determined at the $P < 0.05$ level.

Results

Population size–frequency distributions varied both spatially and temporally. At Station 1, located closest to the mouth of the bay, sea urchin diameters ranged between 15 and 63 mm (mean = 38 mm; densities = 1.4 ind. m^{-2}) in Aug. 1997 (Fig. 2A). In Nov. 1997 the sea urchin diameters had increased significantly, ranging between 20 and 69 mm (mean = 48 mm), whereas the densities (Fig. 3) had declined by more than half (0.6 ind. m^{-2}). No recruits were found in this population in Nov. 1997. In April 1998 sea urchins were not found at Station 1 (corresponding with reduced salinities resulting from recent above-average rainfall), but high densities (average = 45 ind. m^{-2}) of dead sea urchins were found at Beach Station A at the tidemark. Diameters of empty tests (Fig. 4) were similar to the test diameters of live sea urchins in Nov. 1997 (31- to 70-mm test diameter) at Station 1. Densities of dead *L. variegatus* were 45, 3.5, and 3.05 at Beach Stations A, B, and C, respectively. Individuals were no longer found at Station 1 after April 1998.

At Station 2, sea urchins ranged in diameter between 50 and 70 mm (mean = 59 mm; densities = 1.0 ind. m^{-2}) (Fig. 2B) in Nov. 1997. In April 1998 no living sea urchins were found at Station 2, and empty tests were found on Beach Station B (3.5 empty tests m^{-2}) (Fig. 1). The diameters of the tests on the beach were smaller (Fig. 4) than those found at Station 2 during the previous collection. Sea urchins reappeared in July 1998, but densities (0.6 ind. m^{-2}) were significantly lower than they had been in Nov. 1997 (Fig. 3). Test diameters ranged between 28 and 55 mm (mean = 45 mm) and were significantly smaller than those reported in Nov. 1997. Densities of sea urchins declined significantly from July to Dec. 1998 and even further in April 1999 (0.15 ind. m^{-2}). Test diameters did not increase from July to Dec. 1998 and decreased significantly by April 1999 (mean = 28 mm).

At Station 3, located furthest from the mouth of the bay, populations maintained the highest overall densities during the study. In Nov. 1997, at the time of the first collection, sea urchin diameters ranged from 36 to 70 mm (mean = 51 mm; densities = 1.4 ind. m^{-2}) (Figs. 2C, 3, respectively). Test diameters (Fig. 2C) and densities (Fig. 3) decreased significantly in April 1998 (mean = 24 mm; densities = 0.3 ind. m^{-2}), but individuals, in contrast to the other two stations, were still observed. In July 1998 test diameters and densities of sea urchins had increased (mean = 34 mm; densities = 1.1 ind. m^{-2}) but had not yet recovered compared with those of Nov. 1997. In Dec. 1998 densities were similar (1.0 ind. m^{-2}) to those of the previous collection, but test diameters had increased significantly (mean = 52 mm). On the final sampling date (April 1999) size frequencies showed a wider distribution than at any previous time, with diameters ranging from 15 to 63 mm (mean = 37 mm), suggesting a recruitment event had occurred recently. Sea urchin densities (1.4 ind. m^{-2}) were similar to those of Nov. 1997.

Seawater temperatures (Table 2, historical data in Fig. 5) at all three stations ranged from 16.5 (April 1999) to 28 C (Aug. 1999). Salinities (Table 2) ranged from 16 (Aug. 1999) to 41.5 ppt (Dec. 1998). During the mortality event in April 1998, salinities decreased significantly to 19 ppt at Station 1. Salinities increased significantly in July 1998 (maximum = 41 ppt) and remained stable until April 1999. Rainfall recordings (Fig. 6) for Saint Andrew Bay corresponded to these changes in salinity.

Rainfall totals ranged from 9 to 23 cm monthly (Fig. 6). Unusually high rainfall was recorded in March 1998 (54 cm) and again in Sep. 1998 (74 cm). These tropical storms resulted in reductions in bay salinities.

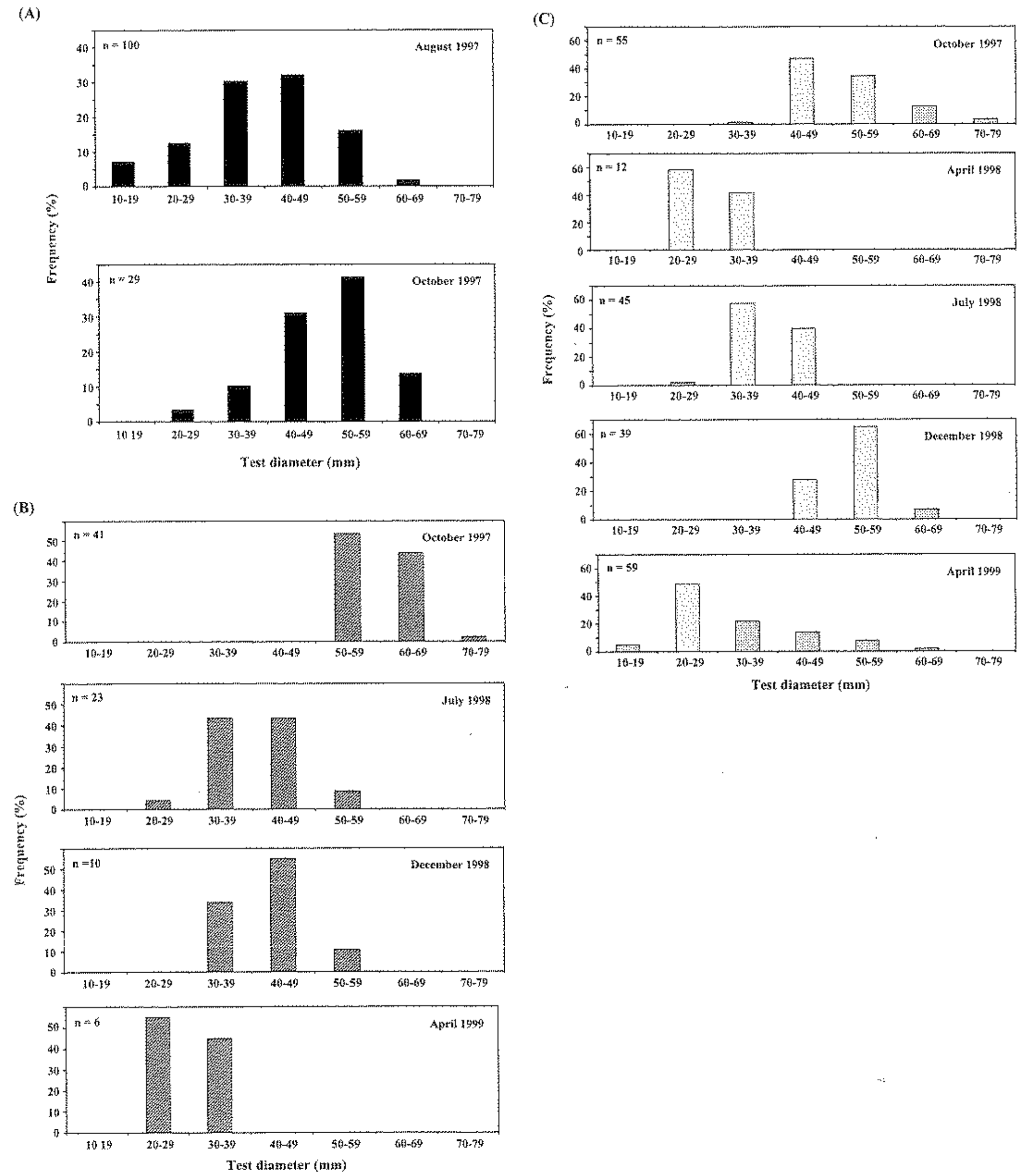
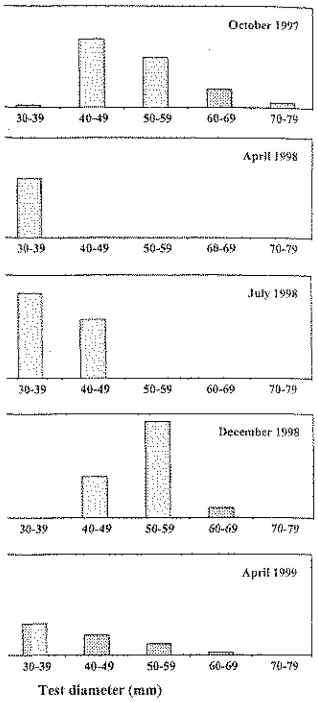


Fig. 2. Size-frequency distributions of *Lytechinus variegatus* at three study sites in Saint Andrew Bay separated into (A) Station 1, located close to the mouth of the bay, (B) Station 2, located along the main body of Shell Island, and (C) Station 3, located on Devil's Point around Tyndall Air Force Base.

Discussion

Population dynamics of *L. variegatus* in Saint Andrew Bay are determined by physical factors, location in the bay, population movement patterns, and recruitment. Population densities changed over the course of the study. These were correlated, in part, to the mortality associated with reduced salinities in the bay as a result of above-average rainfall. They may also have been affected by immigration–emigration of the sea urchins. Population densities were relatively low compared with those reported for the northern Gulf of Mexico (Valentine and Heck, 1991; Beddingfield and McClintock, 2000; Rose et al., 1999) but were similar to those reported for the Itajuru Channel in Brazil (Junqueira et al., 1997). These data suggest the importance of density-independent processes in controlling the distribu-



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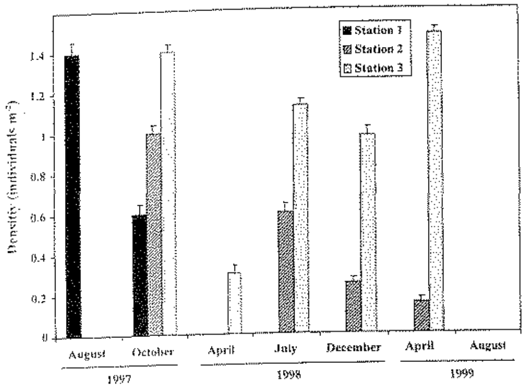


Fig. 3. Densities of *Lytechinus variegatus* from Aug. 1997 (Station 1 only) to Aug. 1999 in Saint Andrew Bay.

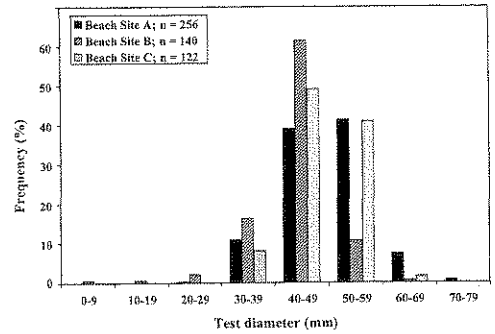


Fig. 4. Size-frequency distribution of empty tests (*Lytechinus variegatus*) in Saint Andrew Bay in April 1998 at three different beach sites. The location of the beach sites is marked in Figure 1. Densities of dead *L. variegatus* were 45, 3.5, and 3.05 at Beach Stations A, B, and C, respectively.

tion and abundance of sea urchins found in shallow waters.

The mortality events that occurred in Saint Andrew Bay in April 1998 and Sep. 1998 were apparently caused by a major decrease in salinities within the bay. March 1998 was characterized by heavy spring rains. These rains, in addition to the drainage of three rivers into the bay, caused a significant decline in salinities. Stations within the bay were affected differentially. *Lytechinus variegatus* had vanished from depths of less than 3 m at Stations 1 and 2, but a few individuals were still found at Station 3. This suggests that currents and winds led to a concentration of freshwater toward the southern part of Saint Andrew Bay (around Station 1). The lowest salinity (19 ppt) was measured at Station 1, the station corresponding to Beach Site A, with the highest densities of empty tests. The salinity was not recorded during the actual rain event and may have been much lower at that time. In Sep. 1998 the highest rainfalls of the 2-yr study period were measured as a result of a tropical storm that affected the northern Gulf of Mexico. No salinity measurements were recorded around the time of this tropical storm, but we suggest that the resulting reduced salinities further decreased sea urchin densities. *Lytechinus variegatus* is an osmotic conformer and is therefore not able to survive salinities below 25 ppt for an extended time period (Lawrence, 1975b; Roller and Stickle, 1993; Lawrence 1996). Echinoderms lack the ability to osmoregulate because of their permeable body wall and the lack of an excretory organ (Stickle and Diehl, 1987). *Lytechinus variegatus* decreases its activity and feeding in response to moderately decreased salinities (Bishop et al., 1994).

Lytechinus variegatus at Station 1, located close to the mouth of the bay, seemed most affected by changes in salinity. Individuals were present at this station during the first two sample dates only. In Nov. various cohorts within the population had increased in size, indicative of a healthy population. The absence of small individuals (<20 mm) indicated that the recruitment had been minimal around Station 1 or that recruits from that year were still too small to be easily detected. After the mortality event in April 1998, the population never recovered during the remainder of the study period. The reasons for this are not clear because

Table 2. Temperature (C) and salinity (ppt) data measured for three different stations in St. Andrew Bay, August 1997–August 1999.

		Aug 1997	Nov 1997	April 1998	July 1998	Dec 1998	April 1999	Aug 1999
Station 1	Temperature	25	22	20.5	21	24	16.5	28
	Salinity	35	34.5	19	41	41.5	40.5	18
Station 2	Temperature		21	20	24.75	22	11.5	26
	Salinity		34.5	22	34.5	41	34	18
Station 3	Temperature		22	20	27.5	24	16.5	25.5
	Salinity		35.5	25	37	35.5	38.5	16

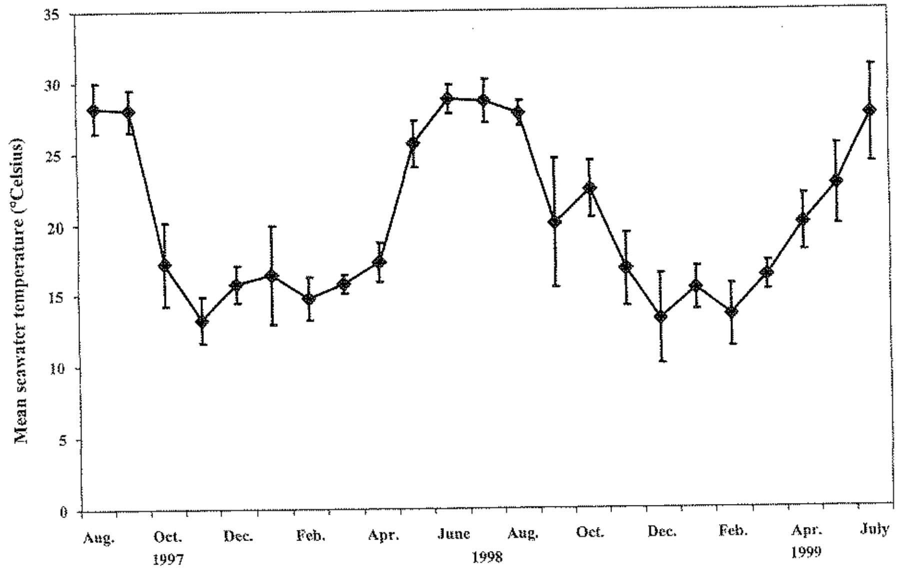


Fig. 5. Air temperature recordings for Saint Andrew Bay from 1997–99 as received from the National Climate Data Center (Station # 86842). Means ± SD.

the seagrass beds of *T. testudinum* appeared in good condition (Boettger and Thompson, pers. obs.). Previous evaluations at this site, several years earlier, found an extensive sea urchin population (Watts, pers. obs.). These data suggest that the population densities can vary annually and that the long-term population structure is quite variable in this shallow-water habitat.

Station 2, located along the north side of Shell Island, displayed population characteristics similar to those of Station 1 during the mortality event, though densities of empty tests along the beach sites were significantly lower than at Station 1. Station 2 was located within a lagoon in Saint Andrew Bay, so minor differences could be explained by water currents and wind patterns. There was a significant change in the population structure from Nov. 1997 to July 1998 at Station 2. In Nov., only large individuals above 50 mm in diameter were found. In July 1998 most of these large

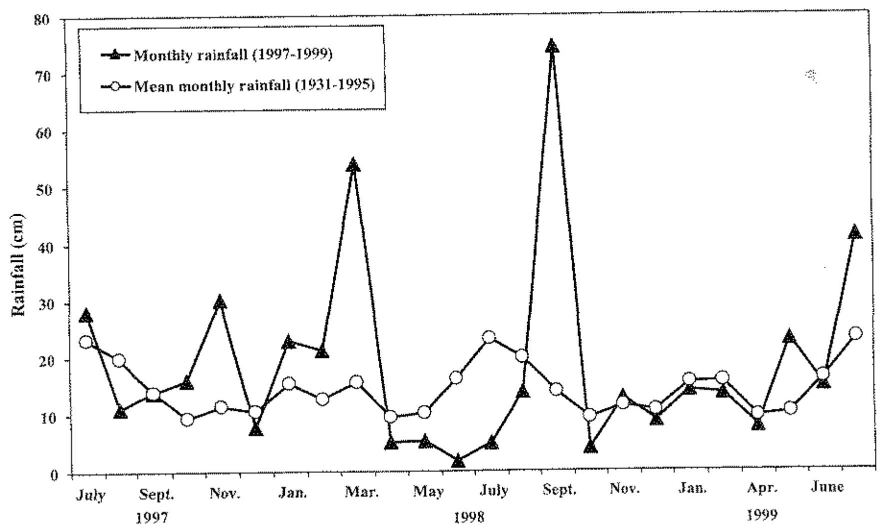
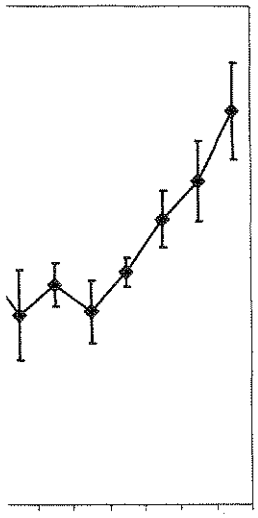


Fig. 6. Absolute and historical monthly rainfalls (cm) in Saint Andrew Bay as from July 1997 to July 1999 as recorded by Station # 86842 of the National Climate Data Center.



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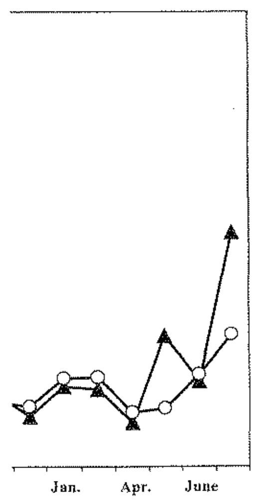

Bay as from July 1997 to July 1999

individuals had disappeared (whether as a result of the mortality event or migration is not known) and were replaced by smaller ones. We suggest that these small sea urchins immigrated into the vicinity of Station 2 because the sizes were too large for recent recruits. By Dec. 1998 the average diameter of the population had increased, and sea urchins were at least 30 mm in diameter. In April 1999 the population structure had changed again, with most sea urchins being between 20 and 39 mm in diameter. This indicates that large individuals had either died or migrated from the area.

The most stable population within the bay was at Station 3. Individuals were found even after the salinity reductions in 1998. This site appeared to sustain a nursery population. Large individuals found in Nov. 1997 were absent in April 1998. They may have migrated into deeper bay waters. The remaining smaller individuals continued to grow through Dec. 1998. Again, in April 1999 the larger animals had generally disappeared from the station. Recruits were found for the first time together with small individuals. Similar associations have been documented in *L. variegatus* by Beddingfield and McClintock (2000).

It appears that *L. variegatus* in Saint Andrew Bay migrate from shallow nursery areas into deeper waters or different sites after reaching between 50 and 69 mm in diameter. Saint Andrew Bay is not as heavily populated as the nearby Saint Joseph's Bay, which contained 13 ind. m^{-2} in *Thalassia testudinum* areas (Beddingfield and McClintock, 2000). The Saint Andrew Bay population of *L. variegatus* could easily be adversely affected by changes in abiotic factors, particularly salinity, because shallow-water populations of *L. variegatus* are subject to multiple disturbances by abiotic factors (reviewed by Watts et al., 2001). It appears that after mass mortality the population recovered through immigration rather than through recruitment, as found for a Brazilian population (Junqueira et al., 1997).

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