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## Food Resource Utilization in the Sea Urchin *Lytechinus variegatus* in Contrasting Shallow-Water Microhabitats of Saint Joseph Bay, Florida

STEPHEN D. BEDDINGFIELD AND JAMES B. MCCLINTOCK

The feeding activity and relative percentages of different foods consumed by the regular sea urchin *Lytechinus variegatus* in three contrasting microhabitats were examined over a 2-yr period in Saint Joseph Bay, FL, at its northern limits of distribution. In 1993, feeding activity levels of individuals at a site dominated by the seagrass *Thalassia testudinum* were higher on average than at a site characterized mostly by sand substrates alone or a site dominated by the seagrass *Syringodium filiforme*. No other significant difference in feeding activity levels was detected between sites or years. Feeding activity was markedly reduced at all sites in winter months of both years. *Lytechinus variegatus* in Saint Joseph Bay displayed generalist feeding behaviors with diets that appeared to be governed by the availability and palatability of food items. Foods consumed by sea urchins varied seasonally at each site, apparently in response to changes in food availability. Some seasonally abundant algae (e.g., the fleshy red alga *Laurencia porteur*) were not consumed, presumably due to chemical defenses. Seasonal depressions in resource utilization and changes in food types likely impact aspects of growth and reproduction of individuals comprising subpopulations of *L. variegatus* that fringe on the northern limits of their biogeographic distribution.

A number of sea urchins display feeding preferences both in the field and in the laboratory (see Lawrence, 1975, for review; Vadas, 1977; Chiu, 1985; Prince and LeBlanc, 1992). Nonetheless, individuals may occur in habitats that support different types or abundances of foods, and intraspecific differences may occur in the diets of sea urchins from different areas (Lasker and Giese, 1954; Lawrence, 1975). Seasonal differences in the diets of sea urchins also occur (see Lawrence, 1975, for review; Chiu, 1985). Such changes in diet may reflect the relative availability of different food items in the environment (Lawrence, 1975). Variations in body size, growth rates, and reproductive output in populations of sea urchins have been related to quantitative and qualitative differences in diets (Fuji, 1967; Ebert, 1968; McPherson, 1969; Dix, 1970, 1972; Lawrence and Lane, 1982; White et al., 1985).

*Lytechinus variegatus* (Lamarck, 1816) is a regular echinoid that inhabits a variety of shallow sublittoral habitats from the coast of North Carolina to Brazil, including the Caribbean and the Gulf of Mexico. The wide variety of substrates on which *L. variegatus* is found include sand flats, sand with shell hash, areas dominated by seagrasses (e.g., *Thalassia testudinum*, *Syringodium filiforme*, *Cymodocea manatorum*, or *Halodule wrightii*), and *Halimeda* algal beds, in addition to hard bottoms covered with algae (Sharp and Gray,

1962; Moore et al., 1963; Kier and Grant, 1965; Greenway, 1976; Lowe and Lawrence, 1976; Serafy, 1979; Vadas et al., 1982; Klinger, 1984; Lessios, 1985; Beddingfield and McClintock, in press).

*Lytechinus variegatus* includes both living and dead plant material in the diet, as well as animal foods (Mortensen, 1943; Moore et al., 1963; Kier and Grant, 1965; Camp et al., 1973; Greenway, 1976, 1995; Klinger, 1982; McClintock et al., 1982; Klinger and Lawrence, 1984; Valentine and Heck, 1991; Heck and Valentine, 1995). Sand grains encrusted with organic material and detritus may also be important components of the diet of *L. variegatus* (Vadas et al., 1982). Animal foods may also be consumed. McClintock et al. (1982) found that *L. variegatus* readily consume food models containing bivalve tissues.

Although diets of *L. variegatus* are known to vary across broad geographic scales, to date no studies have been reported of seasonal variation in feeding activity or diet for any one locality. Accordingly, the present study examines temporal and spatial patterns of food resource utilization in *L. variegatus* from contrasting microhabitats of Saint Joseph Bay, FL. Moreover, because this bay is located at the northern limits of the biogeographic distribution of *L. variegatus*, our findings provide insights on the feeding activities of "fringing" subpopulations of the species.

## MATERIALS AND METHODS

*Study sites.*—Three locations in Saint Joseph Bay, FL (30°N, 85.5°W) were selected as sampling sites for *L. variegatus*, each representative of a discrete habitat type. All three sites were at depths that ranged from 0.75 to 1.5 m over normal tidal cycles. Sites dominated by the seagrass *T. testudinum* (*Thalassia* site) and by sand alone (sand site) were selected within Saint Joseph Peninsula State Park, whereas a third site dominated by the seagrass *S. filiforme* (*Syringodium* site) was located directly offshore of the city of Port Saint Joe (see Beddingfield, 1997, for further details of sites). Both types and abundances of potential plant and animal foods were markedly different among the three study sites and within sites during different seasons. Although a detailed quantitative analysis of the spatial and temporal availability of all potential foods in the field is beyond the scope of the present study, a broad overview of potential foods available at each site is presented below.

The dominant components of the flora and fauna at the *Thalassia* site, 200 m east of the northern point of Eagle Harbor, were dense beds of the seagrass *T. testudinum* (mean  $\pm$  1 SD wet wt = 345  $\pm$  65, 230  $\pm$  24, 69  $\pm$  11, and 104  $\pm$  22 g/m<sup>2</sup> aboveground biomass in July, November, and January 1993 and April 1994, respectively; n = 5) interspersed with rich infaunal populations of the mussel *Modiolus americanus* (mean  $\pm$  1 SD density = 151  $\pm$  51 mussels/m<sup>2</sup> in fall 1993; n = 10). Epibionts, consisting mainly of epiphytic algae (primarily red calcareous algae) and hydroids, occurred (mean  $\pm$  1 SD wet wt = 86  $\pm$  14 and 34  $\pm$  8 g/m<sup>2</sup> in July and November 1993, respectively; n = 5) on grass blades of *T. testudinum*. Decaying drift seagrass was present during all seasons of the year (mean  $\pm$  1 SD wet wt = 30  $\pm$  11, 168  $\pm$  34, 68  $\pm$  17, and 47  $\pm$  9 g/m<sup>2</sup> in July, November, and January 1993 and April 1994, respectively; n = 5).

The sand site was 100 m north of the Saint Joseph Peninsula State Park Marina and consisted of a shallow sand flat with abundant shell hash scattered on the sea floor. During the summer months (June–August 1993 and 1994), sand at this site was covered with a thin (approx. 0.25 mm thick) film of cyanobacteria and the shell hash was covered with encrusting algae (mean  $\pm$  1 SD wet wt = 46  $\pm$  12 and 54  $\pm$  16 g/m<sup>2</sup> in July 1993 and 1994, respectively; n = 5). During the winter months (December–February), the green fleshy algae *Enteromorpha compressa* was abundant (mean  $\pm$  1 SD wet wt

= 586  $\pm$  67 and 672  $\pm$  43 g/m<sup>2</sup> in January 1993 and February 1994, respectively; n = 5) and was found growing on shell fragments. During the fall and early winter months of both years, decaying *T. testudinum* seagrass blades (mean  $\pm$  1 SD wet wt = 278  $\pm$  83 and 311  $\pm$  74 g/m<sup>2</sup> for November 1993 and 1994, respectively; n = 5) were found settled into depressions on the sea floor.

The seagrass *S. filiforme* (manatee grass) constituted the main plant component of the *Syringodium* site (mean  $\pm$  1 SD wet wt = 363  $\pm$  32, 266  $\pm$  46, 45  $\pm$  17, and 64  $\pm$  16 g/m<sup>2</sup> in July, November, and January 1993 and April 1994, respectively; n = 5). *Syringodium filiforme* grass blades were colonized by epibionts (primarily red calcareous algae and hydroids) during the summer and fall (mean  $\pm$  1 SD wet wt = 129  $\pm$  22 and 95  $\pm$  27 g/m<sup>2</sup> in July and November 1993, respectively; n = 5). In contrast to the *Thalassia* site, no infaunal mussels were present. The red fleshy alga *Laurencia porteur* (= *L. porter*) occurred in abundance at both seagrass sites during late spring and summer months.

*Methods.*—At each of the three study sites, the test diameter, feeding activity, and foods being consumed by up to the first 50 *L. variegatus* encountered within a series of up to 15 1-m<sup>2</sup> quadrats, each randomly positioned along a 50-m transect line, were recorded monthly from January 1993 to December 1994. Sea urchins were recorded as actively feeding if, upon immediate examination, plant or animal material was found grasped between their teeth. Percentages of feeding activity of individuals were compared across the three sites by a Kruskal–Wallis nonparametric one-way analysis by ranks and between years within each site on arcsine transformed data with paired t-tests (Zar, 1984). The frequency percentages of dietary items detected in the grasp of the teeth of individuals over the 2-yr study period were compared between sites with a contingency table (Sokol and Rohlf, 1981).

In addition to direct observations of feeding in the field, gut contents of similarly sized adults collected from each site (test diameter = 35–40 mm; n = 10/site/month) were examined monthly to further substantiate natural foods ingested. Only adult sizes were examined to allow direct intersite comparisons among diets of individuals from similar age cohorts. Gut contents were examined under a binocular dissecting microscope, sorted, their volumes determined by measuring the displacement of seawater in a graduated cylinder, and the pro-

TABLE 1. Volumetric percentages of different foods removed from the guts of *Lytechinus variegatus* collected from a *Thalassia*, sand and *Syringodium* site in spring (March, April, May), summer (June, July, August), fall, (Sept, Oct, Nov) and winter (Jan, Feb, March) over a two-year period in Saint Joseph Bay, Florida. Values in parentheses are percentages of individuals observed directly feeding on the same food source in the field (see Figure 1). N = 30 individuals per site per season.

	<i>Thalassia testudinum</i>	<i>Syringodium filiforme</i>	Epibionts	Dead Seagrass	Sand/ Cyanobacteria	<i>Enteromorpha compressa</i>	Encrusting Algae	Other	Unidentified
<i>Thalassia</i> Site									
1993									
Spring	70 (78)	0 (0)	11 (6)	13 (8)	0 (0)	0 (12)	0 (0)	6 (0)	0
Summer	33 (27)	0 (0)	41 (65)	13 (8)	3 (2)	0 (0)	0 (0)	4 (0)	6
Fall	33 (24)	0 (0)	0 (8)	53 (66)	4 (0)	0 (0)	0 (0)	0 (0)	10
Winter	78 (67)	0 (0)	0 (0)	7 (20)	10 (5)	0 (0)	0 (0)	0 (8)	5
1994									
Spring	70 (57)	0 (0)	0 (3)	10 (23)	9 (2)	0 (0)	0 (0)	0 (21)	11
Summer	37 (22)	0 (0)	20 (44)	13 (20)	17 (2)	0 (0)	0 (0)	0 (13)	13
Fall	27 (40)	0 (0)	0 (4)	61 (44)	12 (6)	0 (0)	0 (0)	0 (0)	0
Winter	67 (76)	0 (0)	0 (0)	13 (20)	15 (4)	0 (0)	0 (0)	0 (0)	5
Sand Site									
1993									
Spring	0 (0)	0 (0)	0 (0)	0 (0)	18 (10)	43 (39)	23 (41)	5 (14)	11
Summer	0 (0)	0 (0)	0 (0)	8 (4)	57 (46)	0 (3)	27 (38)	0 (3)	8
Fall	0 (0)	9 (0)	0 (0)	64 (71)	22 (15)	0 (0)	7 (11)	0 (2)	7
Winter	0 (0)	0 (0)	0 (0)	0 (6)	4 (9)	78 (70)	5 (10)	0 (5)	13
1994									
Spring	0 (0)	0 (0)	0 (0)	6 (1)	13 (6)	10 (19)	43 (64)	7 (10)	21
Summer	0 (0)	0 (0)	0 (0)	17 (6)	47 (39)	0 (5)	27 (40)	0 (2)	9
Fall	0 (0)	0 (0)	0 (0)	74 (62)	16 (24)	0 (0)	5 (13)	0 (2)	5
Winter	0 (0)	0 (0)	0 (0)	15 (11)	13 (4)	67 (79)	0 (5)	0 (5)	5
<i>Syringodium</i> Site									
1993									
Spring	7 (12)	75 (63)	0 (6)	11 (4)	3 (10)	0 (0)	0 (1)	0 (6)	4
Summer	11 (8)	47 (35)	37 (50)	0 (1)	0 (2)	0 (0)	0 (0)	0 (4)	5
Fall	15 (4)	38 (37)	0 (0)	37 (60)	0 (0)	0 (0)	0 (0)	0 (0)	10
Winter	10 (3)	49 (65)	0 (0)	23 (34)	6 (0)	0 (0)	0 (0)	3 (0)	9
1994									
Spring	7 (2)	78 (60)	1 (8)	5 (19)	0 (6)	0 (0)	0 (2)	0 (6)	9
Summer	17 (6)	22 (37)	40 (47)	5 (11)	0 (0)	0 (0)	0 (0)	0 (0)	16
Fall	10 (4)	34 (26)	0 (0)	52 (70)	0 (0)	0 (0)	0 (0)	0 (0)	4
Winter	15 (10)	64 (58)	0 (0)	11 (25)	7 (3)	0 (0)	0 (0)	0 (4)	3

portional volumetric percentage of each food type calculated as a function of the total volume of food in sea urchin guts on a given sampling date. A volumetric method of gut content analysis was employed to control for differences in the weights of the various food resources from the different microhabitats and to give a more accurate representation of the amounts of foods ingested by sea urchins.

## RESULTS

Mean ( $\pm 1$  SD) test diameters for individuals recorded over the 2-yr period were  $31.9 \pm 9.6$ ,  $39.9 \pm 7.8$ ,  $39.9 \pm 11.8$  mm for the *Thalassia*,

sand, and *Syringodium* sites, respectively. When examined on an annual basis, significantly ( $P < 0.05$ ) higher percentages, of individuals were observed feeding at the *Thalassia* than the *Syringodium* site in 1993 (40 vs 27%; Fig. 1). No other significant difference in feeding activity levels was detected between sites or years. The incidence of individuals feeding at all three sites increased between January and June of both 1993 and 1994 but declined markedly 2–11-fold between November and December in both years (Fig. 1).

The frequency percentages of dietary items found grasped in the teeth of *L. variegatus* differed significantly ( $P < 0.05$ ) among all sites

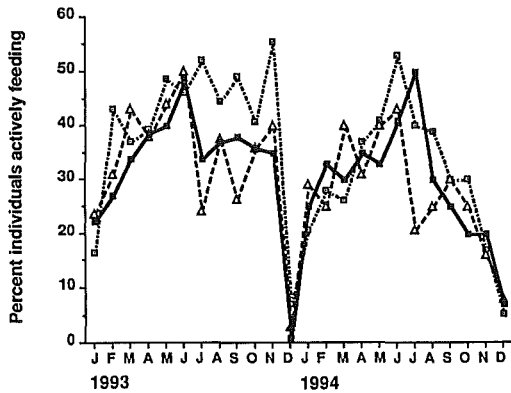


Fig. 1. Monthly percentages of *Lytechinus variegatus* displaying feeding activity at a *Thalassia* site (dashed line with open squares), sand site (dashed line with open triangles), and *Syringodium* site (solid line with closed squares) over a 2-yr period in Saint Joseph Bay, FL.  $n = 26\text{--}50$  individuals per site per month.

during all seasons for almost all food resources (Fig. 2). The exceptions were similar percentages of individuals at the *Thalassia* and *Syringodium* sites feeding on decayed drift seagrass blades and detritus during the fall and winter seasons of both years and similar percentages of sea urchins at these sites feeding on epibionts during summer months. Percentages of individuals at the *Thalassia* and sand sites feeding on decayed drift seagrass blades during the spring months of both years were also similar.

Determinations of gut contents (Table 1) revealed volumetric percentages of ingested foods that were similar in pattern to those determined by direct observations of individuals feeding in the field (Fig. 2). Considerable seasonal variation in diet occurred at all sites. For example, at the *Thalassia* site, 11 and 41% of the diet consisted of epibionts in the spring and summer of 1993, respectively, whereas no epibionts occurred in the diets in the fall and winter of 1993. Epibionts also comprised a greater portion of the diet at the *Syringodium* site in the summer months of both 1993 and 1994. During the fall of both 1993 and 1994, epibionts died off and seagrass blades became scarce. Subsequently, large amounts of decaying drift-seagrass blades became available, and this comprised an important food resource for sea urchins at both seagrass sites during fall months of both years of the study. In the spring and winter of both years, sea urchins at the *Thalassia* and *Syringodium* sites fed directly on live seagrass. The red alga *Laurencia porteaaur* occurred in abundance at both the *Thalassia*

and *Syringodium* sites during the summer months. Nonetheless, only 0.2% of the sea urchins at these sites were found ingesting this alga during the 2-yr study period.

During the spring of both 1993 and 1994, sea urchins at the sand site fed heavily on algae encrusting shell hash (Table 1; Fig. 2). During the summer months, sea urchins fed on both encrusting red algae and cyanobacterial films on the sand. In late fall, the sand site was characterized by the presence of large amounts of decaying drift seagrass. At that time, sea urchins at that site were observed primarily consuming this food source. During the winter months of both years of the study, the green alga *E. compressa* was abundant at the sand site. When present, sea urchins fed almost exclusively on this alga. Although dead and decaying drift seagrass was also abundant during the winter months of both years, only a small percentage of individuals fed on this food source during those periods.

#### DISCUSSION

Percentages of individuals feeding declined dramatically at all sites in winter of both years of the study. Winter seawater temperatures in Saint Joseph Bay during the study period ranged from 1 to 17 C (Beddingfield and McClintock, in press). Kleitman (1941) demonstrated that *L. variegatus* cannot right themselves at 10 C. Therefore, winter seawater temperatures in the bay are seasonally near the lower critical thermal limits for *L. variegatus* (Beddingfield and McClintock, 1994) and are likely responsible for the reduced feeding activities observed. The sea urchin *Strongylocentrotus droebachiensis* also decreases its activity level (righting response) when seawater temperatures decline (Percy, 1973). Feeding activities observed in the present study suggest that limited acclimatization to cold temperatures may occur in *L. variegatus*, with feeding activities of sea urchins first decreasing with falling seawater temperatures (November–December) and rising slowly throughout the remainder of the winter period (January–February) (see also Percy, 1973). Although there appeared to be a strong correlation between increasing spring-time feeding activities and rising spring seawater temperatures, it is also possible that increased feeding activities in the spring were related to increased nutritional demands associated with gametogenesis and spring spawning activities (Beddingfield, 1997; Beddingfield and McClintock, 1998).

The present study supports the conclusion

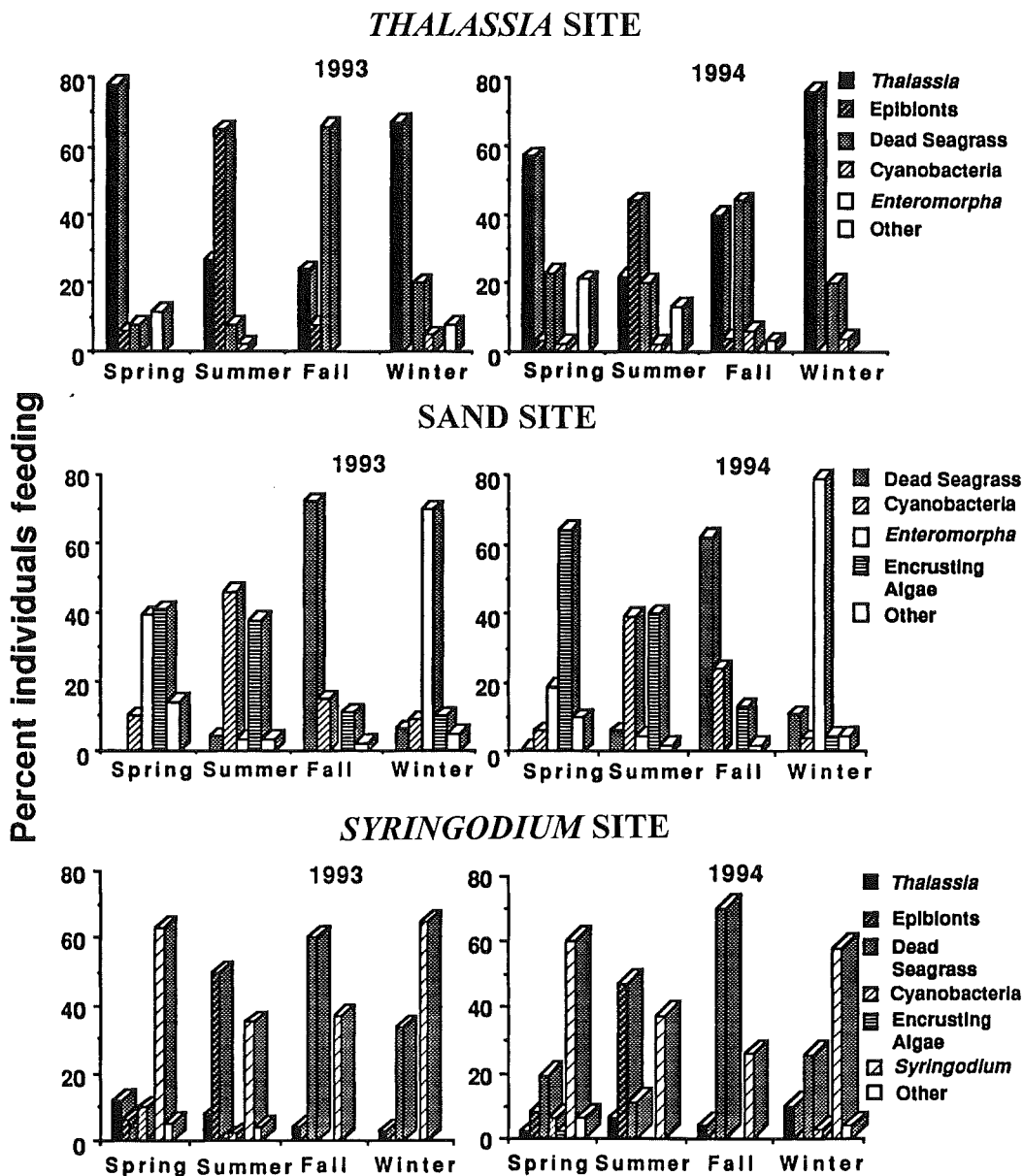


Fig. 2. Percentages of different food items observed in the grasp of the teeth of *Lytechinus variegatus* at *Thalassia*, sand, and *Syringodium* sites in spring (March–May), summer (June–August), fall (September–November), and winter (January–March) over a 2-yr period in Saint Joseph Bay, FL.  $n = 78$ –150 individuals per site per season.

of Vadas et al. (1982) that *L. variegatus* has a diet that is governed by the availability and palatability of food items. Substantial qualitative differences were found in the diets of *L. variegatus* occupying the three different microhabitats sampled in Saint Joseph Bay, FL. Previous studies have indicated that *L. variegatus* examined from other geographic areas are dietary generalists, and our investigations support

these observations. Ernest and Blake (1981) and Klinger (1984) noted that the types of foods eaten by *L. variegatus* in the field are determined by the composition of foods available in the environment. McClintock et al. (1982) found *L. variegatus* did not prefer algal over animal foods. A diverse diet may be necessary to sustain the nutritional requirements for growth in *L. variegatus* (Klinger, 1984).

Gut contents of *L. variegatus*, as well as direct feeding observations, generally reflected the composition of foods at each of the three study sites during different seasons of the year (Beddingfield, 1997; Beddingfield and McClintock, 1998). In summer months, at both the *Thalassia* and *Syringodium* sites, epibionts (primarily calcareous red algae and hydroids) were found heavily fouling the distal tips of seagrass blades. Such encrusting microorganisms were included in the diet of *L. variegatus*. Their inclusion in the diet suggests that although seagrass and fleshy algae are likely of superior nutritional quality to epibiotic calcareous algae and hydroids, sufficient nutrients are associated with these plant and animal epibionts to make them attractive to sea urchins. Seagrass blades were often observed grazed completely free of epibionts. Similarly, other sea urchins consume seagrass blades covered with epibionts (Ott and Maurer, 1977; Traer, 1980; Kitting et al., 1984; Orth and Van Montfrans, 1984; Shepard, 1987; Zavodnik, 1987; Klump et al., 1993).

Sea urchins at the sand site ingested large amounts of the green alga *E. compressa* during the winter and spring of both years of the study. *Enteromorpha* spp. are ephemeral, fleshy algae that lack structural and chemical defenses, making them attractive food items for a variety of marine invertebrate grazers (Lubchenko, 1978). Decaying drift seagrass was very abundant and was the primary food resource utilized by sea urchins in the fall at all sites. The sea urchins *Diadema setosum*, *Echinothrix calamaris*, and *Triploneustes gratilla* similarly feed on detrital material when algae and/or seagrasses are not well represented in the habitat (Maharavo et al., 1994). As seen at all sites, attached seagrasses and algae provide a stable and predictable food resource during the winter in Saint Joseph Bay, whereas drift seagrasses are likely displaced episodically by wave action associated with winter storms. A high percentage of individuals were detected ingesting sand at the sand site during summer months. This is likely incidental ingestion that occurs while sea urchins graze on the thin cyanobacterial layer present on sand grains, although the possibility of utilizing organic material found on encrusting sand cannot be discounted (Johnson and Mann, 1982; Klinger, 1984).

Sea urchins at both the *Thalassia* and *Syringodium* sites exhibited opportunistic feeding aggregations on gastropod egg masses in the spring (Beddingfield, 1997), thus taking advantage of a nutrient-rich but temporally variable food resource. These feeding aggregations were also noted on drifted detrital material

concentrated in depressions on the benthos (Beddingfield, 1997; Beddingfield and McClintock, in press). Similar feeding aggregations of the sea urchin *S. droebachiensis* have been reported (Nestler and Harris, 1994).

Although the red alga *L. porteur* was abundant at both seagrass sites in late spring and summer, *L. variegatus* were only rarely observed feeding on this fleshy alga. Moreover, although *L. variegatus* cover themselves extensively with plant and shell materials, they were never observed to use this red alga as cover (Beddingfield, 1997). McConnell et al. (1982) found that a variety of macroalgae may either inhibit or stimulate feeding in *L. variegatus*. Many species of *Laurencia* are chemically defended and resistant to marine grazers (Hay et al., 1987; Hay and Fenical, 1992). Because this is a fleshy alga that lacks structural defenses, chemical defenses are most likely to explain the lack of ingestion of this potential food resource by *L. variegatus*.

In summary, *L. variegatus* displayed marked seasonality in its feeding activities in Saint Joseph Bay and likely does so in other shallow bay environments of the northern Gulf of Mexico. Feeding almost completely ceased during early winter. Although no comparative seasonal feeding data are available for *L. variegatus*, this pattern is likely restricted to the northern limits of its biogeographic distribution where low winter temperatures occur. The present study also indicates that foods ingested by *L. variegatus* in Saint Joseph Bay vary with habitat and that diets parallel seasonal patterns of dietary resource availability. Such spatial and temporal variation in dietary resource utilization is important because food type influences both somatic growth and reproductive condition in this species (Beddingfield and McClintock, 1998). Moreover, feeding patterns of *L. variegatus* are known to have long-term community effects in subtropical seagrass systems (Heck and Valentine, 1995).

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