

# Diets and coexistence of the sea urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) along the central Florida gulf coast

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**ABSTRACT:** The basis for coexistence of similar species is fundamental in community ecology. One mechanism for coexistence is differentiation of diets. *Lytechinus variegatus* and *Arbacia punctulata* coexist in different microhabitats along the Florida gulf coast. Their great difference in morphology might affect their choice of microhabitats and diet. We analyzed diets of both species at 1 offshore and 1 nearshore site where both occurred in relatively equal numbers, an offshore site dominated by *A. punctulata* and an offshore site dominated by *L. variegatus*. Gut contents were analyzed to determine the diet. *A. punctulata* prim. consumed sessile invertebrates except on dates when algal availability was higher than normal. *L. variegatus* primarily consumed macroflora except on dates when macroflora was extremely limited. Electivity indices revealed no strong preferences for particular species of algae, although *L. variegatus* consumed many drift species. *A. punctulata* and *L. variegatus* both fed in a random manner, although they avoided particular species of algae known to contain high concentrations of secondary metabolites. The diet of *A. punctulata* was correlated with algae only over rubble outcroppings at the offshore site with the highest biomass. Diets of offshore populations were more similar to each other, regardless of the presence of conspecifics, than to those of populations at Caspersen Beach (nearshore site). As diets do not overlap, distribution of individuals at a location would not be affected by interspecific competition for food. However, intraspecific competition may be high due to low site productivity.

**KEY WORDS:** Sea urchins · *Arbacia punctulata* · *Lytechinus variegatus* · Diet · Gulf of Mexico · Coexistence

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## INTRODUCTION

Tokeshi (1999, p. 1) noted that species coexistence is 'beguilingly simple and, yet, is a remarkably accurate description of the natural world' and that 'the theme of coexistence of species is central in community ecology'. Pairs of sea urchin species coexist in numerous habitats. They may belong to different genera, e.g. *Paracentrotus lividus* (Lamarck) and *Arbacia lixula* (Linnaeus) in the Mediterranean (Boudouresque & Verlaque 2001) and *Loxechinus albus* (Molina) and *Tetrapygus niger* L. Agassiz (Vásquez 2001) along the Chilean coast or be of the same genus with distinct morphologies, e.g. *Strongylocentrotus purpuratus* (Stimpson) and *Strongylocentrotus franciscanus*

(Agassiz) (Tegner 2001). Typically species found in pairs differ in microhabitats and diets.

The sea urchins *Lytechinus variegatus* (Lamarck) and *Arbacia punctulata* (Lamarck) occur throughout the Gulf of Mexico and the Caribbean in a variety of environments (Hendler et al. 1995). Along the central Florida gulf coast they usually occupy distinct microhabitats, *L. variegatus* on sand and *A. punctulata* on rock (Hill & Lawrence 2003). Although the diet of *L. variegatus* in seagrass beds has been well documented, few studies have recorded the diet at depths greater than 5 m. In shallow water, it is a generalist grazer of fresh and detrital algae, seagrasses (Moore et al. 1963, Lowe & Lawrence 1976, Vadas et al. 1982, Keller 1983, Greenway 1995, Couto 1998, Beddingfield

& McClintock 1999), and occasionally animals (Lowe & Lawrence 1976). The diet of *A. punctulata* is not well documented. Parker (1932) and Harvey (1956) stated that it is an omnivore, and Karlson (1975) called it a generalized carnivore. *A. dufresnei* is primarily carnivorous in Argentinian waters (Penchaszadeh & Lawrence 1999). The Mediterranean *A. lixula* feeds on algae and invertebrates (Frantzis et al. 1988), although studies on interaction between *Paracentrotus lividus* and *A. lixula* have focused primarily on herbivory (Benedetti-Cecchi & Cinelli 1995, Benedetti-Cecchi et al. 1998, Bulleri et al. 1999, 2002). Understanding the feeding habits of sea urchins is essential to assess the impact of these animals within a community and their interactions with each other and their prey.

Very few studies document the feeding habits of *Lytechinus variegatus* and *Arbacia punctulata* outside seagrass beds. However, *L. variegatus* and *A. punctulata* coexist at many offshore locations with highly variable algal communities in the Gulf of Mexico (Cobb & Lawrence 2003, Hill & Lawrence 2003). Therefore, it is reasonable to assume that the diets and interactions of *L. variegatus* and *A. punctulata* will also vary between these populations. In this study, we asked (1) how the diets of *L. variegatus* and *A. punctulata* overlap, (2) if diets differ when the species coexist and when only 1 species dominates a site, (3) if each species selects specific foods or feeds randomly, and (4) if each species shows a preference for feeding over sand or rubble.

## MATERIALS AND METHODS

**Field observations and collection.** Three offshore sites and 1 nearshore site along the central west coast of Florida (Fig. 1) were selected based on *a priori* knowledge of sea urchin populations. Observations were made and specimens collected at all sites using SCUBA. Collection dates, GPS coordinates, depths, and water temperature are given in Table 1. Site 1, approximately 37.5 km offshore, was dominated by *Arbacia punctulata*, although individuals of *Lytechinus variegatus* were found occasionally. The substratum consisted primarily of flat, rubble outcroppings of limestone with sparse patches of sand. Macroalgae were evenly distributed and included large stands of *Sargassum* sp. several meters in length. Sessile invertebrates were common and primarily included sponges and ascidians. Site 1 is 15.1 km west of Sites 2 and 3.

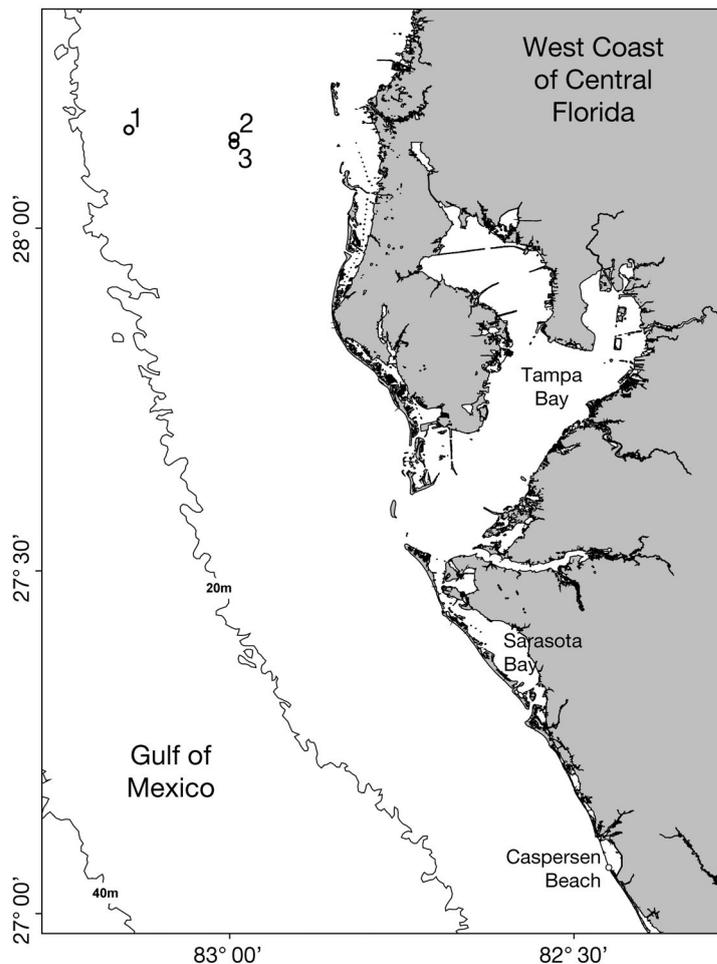


Fig. 1. Locations of offshore (1–3) and near-shore (Caspersen Beach) sites on the central Florida gulf coast shelf

At Site 2, both *Lytechinus variegatus* and *Arbacia punctulata* were present in large numbers. Large limestone outcroppings were moderately scattered over swaths of sand. *L. variegatus* was often found on sand, heaped with various shells or algae, while *A. punctulata* was only found attached to rubble. Sponges, ascidians, and some macroalgae were found attached to rubble outcroppings. Site 2 is only 193 m from Site 3.

Only *Lytechinus variegatus* was present at Site 3, which consisted primarily of barren sand. A few natural outcroppings were sparsely distributed and smaller in size than those at Site 2. A few concrete bricks acted as an artificial reef substratum for some ascidians and other sessile invertebrates.

The nearshore site is approximately 300 m off Caspersen Beach. Both species of sea urchins were found in similar numbers. Large rubble outcroppings were abundant on sand flats at approximately 6 m in depth. *Arbacia punctulata* was only present on rubble outcroppings while *Lytechinus variegatus* was found on

Table 1. Sampling locations, depths and dates in the Gulf of Mexico. Water temperature is also shown at sampling sites. Water temperature was lowest at Caspersen Beach on January 17, 2000. Dash indicates not measured

	Site 1	Site 2	Site 3	Caspersen
Location	28° 8.56' N 83° 8.82' W	28° 7.56' N 82° 59.70' W	28° 7.45' N 82° 59.70' W	27° 4' N 82° 27' W
Depth (m)	17.7	11.9	11.9	5.8
	Water temperature (°C)			
Sampling date				
Sep 29, 1999	–	–	–	27.2
Oct 2, 1999	26.7	26.7	26.7	–
Jan 17, 2000	–	–	–	17.2
Apr 8, 2000	21.7	21.7	23.3	–
Jun 15, 2000	–	–	–	29.4
Aug 23, 2000	–	–	–	30.0
Nov 12, 2000	22.2	21.7	21.7	–

both substratum types. Caspersen Beach closely resembles Site 2, although rubble outcroppings merge into sand patches, while microhabitats at Site 2 are discrete. Limestone outcroppings supported a number of species of ascidians, sponges, hydroids, and gorgonians. Macroalgae were sparsely distributed over rubble at sampling depths. Drift algae were common over sand at most depths, and large stands of red macroalgae and *Caulerpa* spp. were noted in areas of high hydrodynamics at approximately 3.5 m in depth.

Ten specimens of the dominant species of sea urchin (or both species if each was equally abundant) were collected from each site for gut content analysis. Each sea urchin was injected with a 4% formalin solution (Vadas 1985) to preserve gut contents. Sea urchins of similar size were collected haphazardly from both sand and rubble. Samples were collected from all offshore sites in the fall of 1999, and spring and fall of 2000. During the spring of 2000, an algal bloom prevented divers from locating rubble outcroppings to collect samples over hard substrata at 1 offshore site. Nearshore collections at Caspersen Beach were made in the fall of 1999, and winter, spring, and summer of 2000.

Samples of macroalgae and plants (collectively referred to as flora) were collected from quadrats over rubble and sand, along with the sea urchins, to document the species present within each habitat and to estimate available biomass at each site. These data are published in Cobb & Lawrence (2003).

**Measurements of sea urchin size and calculation of repletion index.** Test diameter was measured and wet weight obtained for each sea urchin prior to dissection. A repletion index was calculated according to Régis (1980) and Verlaque & Nédelec (1983):

$$(\text{wet weight of gut contents} \times 100) / \text{wet body weight} \quad (1)$$

Differences in size and repletion indices between sites were determined by ANOVA and Tukey's multiple comparison test.

**Gut content analysis.** Gut contents were analyzed using the point-count method described by Jones (1968) to determine abundance of each item in the gut as done by Verlaque (1984) and Frantzis et al. (1988). Gut contents were sieved through a 595  $\mu\text{m}$  sieve to remove fine sediment and items too small to identify. Then 2 ml of the remaining gut contents were placed into a petri dish with a 2.5  $\times$  2.5 cm grid. Gridlines were spaced in increments of 25 mm resulting in 121 intersections. The frequency with

which each specimen in the gut contacted the intersections of the grid was recorded and used to determine the relative abundance of each food type within the gut. Five replicates were analyzed for each sea urchin to calculate average abundance and to insure consistency.

Plant and macroalgal specimens in the gut were identified as with field specimens. All samples were separated by species and identified by external morphology and examination of cross sections according to Dawes (1974) with taxonomic names corrected using Wynne (1986). In some cases, gut specimens were indistinguishable and had to be grouped into broader categories. For example, species of the genera *Micropeuce*, *Polysiphonia*, *Murrayella*, and *Lophosiphonia* were counted under the group name 'Family Rhodomelaceae (4)'. Other members of the family Rhodomelaceae distinguishable from these 4 genera were counted separately. To avoid confusion and simplify quantification, fragments of material covered by several species of minute epiphytes were grouped together as 'epiphytes'.

Animals in the gut were identified to the genus level whenever possible. Due to the difficulty in accurately identifying partially digested fragments, most animals were grouped into higher taxa. References used to identify most animals were Sterrer (1986) and Ruppert & Fox (1988). Hydroids could often be classified to genus according to Fraser (1944). Some bryozoans were identifiable according to Shier (1964); however, most cheilostomes and cyclostomes could not be classified beyond order. Fragments of crustaceans other than barnacles were often too small to identify species. Some tunicates could be classified according to Van Name (1945) and Plough (1978). Animals were grouped into phyla for statistical analysis.

The total number of grid intersections using the point-count method for all animal and floral material consumed by each sea urchin were averaged for each site and collection date. Flora and fauna consumed by each species of sea urchin were compared using a paired Student's *t*-test or the Wilcoxin signed rank test.

The contingency coefficient (*C*) was used to measure the degree of association between the diet of sea urchins and different sites and sampling dates:

$$C = \sqrt{\chi^2 / (N + \chi^2)} \quad (2)$$

The frequency of each food was used to calculate chi-square ( $\chi^2$ ), and the sum of all observed frequencies (*N*) was used to compute *C*. Values of *C* were also used to measure the similarity of the diets of coexisting sea urchins at Site 2 and Caspersen Beach.

The Index of Proportional Similarity (*Sc*) of Czekański (as used in Verlaque & Nédelec 1983) was used to compare floral diet with floral availability of each microhabitat within a site to determine if sea urchins were feeding over specific substrates:

$$Sc = \sum \text{MIN}(P_i, Q_i) / 100 \quad (3)$$

Variables  $P_i$  and  $Q_i$  represent percentage abundance of food item *i* in groups *P* and *Q*, which in this case is food *i* consumed by one sea-urchin species and availability of food *i* in the environment. The Index of Proportional Similarity is the sum of the minimum (MIN, the lower of the 2 values  $P_i$  and  $Q_i$ ) percentage abundance of each food item, divided by 100. This index was used to compare flora consumed by each sea urchin species with available flora over rubble, sand, and rubble and sand combined. Flora over sand was also compared with flora over rubble to calculate differences between microhabitats at each site.

Abundance of each floral species consumed by *Arbacia punctulata* and *Lytechinus variegatus* was compared with availability of floral material at each site using Strauss's Food Selectivity Index (*L*) to determine random or selective feeding of each food by sea urchins (Strauss 1979):

$$L = r_i - p_i \quad (4)$$

where  $r_i$  is relative abundance of food *i* in the gut and  $p_i$  is relative abundance of food *i* in the environment. Therefore Strauss's index ranges from -1.0 (avoidance) to +1.0 (preference). Values were categorized as follows:

Index range		Selectivity
-1.00	to -0.75	Strong avoidance
-0.74	to -0.25	Moderate avoidance
-0.24	to 0.24	Random feeding
0.25	to 0.74	Moderate preference
0.75	to 1.00	Strong preference

## RESULTS

### Size and repletion index

Size of *Arbacia punctulata* did not vary greatly between collection dates at most sites (Table 2). Repletion indices were greater at Site 1 than at either Site 2 or Caspersen Beach.

*Lytechinus variegatus* was significantly larger at both Sites 2 and 3, and showed much less variation among sampling dates than individuals at Caspersen Beach (Table 2). Repletion indices fluctuated considerably between collection dates although no distinction between sites was detected.

### Diet composition

*Laurencia* spp. (covered with epiphytes, and other small epiphytic red algae of the Rhodomelaceae) were the most frequently consumed macroflora by *Arbacia punctulata* at Site 1 (Table 3). *A. punctulata* primarily ingested small epiphytic algae or drift algae at all other sites. *Lytechinus variegatus* frequently consumed a greater diversity of macroflora than *A. punctulata*. Both sea urchins consumed a wide diversity of sessile invertebrates at all locations, particularly hydrozoans, ectopods, and barnacles (Table 4).

Table 2. *Arbacia punctulata* and *Lytechinus variegatus*. Test diameter (mm) and repletion indices at offshore and nearshore sites in the Gulf of Mexico. (mean ± SD; n/p: species not present; n/a: data not available; n = 7 for *L. variegatus* in August 2000; n = 10 on all other collection dates)

	<i>Arbacia punctulata</i>		<i>Lytechinus variegatus</i>	
	Test diameter	Repletion index	Test diameter	Repletion index
Site 1				
Oct 99	39.1±4.1	5.5±1.3	n/p	n/p
Apr 00	33.9±6.7	9.7±1.6	n/p	n/p
Nov 00	40.8±4.6	7.3±1.9	n/p	n/p
Site 2				
Oct 99	30.4±4.2	4.4±2.7	73.1±2.7	6.8±1.8
Apr 00	30.9±4.3	5.2±2.1	74.7±2.1	11.5±3.1
Nov 00	36.3±3.2	4.9±1.7	71.7±2.9	7.5±2.0
Site 3				
Oct 99	n/p	n/p	73.6±2.9	8.3±1.8
Apr 00	n/p	n/p	73.0±3.7	13.2±3.5
Nov 00	n/p	n/p	73.8±2.4	6.0±1.2
Caspersen				
Sep 99	27.9±4.1	2.5±0.8	46.9±3.9	7.1±3.3
Jan 00	n/a	n/a	58.6±2.8	10.1±3.1
Jun 00	30.7±5.1	3.7±2.5	57.3±3.8	7.4±2.3
Aug 00	38.3±6.5	4.5±1.3	62.7±7.0	5.1±1.8

Table 3. *Arbacia punctulata* and *Lytechinus variegatus*. Frequency of ingested flora (n = 10). 1: Site 1, 10/2/99 (mo/d/yr); 2: Site 1, 4/8/00; 3: Site 1, 11/12/00; 4: Site 2, 10/2/99; 5: Site 2, 4/8/00; 6: Site 2, 11/12/00; 7: Site 3, 10/2/99; 8: Site 3, 4/8/00; 9: Site 3, 11/12/00; 10: Caspersen, 9/29/99; 11: Caspersen, 1/17/00; 12: Caspersen, 6/15/00; 13: Caspersen, 8/23/00

Collection	<i>Arbacia punctulata</i>									<i>Lytechinus variegatus</i>									
	1	2	3	4	5	6	10	12	13	4	5	6	7	8	9	10	11	12	13
Cyanophyta	1	1	0	1	0	0	0	4	2	0	0	0	0	0	3	0	0	0	1
Chrysophyta	0	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0	0	1
Chlorophyta																			
<i>Bryopsis pennata</i>	0	0	0	0	0	0	0	0	0	0	5	0	1	7	0	0	0	0	0
<i>Caulerpa</i> spp.	0	0	0	0	0	0	1	0	3	0	1	0	7	4	0	0	0	0	3
<i>Cladophora</i> spp.	0	5	0	4	7	0	1	1	2	1	10	0	0	9	3	0	0	0	1
<i>Codium</i> spp.	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0
<i>Enteromorpha</i> spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Pseudocodium floridanum</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0
<i>Udotea</i> spp.	2	1	2	0	0	0	0	0	0	0	2	0	2	1	1	0	0	0	0
Phaeophyta																			
<i>Cladosiphon occidentalis</i>	0	4	0	0	0	0	0	0	0	0	3	0	0	6	0	0	0	0	0
<i>Dictyota</i> spp.	5	4	1	2	1	0	0	0	3	10	3	1	7	1	1	0	1	0	6
<i>Lobophora variegata</i>	0	0	0	1	2	1	0	0	0	0	0	1	0	0	2	0	0	0	0
<i>Sargassum</i> spp.	0	0	0	0	0	0	0	0	0	0	8	4	0	8	6	0	1	0	0
<i>Sphacelaria tribuloides</i>	0	0	0	0	1	3	0	0	0	2	6	3	0	4	3	0	0	0	0
Rhodophyta																			
<i>Acanthophora muscoides</i>																			
<i>Agardhiella</i> spp.	0	0	0	0	0	0	1	0	2	0	0	0	1	2	1	6	7	9	4
<i>Amphiroa</i> spp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Batophora oerstedii</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Botryocladia occidentalis</i>	3	1	0	0	0	0	0	0	0	0	2	0	0	0	0	9	1	0	0
<i>Caloglossa leprieuri</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Centroceras</i> spp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2
<i>Ceramium</i> spp.	0	4	0	0	5	0	0	7	6	1	10	0	0	8	0	1	0	0	5
<i>Champia parvula</i>	0	2	0	0	0	1	0	0	1	1	4	0	0	5	0	0	0	1	2
<i>Chondria</i> spp.	0	2	1	0	0	0	0	0	0	0	2	0	0	1	0	0	2	0	0
<i>Dasya</i> spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Euchema nudum</i>	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	2	0	2	1
Family Rhodomelaceae (4)	3	7	0	0	1	0	0	7	4	5	7	0	2	6	1	0	1	8	1
<i>Gelidium</i> spp.	0	0	0	1	1	2	0	0	0	1	0	0	0	1	1	1	1	0	4
<i>Gracilaria</i> spp.	0	0	1	0	1	0	0	0	1	0	1	0	3	0	1	0	4	10	5
<i>Hypnea</i> spp.	0	0	0	0	0	0	1	3	7	0	1	0	0	0	0	7	7	10	6
<i>Jania</i> spp.	0	0	1	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0
<i>Kylinia crassipes</i>	0	0	0	0	0	0	1	0	0	0	10	1	0	9	2	0	0	0	0
<i>Laurencia</i> spp.	6	8	5	2	1	0	0	0	0	1	1	2	0	0	1	2	0	0	0
<i>Lithothamnion</i> spp.	0	0	8	1	4	2	0	0	0	5	4	7	2	3	7	0	0	0	0
<i>Spyridia filamentosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1
Epiphytes	0	8	8	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0
Unidentifiable algae	5	6	5	0	1	0	2	5	8	3	9	2	4	6	7	4	5	5	7
Anthophyta																			
<i>Thalassia testudinum</i>	1	0	0	0	0	0	0	0	0	7	4	10	4	3	6	0	1	1	0
Unidentifiable plant	0	0	0	0	0	0	0	0	0	0	3	1	2	1	2	0	2	1	0

Comparison of the amount of flora and fauna in the gut contents of *Arbacia punctulata* showed that all populations normally ingested more animals than plants or ingested both in equal proportions (Fig. 2). However, *Lytechinus variegatus* consumed significantly more flora than fauna during the spring and summer at all sites (Fig. 3). Both species consumed significantly more animals than flora in November 2000 at all offshore locations and during October 1999 at Site 3.

Diets of different populations within species are compared in Table 5A. The diet of *Arbacia punctulata*

at Site 1 during October 1999 was significantly different from the diet of populations at all other sites. The diet of *A. punctulata* at Site 1 was also significantly different from specimens at Caspersen Beach on all collection dates. *Lytechinus variegatus* at Caspersen Beach had very little overlap in diet between dates and was significantly different from all offshore collections.

The diet of *Arbacia punctulata* and *Lytechinus variegatus* was also compared at sites where these species coexist (Table 5B). The diets of coexisting sea urchins

Table 4. *Arbacia punctulata* and *Lytechinus variegatus*. Frequency of ingested fauna (n = 10). 1: Site 1, 10/2/99 (mo/d/yr); 2: Site 1, 4/8/00; 3: Site 1, 11/12/00; 4: Site 2, 10/2/99; 5: Site 2, 4/8/00; 6: Site 2, 11/12/00; 7: Site 3, 10/2/99; 8: Site 3, 4/8/00; 9: Site 3, 11/12/00; 10: Caspersen, 9/29/99; 11: Caspersen, 1/17/00; 12: Caspersen, 6/15/00; 13: Caspersen, 8/23/00. See Cobb (2002) for a more detailed list of animals consumed by sea urchins

Collection	<i>Arbacia punctulata</i>									<i>Lytechinus variegatus</i>									
	1	2	3	4	5	6	10	12	13	4	5	6	7	8	9	10	11	12	13
Porifera	3	3	7	1	0	6	4	1	5	2	3	3	1	0	1	2	4	0	2
Cnidaria	8	5	6	4	0	2	4	3	5	10	4	2	6	5	10	6	7	3	3
Ectoprocta	7	6	5	3	8	7	0	0	1	6	8	10	5	6	9	0	5	1	0
Sipuncula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Mollusca	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1
Annelida	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0
Arthropoda																			
<i>Balanus</i> sp.	0	0	0	7	0	10	9	10	7	10	4	10	10	9	10	3	2	10	6
Errant Crustacea	0	1	0	0	0	0	2	1	1	7	3	7	3	0	8	2	1	1	2
Chordata	5	1	7	3	1	10	0	0	0	7	4	9	5	1	7	0	0	0	0
Unidentifiable tube dweller	0	0	0	3	0	3	2	2	7	9	10	6	10	3	7	1	8	1	6
Unidentifiable animal	8	7	8	0	1	0	1	0	1	3	0	2	1	1	2	0	3	3	4
Unknown (flora or fauna)	3	0	1	1	1	2	2	0	3	2	6	4	5	3	8	1	6	0	1

**Feeding selectivity**

Czekanowski's Index of Proportional Similarity showed no strong correlations between the diet of *Arbacia punctulata* and *Lytechinus variegatus* with the available flora found over different substrates (Table 6). Moderate similarity (25 to 75%) was noted at Site 1 between the diet of *A. punctulata* and flora found over rubble in October 1999 and April 2000. The diet of *L. variegatus* was also moderately similar to flora available over sand and rubble at Caspersen Beach in June 2000. This was one of 3 collections when flora was equally abundant over sand and rubble, as indicated by the high index of similarity in the last column of Table 6.

Comparison of the available proportions of flora in each habitat and flora consumed by sea urchins using

were significantly different during the fall of 1999 at both Site 2 and Caspersen Beach, and during June 2000 at Caspersen Beach.

Stauss's Feeding Selectivity Index indicates that *Arbacia punctulata* and *Lytechinus variegatus* tend to graze in a random manner on most species of flora.

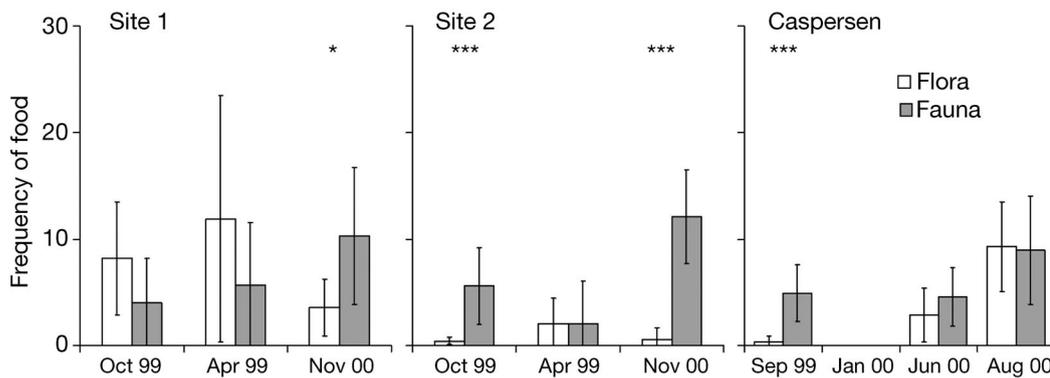


Fig. 2. *Arbacia punctulata* Frequency of ingested flora and fauna by point counts. Error bars represent 95% confidence interval. (n = 10). \*p < 0.05, \*\*\*p < 0.001

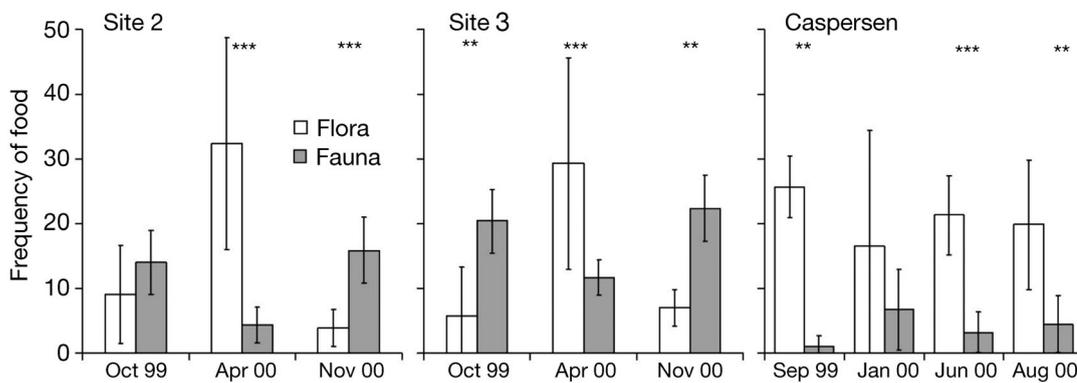


Fig. 3. *Lytechinus variegatus*. Frequency of ingested flora and fauna by point counts. Error bars represent 95% confidence interval. (n = 10 on all collection dates except in August 2000, where n = 7). \*\*p < 0.01, \*\*\*p < 0.001

Table 5. *Arbacia punctulata* and *Lytechinus variegatus*. Contingency coefficient values of the diets (flora and fauna) of (A) each species between different sites and dates and (B) between coexisting species at Site 2 and Caspersen Beach. Possible values range from 0.00 (identical diets) to 1.00 (dissimilar diets). Underlined values indicate statistically significant comparisons (p < 0.05)

(A) <i>Arbacia punctulata</i>		Site 1			Site 2			Caspersen			
		Oct 99	Apr 00	Nov 00	Oct 99	Apr 00	Nov 00	Sep 99	Jun 00	Aug 00	
Site 1	Oct 99	0.00	<u>0.54</u>	0.53	<u>0.55</u>	<u>0.66</u>	<u>0.64</u>	<u>0.66</u>	<u>0.71</u>	<u>0.70</u>	
	Apr 00	-	0.00	0.51	<u>0.55</u>	<u>0.60</u>	<u>0.61</u>	<u>0.69</u>	<u>0.66</u>	<u>0.67</u>	
	Nov 00	-	-	0.00	0.53	0.65	0.60	<u>0.66</u>	<u>0.71</u>	<u>0.68</u>	
Site 2	Oct 99	-	-	-	0.00	<u>0.64</u>	0.53	0.57	<u>0.64</u>	<u>0.66</u>	
	Apr 00	-	-	-	-	0.00	0.62	0.71	0.60	0.65	
	Nov 00	-	-	-	-	-	0.00	0.55	0.61	0.61	
Caspersen	Sep 99	-	-	-	-	-	-	0.00	0.57	0.54	
	Jun 00	-	-	-	-	-	-	-	0.00	0.41	
	Aug 00	-	-	-	-	-	-	-	-	0.00	
<i>Lytechinus variegatus</i>		Site 3			Site 2			Caspersen			
		Oct 99	Apr 00	Nov 00	Oct 99	Apr 00	Nov 00	Sep 99	Jan 00	Jun 00	Aug 00
Site 3	Oct 99	0.00	<u>0.59</u>	0.48	<u>0.54</u>	<u>0.67</u>	0.51	<u>0.67</u>	<u>0.65</u>	<u>0.66</u>	<u>0.64</u>
	Apr 00	-	0.00	0.52	<u>0.61</u>	0.49	<u>0.59</u>	<u>0.68</u>	<u>0.65</u>	<u>0.64</u>	<u>0.66</u>
	Nov 00	-	-	0.00	0.51	<u>0.61</u>	0.46	<u>0.68</u>	<u>0.65</u>	<u>0.66</u>	<u>0.67</u>
Site 2	Oct 99	-	-	-	0.00	<u>0.63</u>	0.40	<u>0.68</u>	<u>0.66</u>	<u>0.65</u>	<u>0.66</u>
	Apr 00	-	-	-	-	0.00	<u>0.63</u>	<u>0.67</u>	<u>0.64</u>	<u>0.64</u>	<u>0.65</u>
	Nov 00	-	-	-	-	-	0.00	<u>0.68</u>	<u>0.66</u>	<u>0.67</u>	<u>0.66</u>
Caspersen	Sep 99	-	-	-	-	-	-	0.00	<u>0.62</u>	<u>0.62</u>	<u>0.60</u>
	Jan 00	-	-	-	-	-	-	-	0.00	<u>0.57</u>	<u>0.61</u>
	Jun 00	-	-	-	-	-	-	-	-	0.00	0.53
	Aug 00	-	-	-	-	-	-	-	-	-	0.00
(B) <i>Arbacia punctulata</i> vs. <i>Lytechinus variegatus</i>		Site 2						Caspersen			
		Oct 99	Apr 00	Nov 00	Sep 99	Jun 00	Aug 00	Sep 99	Jun 00	Aug 00	
			<u>0.60</u>			<u>0.60</u>			<u>0.60</u>		
			0.57			<u>0.59</u>					
			0.56			0.53					

Table 6. *Arbacia punctulata* and *Lytechinus variegatus*. Czekanowski's Index of Proportional Similarity of the diet (macroflora only) of sea urchins to different microhabitats within offshore and nearshore sites. Possible values range from 0.00 (dissimilar) to 1.00, which indicates identical proportions of algae species in the gut of the sea urchins and in the environment. Algal availability over sand and rubble substrates is also compared in the last column. n/a: comparison is not applicable because sea urchins were not present or data is unavailable

Site	Date (mo/d/yr)	<i>A. punctulata</i>		<i>A. punctulata</i> × Rubble and sand	<i>L. variegatus</i>		<i>L. variegatus</i> × Rubble and sand	Sand × Rubble
		× Rubble	× Sand		× Rubble	× Sand		
Site 1	10/2/99	0.58	0.28	0.58	n/a	n/a	n/a	0.26
	4/8/00	0.51	0.25	0.50	n/a	n/a	n/a	0.25
	11/12/00	0.37	0.37	0.37	n/a	n/a	n/a	0.34
Site 2	10/2/99	0.24	0.24	0.24	0.25	0.13	0.23	0.88
	4/8/00	0.05	0.01	0.04	0.05	0.01	0.04	0.02
	11/12/00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Site 3	10/2/99	n/a	n/a	n/a	0.24	0.00	0.00	0.00
	4/8/00	n/a	n/a	n/a	n/a	0.31	n/a	n/a
	11/12/00	n/a	n/a	n/a	0.34	0.34	0.34	0.81
Caspersen Beach	9/29/99	0.00	0.00	0.00	0.02	0.00	0.00	0.00
	1/17/00	n/a	n/a	n/a	0.37	0.00	0.00	0.00
	6/15/00	0.27	0.27	0.27	0.47	0.56	0.50	0.74
	8/23/00	0.24	0.33	0.36	0.25	0.27	0.31	0.22

Macroflora consumed with moderate to strong index values are listed in Tables 7 & 8. Both sea urchins exhibited a moderate to strong avoidance for species of *Halimeda*, *Dictyota*, and *Helminthocladia*. Moderate avoidance was noted for *Laurencia* spp. and *Caulerpa* spp. by *A. punctulata*, while the preference of *L. variegatus* for these species fluctuated with date. Both species of sea urchins showed a preference for *Botryocladia occidentalis* and *Agardhiella* spp. on some dates and avoided these species on other occasions. Neither sea urchin strongly favored any species of algae.

## DISCUSSION

A primary factor controlling diets of benthic herbivores is availability of food. With the exception of offshore Site 1, a highly variable diversity of flora occurred at both nearshore and offshore sites (Cobb & Lawrence 2003). Although Site 1 was only 15 km from Sites 2 and 3, which were only 193 m apart, floral community composition varied greatly (Cobb & Lawrence 2003).

Given the low abundance of macroalgal availability at most sites and limited distance chemoreception of sea urchins (De Ridder & Lawrence 1982), the likelihood of frequent encounters of attached algae by sea urchins should be low. With limited availability of

attached fleshy macroalgae and plants in the Gulf (Cobb & Lawrence 2003), consumers may be forced to rely on other sources of food such as encrusting coralline algae, drift algae, and animals.

High repletion indices for *Arbacia punctulata* at Site 1 indicate high consumption, suggesting food is not a limited resource and reducing the probability of intraspecific competition for food. Lower repletion indices support the conclusion that Site 2 is nutritionally poor in comparison to Site 1. Caspersen Beach also consistently had low repletion indices. Caspersen Beach may be food limited but possibly not to the same extent as Site 2.

*Lytechinus variegatus* at Sites 2 and 3 may rely heavily on food other than attached algae. This is indicated by peaks in the repletion index during April 2000 which coincided with the spring bloom of drifting *Cladophora* spp., although total floral biomass was not significantly higher during the spring than in the fall. High repletion indices during January 2000 at Caspersen Beach are inconsistent with previous behavioral patterns of *L. variegatus*. *L. variegatus* normally decreases feeding activity in the winter when food is limited and temperatures are low (Klinger & Lawrence 1984). However, the repletion index does not indicate when feeding occurred, as gut passage time increases when feeding decreases. Dietary preference is often difficult to determine in the field due to variability in the supply of food, which can result

Table 7. *Arbacia punctulata* Feeding selectivity. Values range from -1.00 (avoidance) to 1.00 (preference) with 0.00 indicating random feeding. Only foods with values greater than 0.24 or less than -0.24 are included. All other food found in the gut was ingested randomly on all dates. Dashes indicate days when a species of algae was not present in either the gut or in the environment

Site Species	Date (mo/d/yr)			Date (mo/d/yr)			Date (mo/d/yr)		
	Rubble	Sand	Rubble & sand	Rubble	Sand	Rubble & sand	Rubble	Sand	Rubble & sand
Site 1	10/2/99			4/8/00			11/12/00		
<i>Caulerpa</i> sp.	-0.03	-0.49	-0.04	0.00	-0.03	-0.01	-	-	-
<i>Halimeda discoidea</i>	-0.10	-	-0.10	-0.02	-0.67	-0.10	-0.01	-	0.00
<i>Botryocladia occidentalis</i>	0.21	0.29	0.22	-0.05	0.01	-0.04	-0.01	0.00	-0.01
<i>Laurencia</i> spp.	-0.15	0.22	-0.14	-0.31	0.11	-0.26	-0.53	-0.29	-0.48
Site 2	10/2/99			4/8/00			11/12/00		
<i>Caulerpa prolifera</i>	-	-	-	-	-	-	-	-1.00	0.00
<i>Halimeda discoidea</i>	-	-0.12	-0.02	-0.38	-	-0.34	-0.17	-	-0.17
<i>Dictyota</i> spp.	-0.64	-0.64	-0.64	0.03	0.03	0.03	0.00	-	0.00
<i>Agardhiella subulata</i>	-	-	-	-0.56	-	-0.50	-	-	-
<i>Botryocladia occidentalis</i>	-	-	-	-	-	-	-0.83	-	-0.83
<i>Gelidium</i> spp.	0.10	0.10	0.10	0.26	0.26	0.26	0.25	0.25	0.25
<i>Helminthocladia</i> sp.	-	-	-	-0.01	-0.99	-0.12	-	-	-
<i>Lobophora variegata</i>	0.10	0.10	0.10	0.05	0.05	0.05	0.38	0.38	0.38
Caspersen Beach	9/29/99			6/15/00			8/23/00		
<i>Sargassum filipendula</i>	-0.62	-	-0.62	-	-	-	-0.01	-	-0.01
<i>Agardhiella</i> spp.	0.44	0.44	0.44	-	-	-	0.04	0.04	0.04
<i>Chondria</i> spp.	-	-	-	-	-	-	-0.38	-	-0.22
Family Rhodomelaceae (4)	-	-	-	0.44	0.45	0.44	0.21	0.21	0.21
<i>Gracilaria</i> spp.	-0.36	-	-0.36	-	-0.26	-0.02	0.12	-0.52	-0.16
<i>Hypnea</i> spp.	0.11	0.11	0.11	-0.72	-0.47	-0.70	-0.08	0.01	-0.04

Table 8. *Lytechinus variegatus*. Feeding selectivity. Values range from -1.00 (avoidance) to 1.00 (preference) with 0.00 indicating random feeding. Only foods with values greater than 0.24 or less than -0.24 are included. All other food found in the gut was ingested randomly on all dates. Dashes indicate days when a species of algae was not present in either the gut or in the environment

Site Species	Date (mo/d/yr)											
	Rubble	Sand	Rubble & sand									
Site 2	10/2/99			4/8/00			11/12/00					
<i>Caulerpa</i> spp.	-	-	-	0.01	0.01	0.01	-	-1.00	0.00			
<i>Halimeda discoidea</i>	-	-0.12	-0.02	-0.38	-	-0.34	-0.17	-	-0.17			
<i>Dictyota</i> spp.	-0.75	-0.75	-0.75	0.00	0.00	0.00	0.04	0.04	0.04			
<i>Agardhiella subulata</i>	-	-	-	-0.56	-	-0.50	-	-	-			
<i>Botryocladia</i> <i>occidentalis</i>	-	-	-	0.04	0.04	0.04	-0.83	-	-0.83			
<i>Helminthocladia</i> sp.	-	-	-	-0.01	-0.99	-0.12	-	-	-			
<i>Laurencia</i> spp.	0.46	0.46	0.46	0.07	0.07	0.07	0.46	0.46	0.46			
Site 3	10/2/99			4/8/00			11/12/00					
<i>Caulerpa</i> spp.	0.36	0.36	0.36	-	-0.68	-	-	-0.19	-0.04			
<i>Halimeda discoidea</i>	-	-	-	-	-	-	-0.54	-	-0.51			
<i>Botryocladia</i> <i>occidentalis</i>	-0.30	-	-0.30	-	-	-	-	-	-			
Caspersen Beach	9/29/99			1/17/00			6/15/00			8/23/00		
<i>Sargassum</i> sp(p).	-0.62	-	-0.62	0.02	0.02	0.02	-	-	-	-0.01	-	-0.01
<i>Agardhiella</i> spp.	0.12	0.12	0.12	0.23	0.58	0.23	0.14	0.14	0.14	0.08	0.08	0.08
<i>Botryocladia</i> <i>occidentalis</i>	0.61	0.63	0.61	0.01	0.01	0.01	-	-	-	-0.06	-0.01	-0.04
<i>Chondria</i> sp(p).	-	-	-	-0.53	0.01	-0.53	-	-	-	-0.38	-	-0.22
<i>Gracilaria</i> spp.	-0.36	-	-0.36	0.14	0.14	0.14	0.09	-0.17	0.07	0.06	-0.58	-0.21
<i>Hypnea</i> spp.	0.07	0.07	0.07	0.05	0.05	0.05	-0.52	-0.27	-0.50	-0.06	0.03	-0.02

in a change in food preference over time as resources become limited (Boudouresque & Verlaque 2001). While some sea urchins are strictly herbivorous or carnivorous, the sea urchins in this study are clearly omnivorous and change their diet based on resource availability.

*Arbacia punctulata* consumed equal proportions of flora and fauna only during periods when attached and drifting macroflora were very abundant, such as October 1999 and April 2000 at Site 1. During seasons of moderate to low floral biomass, for example November 2000 at Site 1 or fall collections at Site 2 (Cobb & Lawrence 2003), *A. punctulata* consumed animals almost exclusively. Strauss's Selectivity Index indicates that *A. punctulata* consumed almost all species of algae in a random manner. This implies that *A. punctulata* is a general omnivore when algal abundance is high and is normally carnivorous when algal availability is moderate to low, as is often the case on the Florida gulf coast shelf.

In contrast to *Arbacia punctulata*, *Lytechinus variegatus* exhibits a stronger preference for algal and plant matter than animals. At Sites 2 and 3, *L. variegatus* primarily consumed animals when macroflora abundance was low. However, during April 2000, when combined macroflora biomass over rubble and sand was moderately high and drift algae were very abundant (Cobb &

Lawrence 2003), *L. variegatus* consumed significantly more algal matter. Macroflora abundance at Caspersen Beach was low to moderate on all dates (Cobb & Lawrence 2003); however, *L. variegatus* consumed much more algal matter than animals, except in January 2000. Like *A. punctulata*, random feeding was more common than selection at all sites. This is consistent with laboratory experiments, suggesting that *L. variegatus* detects food only within 8 cm (Klinger & Lawrence 1984). Random feeding has been documented in seagrass beds based primarily on macroflora availability (Vadas et al. 1982).

Because *Arbacia punctulata* and *Lytechinus variegatus* primarily fed in a random manner and showed no strong preferences for any species of algae, neither sea urchin ate large quantities of particular species. Both sea urchins often avoided the calcareous species *Halimeda discoidea* and 2 fleshy species *Dictyota* spp. and *Helminthocladia* sp. As *Sargassum* sp. was qualitatively observed to be in high abundance at Site 1, it can be assumed that *A. punctulata* also avoided consumption of this species. All of these species contain large amounts of secondary metabolites that deter herbivory (Hay & Fenical 1988). *Laurencia* spp. and *Caulerpa* spp., 2 genera that contain anti-herbivory compounds, were often avoided during periods of high algal availability, and consumed in greater quantities by *L. varie-*

*gatus* during fall collections when floral biomass was low. The Mediterranean sea urchin *Paracentrotus lividus* consumes less palatable species such as *Codium fragile* and encrusting algae when resources are limited (Boudouresque & Verlaque 2001).

At Caspersen Beach *Arbacia punctulata* did not consume large amounts of *Sargassum filipendula*, *Gracilaria* spp., or *Hypnea* spp. In laboratory experiments species of *Sargassum* and *Dictyota* are avoided by *A. punctulata*, presumably due to secondary metabolites (Hay et al. 1986, Cronin & Hay 1996, Cronin et al. 1997), while species of *Gracilaria* and *Hypnea* are considered preferred foods (Hay & Fenical 1988). One explanation is that these species occur more often as drift algae at Caspersen Beach and may not be available to *A. punctulata* because it lacks suckered podia, which facilitates the capture of drifting food (De Ridder & Lawrence 1982). However, the arbacioid *Tetrapygyus niger* captures drift algae (Rodríguez 2003). *Lytechinus variegatus* frequently fed on many species of drift algae with the exception of *Sargassum* sp. at Caspersen Beach. Drift Rhodophyta were still consumed in lower proportions than found in the environment. Unlike *A. punctulata*, *L. variegatus* possesses podia with suckers (Flammang 1996) and captures drift algae (J. Cobb unpubl. data). Although drift algae were collected in habitat sampling, it is highly probable that its biomass was underestimated. Feeding on drift algae may explain how *L. variegatus* consumed greater quantities of algae at Caspersen Beach, and during spring collections at offshore sites, than appeared available from floral biomass estimates.

In addition to macroflora, both species consumed a diverse range of animals, many of which contained indigestible structures. Ascidians of the family Didemnidae, which possess stellate spicules of calcium carbonate, often epiphytized *Laurencia* sp. and were frequently consumed by *Arbacia punctulata*. Other animals primarily included sessile species such as encrusting bryozoans, barnacles, hydrozoans, sponges, and tube dwelling organisms. Errant invertebrates such as mollusks and crustaceans were consumed less frequently. Consumption of animals with large quantities of inorganic material suggests that sea urchins may feed indiscriminately on animals as well as algae. However, sampling may be biased with respect to soft-bodied organisms that would be rapidly digested and difficult for researchers to identify.

Restricted feeding by *Arbacia punctulata* to a particular substrate could not be detected by Czekanowski's index, except when algal availability was exceptionally high over rubble at Site 1. In this case *A. punctulata* exhibited a moderate preference for algae over rubble. No other correlation with substrate was detected at Site 2, Site 3, or Caspersen Beach for *A.*

*punctulata* or *Lytechinus variegatus*. The probability of detecting a true pattern between the feeding of sea urchins and a particular substrate by a similarity index is greatly diminished by low abundance of each algal species and the tendency of *A. punctulata* to consume large quantities of animals. In addition, available flora over rubble and sand were quite similar on some dates. This observation is attributed to extremely low diversity and biomass of macroflora. Although the reliability of Czekanowski's index can be questioned when flora are sparse, *A. punctulata* was always observed on rubble outcroppings and *L. variegatus* was primarily found on sand. Many sessile animals consumed, such as sponges, tunicates, and hydroids, were only observed on rubble outcroppings. This implies that *A. punctulata* and *L. variegatus* fed on rubble at least during periods when algal availability was low. Some species of algae consumed by *L. variegatus*, such as *Caulerpa*, were only observed over sand or shell hash. Based on qualitative observations it is likely that *L. variegatus* at least feeds on both types of substrate.

All collections in this study were conducted during the day, although feeding preferences over different substrates may change during the night. Laboratory experiments by Hay et al. (1986) demonstrated that chemotaxis and feeding preferences of *Arbacia punctulata* show diurnal rhythms. Like the tropical sea urchin *Diadema setosum* (Lawrence & Hughes-Games 1972), *A. punctulata* and *Lytechinus variegatus* feed more during the night (J. Cobb unpubl. data).

As *Arbacia punctulata* tends to consume large quantities of animals while *Lytechinus variegatus* primarily consumes plants and algae, it is not surprising that very little overlap in the diet of these species was detected using the contingency coefficient at either Caspersen Beach or Site 2. Interspecific competition is therefore unlikely, except under conditions of extremely low flora availability, such as those observed at Site 2 in 2000, when both species may feed solely on animals. This is also supported by comparison of diets between sampling sites that contain 1 species of sea urchin and sites with both species. Comparisons between offshore sites indicate moderate overlap between the diets of sea urchins of the same species which solely dominate an area (*A. punctulata* at Site 1 or *L. variegatus* at Site 3) and sites where species co-exist (Site 2). If interspecific competition for food existed, we would expect a shift in diet of both species at Site 2 because of the presence of a competitor. Differences in diet of offshore populations and nearshore populations are most likely attributed to differences in diversity of algae available at these sites, although this can not be verified without proper replicates. Macroalgae diversity was more similar between offshore locations compared to Caspersen Beach.

In summary, diets of *Arbacia punctulata* and *Lytechinus variegatus* do not overlap significantly at sites along the Florida gulf coast shelf. Both species feed randomly on most species of algae when available. Competition for food is unlikely as *A. punctulata* primarily consumes animal foods while *L. variegatus* primarily consumes algae and plants. Shallow sites less than 12 m in depth appear to exhibit more variability in community composition with season. When floral biomass decreases at these locations, competition for food may increase as both species consume larger quantities of animals. Drift algae may also play an important role in the diet of *L. variegatus* at sites of low floral biomass. Tokeshi (1999) stated that a small overlap in resource utilization is likely due to (1) competition over evolutionary and/or contemporary time, (2) independent evolutionary diversification in niche characteristics, or (3) phylogenetic distance between species resulting in little overlap in niche characters, including pattern of resource use. We do not know whether the progenitors of *Arbacia punctulata* and *Lytechinus variegatus* competed. Our observations indicate they do not compete now as they occupy distinct microhabitats except in heterogeneous situations. This seems to be the result of their distinct morphological characteristics.

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