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Habitats and Characteristics of the Sea Urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) on the Florida Gulf-Coast Shelf

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With 6 figures and 3 tables

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Abstract. *Lytechinus variegatus* and *Arbacia punctulata* have been studied primarily in inshore, shallow-water areas. However, they are abundant in deeper waters on the Florida gulf-coast shelf and seem important components of the benthic communities there. *Lytechinus variegatus* occurs alone on sand bottoms and *A. punctulata* occurs alone on rubble bottoms in these deeper waters. The species also co-occur there on heterogeneous bottoms, each in a distinct microhabitat with *A. punctulata* on rubble and *L. variegatus* on surrounding sand. Characteristics of the sea urchins in these different deeper-water habitat types and at one nearshore site with a heterogeneous rubble-sand bottom were compared. Over the 2-year study, offshore individuals of both species had low gut and gonad indices and the maximum size of individuals did not change. This suggests food limitation and low production. Offshore, *A. punctulata* had a higher Aristotle's lantern index and lower gut and gonad indices in populations where it co-occurred with *L. variegatus* compared to populations where it occurred alone. The Aristotle's lantern index of *L. variegatus* did not differ among the offshore sites. Neither species seemed food limited at the nearshore site. Although productivity is lower at the offshore sites, both species extend their distribution and reproduction potential by existing there.

Problem

Co-occurring species tend to use different resources (Begon *et al.*, 1996; Putman & Wratten, 1984; Stiling, 1999). In a review of 76 studies, Schoener (1974) found that habitat was the resource that differed most frequently (55 %), followed by diet (40 %) and time (5 %). In a review of 37 fish species, Ross (1986) found diet differed most (57 %), followed by habitat (32 %) and time (11 %).

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This also seems true for sea-urchin species co-occurring in shallow water. They tend to differ in physical characteristics that affect their habitat potential. The congeners *Strongylocentrotus franciscanus* (Agassiz) and *Strongylocentrotus purpuratus* (Stimpson) co-occur, but large differences in test diameter and relative spine length result in differences in susceptibility to predation, behavior, and habitat partitioning (Tegner, 2001). Both species feed on algal detritus or drift material as well as attached algae. In the Mediterranean, *Paracentrotus lividus* (Lamarck) can co-occur with *Arbacia lixula* (Linnaeus) (Boudouresque & Verlaque, 2001). They differ in vertical zonation, with *A. lixula* dominant at upper levels and *P. lividus* at lower ones. Although overlapping in habitat, their diets differ. The former is mainly a browser of coarsely branched erect algae with the capacity to capture drift material and the latter is a grazer that cannot capture drift material. When erect algae are not present, *P. lividus* shifts its diet to overlap with that of *A. lixula*. *Loxechinus albus* (Molina) and *Tetrapygus niger* L. Agassiz co-occur on the northern Chilean coast (Vásquez, 2001). Contreras & Castilla (1987) and Vásquez (1992) suggested overgrazing by *Tetrapygus niger* and the gastropod *Tegula tridentata* Potiez & Michaud decreases the abundance of *L. albus*. In contrast, Viviani (1975) suggested *L. albus* would outcompete *T. niger* in northern Chile. Like the paired *P. lividus* – *A. lixula, L. albus* has the ability to capture drift material while the arbacioid *T. niger* does not (Contreras & Castilla, 1987). In the Beagle Channel, both *Arbacia dufresnei* (Blainville) and *L. albus* co-occur on boulders, but *A. dufresnei* eats invertebrates and *L. albus* eats algae (Vásquez *et al.*, 1984)

Lytechinus variegatus (Lamarck) occurs in shallow water from North Carolina to Santos, Brazil, and throughout the Caribbean and the Gulf of Mexico (Serafy, 1979). The species usually thought of as inhabiting seagrass beds, but it can occur on rock, shell-hash, sand, and hard bottoms and consumes such a variety of food that it can be classified as an omnivore (Watts *et al.*, 2001). *Arbacia punctulata* (Lamarck) occurs in shallow water from Massachusetts to Cuba and the Yucatan Peninsula, from Texas to Florida in the Gulf of Mexico, the coast from Panama to French Guiana and in the Lesser Antilles (Serafy, 1979). It is found on rocky, sandy, or shelly bottoms (Serafy, 1979). It also is omnivorous, consuming a wide variety of prey (Wahl & Hay, 1995) although Karlson (1978) classified it as a generalized carnivore. The two species are members of different orders: *L. variegatus* (Temnopleuroida) has the advanced camarodont lantern and the tube feet on its dorsal surface have well-developed suckers whereas *A. punctulata* (Arbacioida) has the less advanced stirodont lantern and the tube feet on its dorsal surface lack well-developed suckers.

Despite these differences and the usual lack of co-occurrence, the two species can be found together. Both species co-occur on sandy shell bottoms at 2 to 4 fathoms depth at Beaufort, North Carolina (Sharp & Gray, 1962). *Arbacia punctulata* can be found rarely along with *L. variegatus* in seagrass beds (*e.g.* Kier, 1975; J. Valentine, pers. comm.). Dredging showed a high degree of association of *A. punctulata* and *L. variegatus* on the central Florida gulf-coast shelf on quartz sand and crushed shell in association with limestone outcroppings (Serafy, 1979), but did not discriminate microhabitats.

Knowledge of the abundance and distribution of species is not sufficient to understand how well they function in specific habitats. Density and size of sea urchins are not necessarily coupled because the latter is dependent upon food availability (Ebert, 1968). Size, however, is difficult to use to evaluate habitat quality except in long-term studies as it may indicate age rather than food availability. In sea urchins, body compartment indices can be used as an indication of food availability. An inverse relationship between the Aristotle's lantern index and food availability has been reported (Ebert, 1980; Edwards & Ebert, 1991; Levitan, 1991; McShane & Anderson, 1997), although there is disagreement as to whether this results from increased lantern growth or test shrinkage (Ebert, 2001). Lawrence *et al.* (1996, 1998) did not find this inverse relationship for two sea urchin species. As the size of the gut and gonads depends on food availability (Lawrence & Lane, 1982), the respective indices can be used to indicate nutritional condition and habitat quality.

Hill & Lawrence (1999) suggested that the different structural characteristics of *Lytechinus variegatus* and *Arbacia punctulata* indicate different life-history strategies, *L. variegatus* being more ruderal and *A. punctulata* more stress-tolerant. They found physiological characteristics to support this conclusion. The co-occurrence of *Lytechinus variegatus* and *Arbacia punctulata* on the Florida gulf-coast shelf provides an unusual opportunity to compare their characteristics and production on a major geographic feature of the eastern Gulf of Mexico.

Material and Methods

1. Collecting sites

The study sites are on the Florida gulf-coast shelf (Fig. 1). The locations, depths, dates of sampling and observation, and characteristics of the sites are given in Table 1. Four sites (1–4) are approximately 19 km offshore Tampa, three at depths of 13 m and one at 20 m. One site (5, Caspersen Beach) is only 0.3 km offshore at a depth of 7 m. Two sites were homogeneous, one (1) consisting of a rubble bottom, the other (2) of sand. The other three sites (3 to 5) were heterogeneous with rubble patches surrounded by sand. Macroalgae and colonial sessile invertebrates were found on the rubble. Collections and observations were not made at some dates because of logistics.

2. Densities and size frequency distribution

Two transects were made at each site by SCUBA to measure sea urchin density. A 30 m straight line was placed haphazardly on the substratum. The individuals one meter along either side of the transect were counted and the density [indiv. $\cdot$ m^{-2}] calculated. The average of these two transects was calculated. The horizontal diameter of the test of individuals collected haphazardly was measured with vernier calipers to the nearest 0.1 mm.

3. Body compartment indices

Ten individuals of the modal size of each species were weighed and dissected into body compartments: test (including spines), Aristotle's lantern, gut, and gonads. The compartment indices were calculated as the [(wet weight of compartment / wet body weight) $\cdot$ (100)].

4. Statistics

A comparison between sites was made at each collection time. Results were analyzed by ANOVA (the Tukey test was used for multiple comparisons) and chi-square tests. The null hypothesis was that the sites did not differ. The test diameter data for *Lytechinus variegatus* in November 1998 and March 1999 could not be transformed successfully and were therefore analyzed by a Kruskal Wallis one-way ANOVA on ranks and Dunn's multiple comparison test. All analyses were done with Sigmastat using a 1 % significance level.

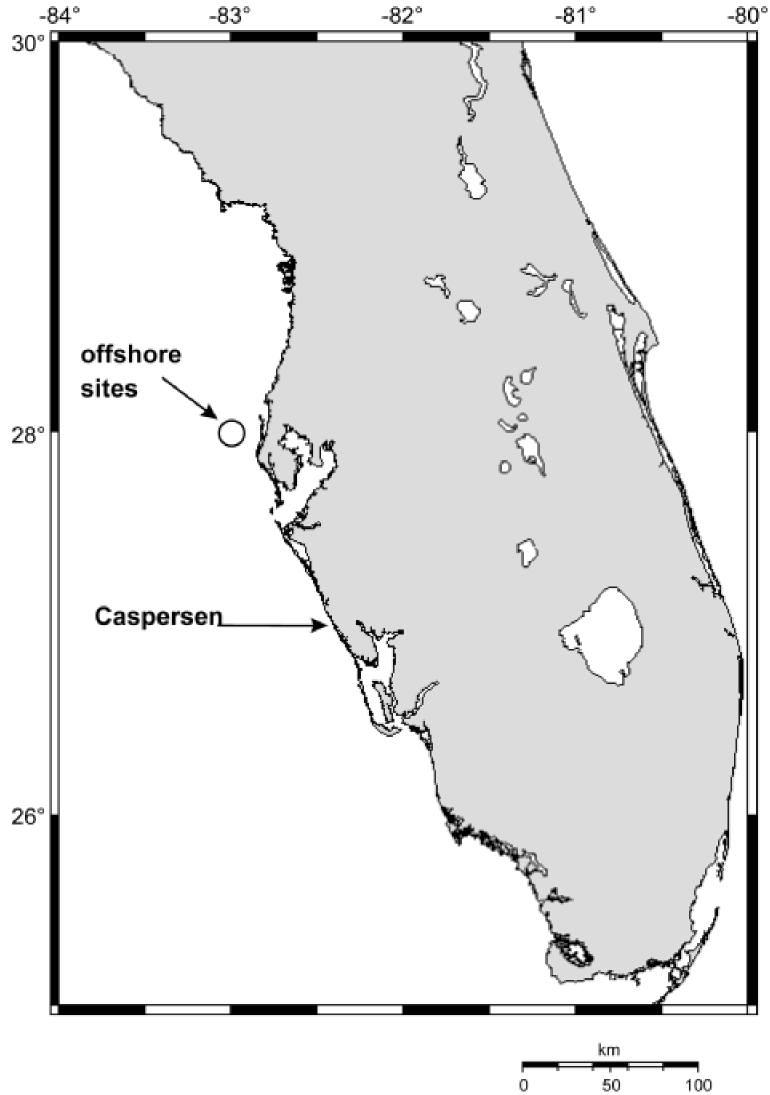

Fig. 1. Map of the west coast of Florida and the Gulf of Mexico showing the offshore and nearshore (Caspersen) sites sampled.

Results

1. Occurrence of species at the sites

The occurrence of the species at the different sites is given in Table 1. Only *Arbacia punctulata* occurred at offshore site 1 consisting of rubble and only *Lytechinus variegatus* occurred at offshore site 2 consisting of bare sand. Both species inhabited offshore sites 3 and 4 and nearshore site 5, consisting of both bare sand and rubble. At these sites,

Table 1. *Arbacia punctulata* and *Lytechinus variegatus*: Location, depth and distance from shore of collection sites, dates of collection, and characteristics of collection sites.

site and species	location, depth distance from shore	dates	characteristics
1. *Arbacia punctulata*	28°08.56′ N 83°08.82′ W 20 m *ca.* 19 km	Feb 1998 Nov 1998 Mar 1999 Oct 1999	Rubble (10 cm high) with some macroalgae and sponges. Homogeneous habitat.
2. *Lytechinus variegatus*	28°07.34′ N 82°59.70′ W 13 m *ca.* 19 km	Nov 1998 Mar 1999 Oct 1999	Bare sand. Homogeneous habitat.
3. *Arbacia punctulata* and *Lytechinus variegatus*	28°07.56′ N 82°59.70′ W 13 m *ca*. 19 km	Sep 1997 Feb 1998 Nov 1998 Mar 1999 Oct 1999	Patches of rock and rubble (10 to 50 cm high) surrounded by bare sand. Rubble patches distinct from sand. Rubble covered with macroalgae, sponges, and ascidians. Heterogeneous habitat. *Arbacia punctulata* occurs on the rock/rubble; *Lytechinus variegatus* occurs on the sand.
4. *Arbacia punctulata* and *Lytechinus variegatus*	28°07.45′ N 82°59.70′ W 13 m *ca*. 19 km	Nov 1998 Mar 1999	Patches of rubble (10 cm high) surrounded by bare sand. Rubble patches merge into sand. Rubble covered with macroalage. Heterogeneous habitat. *Arbacia punctulata* occurs on the rubble; *Lytechinus variegatus* occurs primarily on the sand, occasionally on the rubble.
5. *Arbacia punctulata* and *Lytechinus variegatus*	27°07′ N 82°27′ W 7 m *ca.* 0.3 km	Sep 1997 Nov 1998 Mar1999 Oct 1999	Patches of rubble (10 cm high) surrounded by bare sand. Rubble patches merge into sand. Rubble covered with macroalage. Heterogeneous habitat. Both *Arbacia punctulata* and *Lytechinus variegatus* occur on the rubble; *L. variegatus* occurs on the sand.

L. variegatus was found on the sand and *A. punctulata* occurred on the rubble during the day but moved onto the sand during the night.

2. Density and size-frequency distribution

Sea urchin density at the different sites is given in Table 2. For both species at all sites and dates, the average density calculated for the two transects ranged from approximately 0.06 to 1.25 indiv. $\cdot$ m^{-2}. Densities < 0.10 indiv. $\cdot$ m^{-2} occurred at the deepest offshore site 1 where *Arbacia punctulata* occurred alone, and on one occasion for both *A. punctulata* and *Lytechinus variegatus* where they co-occurred at offshore site 4.

Table 2. *Arbacia punctulata* and *Lytechinus variegatus*. Densities (indiv. $\cdot$ m^{-2} for two 2 m × 30 m transects, T1 and T2, and the average) at different sites. See Table 1 for site locations and descriptions.

	Arbacia punctulata				*Lytechinus variegatus*			
	site 1	site 3	site 4	site 5	site 2	site 3	site 4	site 5
Nov 98								
T1	–	0.28	0	0.17	0.52	0.38	0.05	0.42
T2	–	0.25	0.15	0.53	0.53	0.48	0	0.28
average	–	0.27	0.08	0.35	0.53	0.43	0.03	0.35
Mar 99								
T1	–	0.13	0.07	0.55	0.80	0.23	0.23	0.73
T2	–	0.60	0.07	0.37	0.45	0.40	0	0.47
average	–	0.37	0.07	0.46	0.63	0.32	0.12	0.60
Oct 99								
T1	0.05	0.30	–	0.15	0.40	0.28	–	1.63
T2	0.07	0.15	–	0.38	0.15	0.17	–	0.87
average	0.06	0.22	–	0.27	0.28	0.22	–	1.25

Large *Arbacia punctulata* were consistently present at the deepest offshore site, where they occurred alone in low densities, with 42 to 65 % of the individuals being > 30 mm in diameter (Fig. 2). *Arbacia punctulata* at offshore sites 3 and 4 were small, with only 2 to 31 % of the individuals being > 30 mm (Fig. 4 and Fig. 5). In contrast, individuals at nearshore site 5 were large, with 24 to 82 % of the individuals being > 30 mm (Fig. 6). Large *Lytechinus variegatus* also occurred at the offshore sites, 59 to 93 % of the individuals being > 60 mm in diameter. Individuals at offshore site 2, where the species occurred alone, were no larger than those that co-occurred at the two offshore sites with *A. punctulata* (Figs. 3, 4 and Fig. 5). At nearshore site 5, less than 30 % of the *L. variegatus* was > 60 mm on the two collections (Fig. 6).

The size-frequency distributions of *Arbacia punctulata* typically were bi- or polymodal. Single modes are apparent only for offshore site 3 in November 1998 and nearshore site 5 in March 1999 (Fig. 4 and Fig. 6). *Lytechinus variegatus* at offshore site 2, where it occurred alone, and at offshore site 4, where it co-occurred with *A. punctulata,* had single modes in November 1998 and March 1999 (Fig. 3 and Fig. 5). Small *L. variegatus* were found at offshore site 3 in February 1998 (Fig. 4).

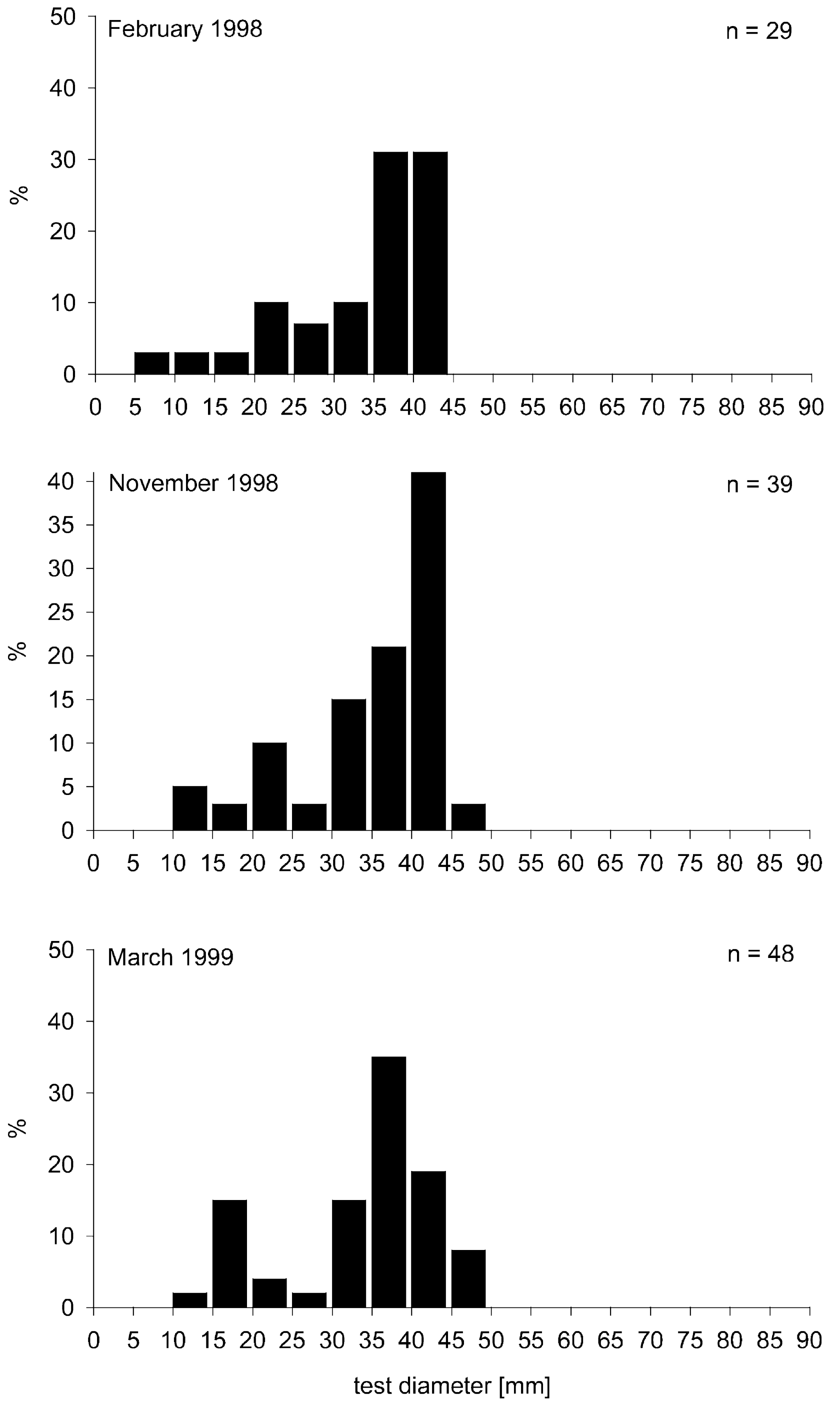

Fig. 2. Size-frequency distributions of *Arbacia punctulata* at site 1 over time.

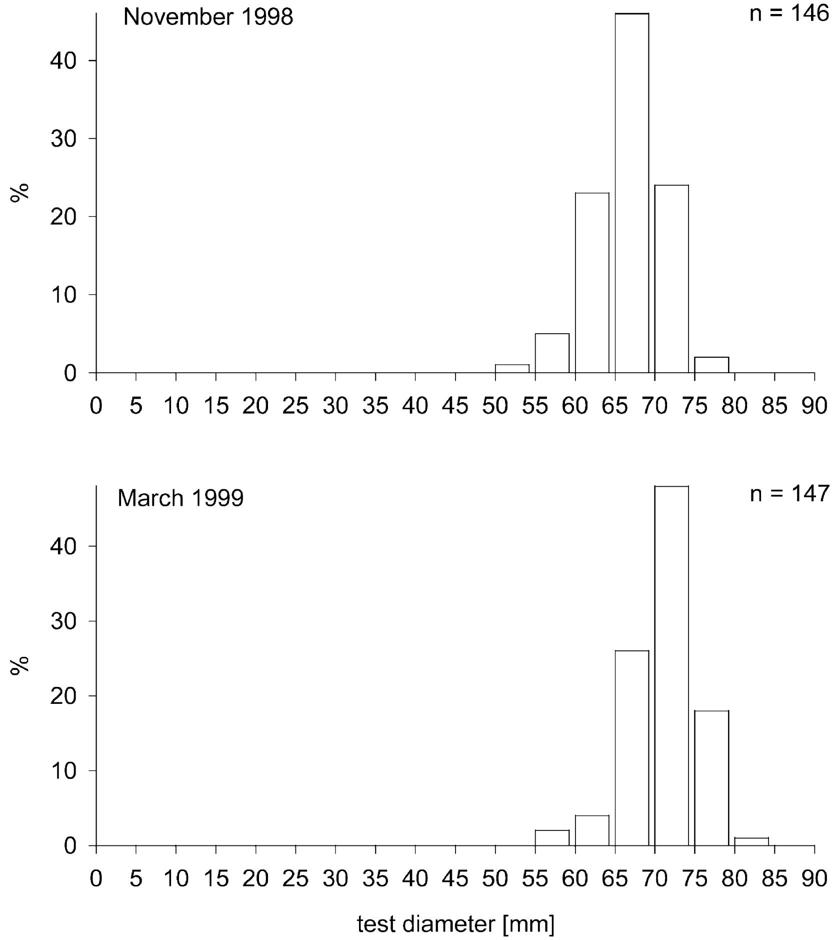

Fig. 3. Size-frequency distributions of *Lytechinus variegatus* at site 2 over time.

3. Compartment indices

The body sizes of dissected individuals of each species did not differ significantly except for *Lytechinus variegatus* from nearshore site 5. Dissected individuals from this site were significantly smaller than individuals at the other sites (Table 3).

The test index of each species from the different sites did not differ. For all but the September 1997 collections, the lantern index of *Arbacia punctulata* at offshore sites 3 and 4, where both species occur, was significantly higher than at offshore site 1 (where it occurred alone) or the nearshore site (where it co-occurred with *Lytechinus variegatus*) (Table 3). At each site, the gut index of *A. punctulata* was higher in the spring than in the fall, although the values differed with year. High indices were calculated for February 1998 at both site 1, where *A. punctulata* occurred alone, and site 3, where it co-

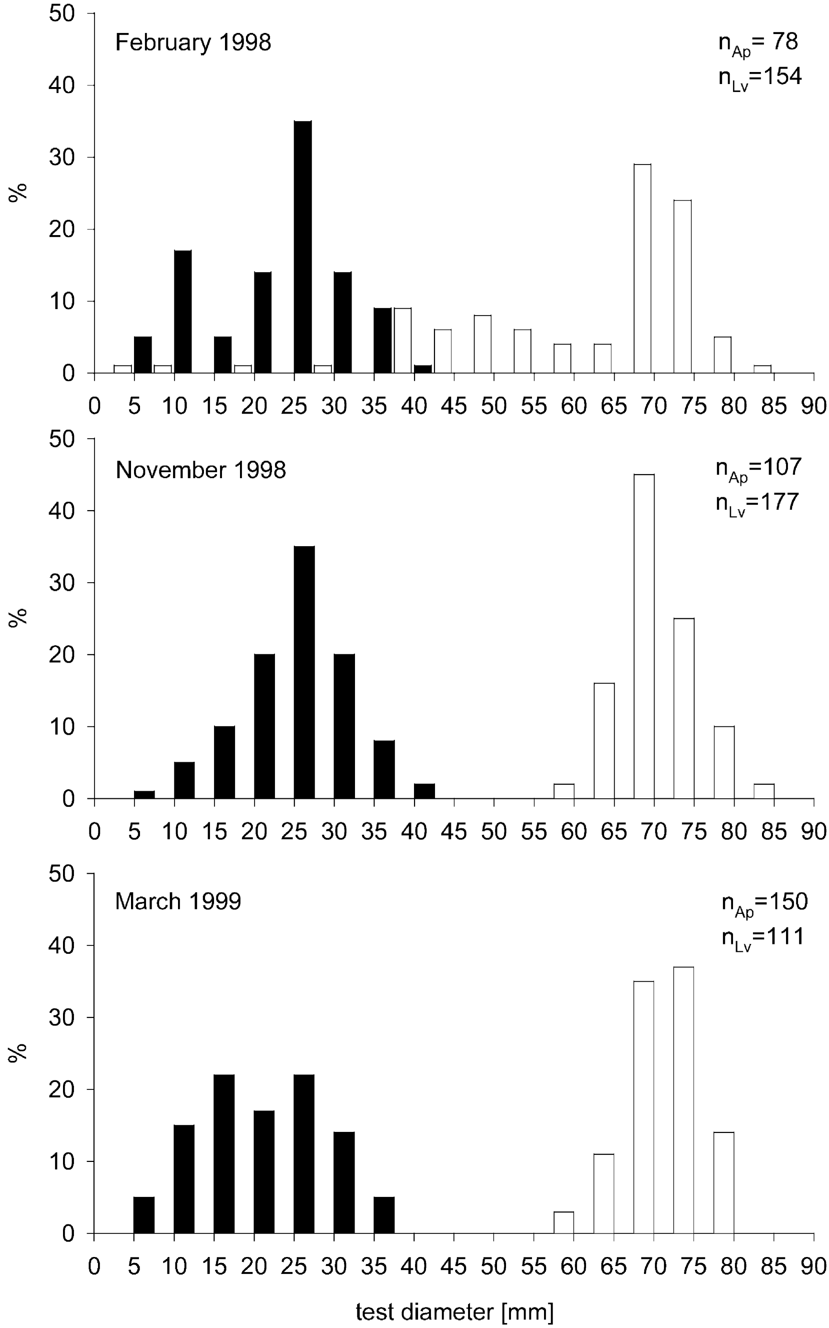

Fig. 4. Size-frequency distributions of *Arbacia punctulata* (filled bars) and *Lytechinus variegatus* (open bars) at site 3 over time.

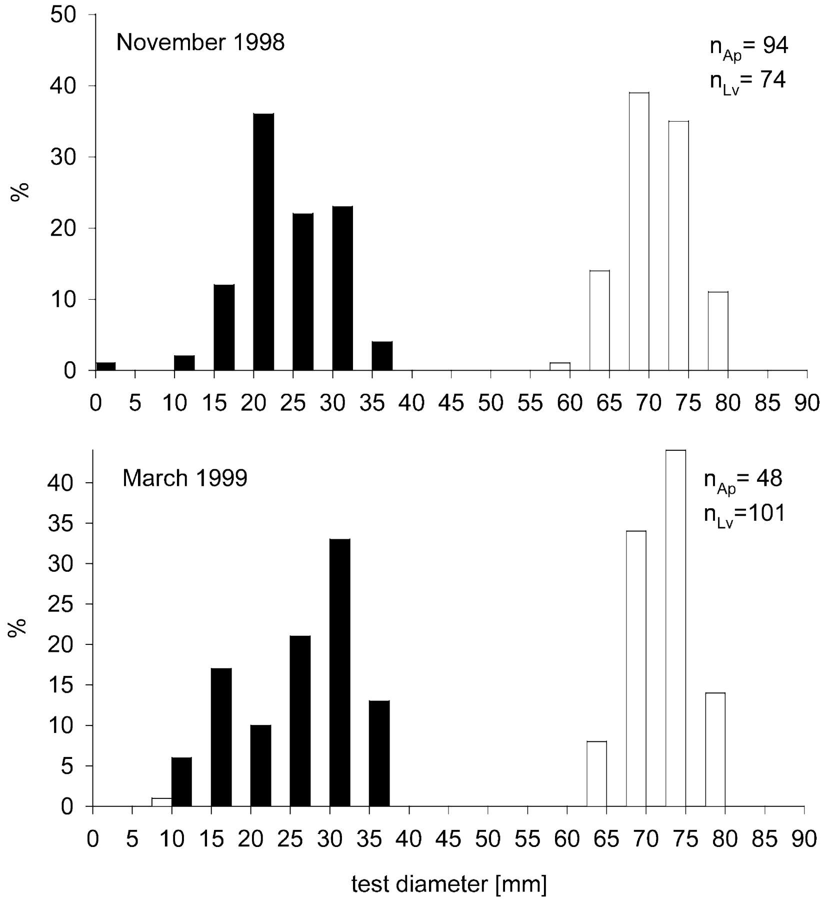

Fig. 5. Size-frequency distributions of *Arbacia punctulata* (filled bars) and *Lytechinus variegatus* (open bars) at site 4 over time.

occurred with *L. variegatus*. The gonad indices of *A. puntulata* were also higher in spring than fall at each site. In spring of both 1998 and 1999, individuals at offshore site 3 (where both species occurred) had a significantly lower gonad index than those at offshore site 1, where they occurred alone. The highest gonad index by far was at nearshore site 5 in spring 1999.

In contrast to *Arbacia punctulata*, lantern indices of *Lytechinus variegatus* did not differ with site. The gut index of *L. variegatus* was significantly higher at nearshore site 5 than at the other sites. The gonad index of *L. variegatus* was higher in spring than fall at all sites. In both fall 1998 and spring 1999, the gonad index at nearshore site 5 was significantly greater than at the offshore sites.

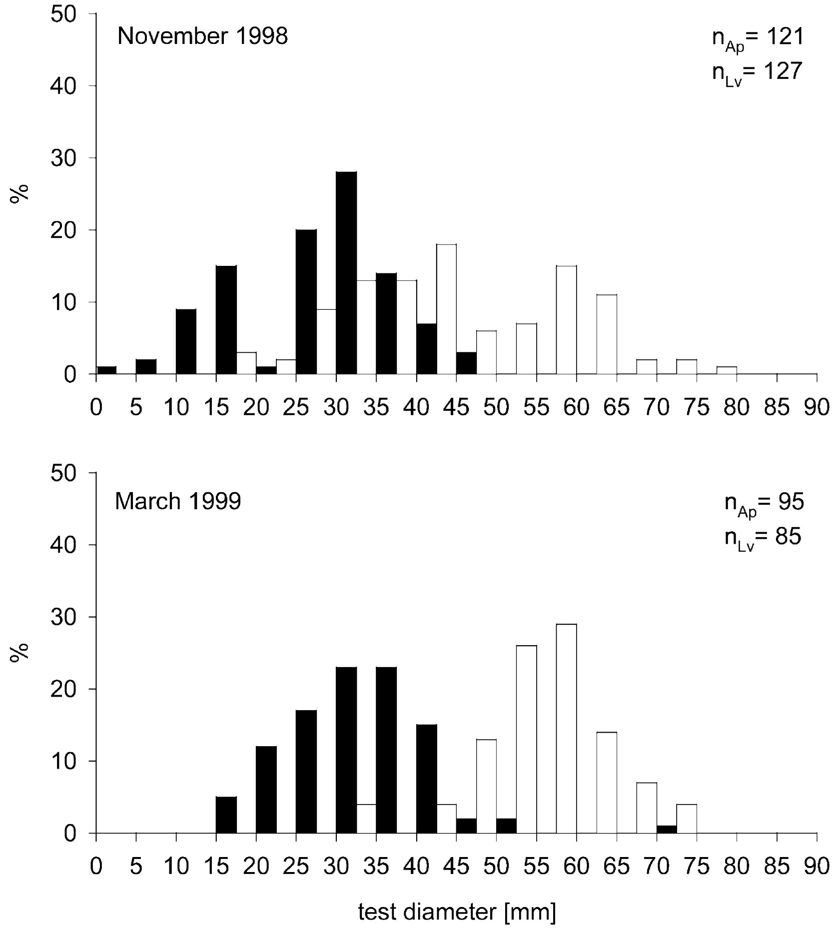

Fig. 6. Size-frequency distributions of *Arbacia punctulata* (filled bars) and *Lytechinus variegatus* (open bars) at site 5, Caspersen Beach, over time.

Discussion

The occurrence of *Arbacia punctulata* and *Lytechinus variegatus* at the offshore sites indicates a distinct difference in microhabitats. *Arbacia punctulata* was associated with a hard substratum and *L. variegatus* with a sand substratum. In contrast, they did not occupy microhabitats at the nearshore site, where *L. variegatus* occurred not only on sand but with *A. punctulata* on rubble.

The situation is similar in other pairs of co-occurring sea urchin species. The observations of Kempf (1962), Neill & Larkum (1965), Régis (1981), and Maggiore *et al.* (1987) all suggest difference in the habitat of *Arbacia lixula* and *Paracentrotus lividus* in the northwest Mediterranean. *A. lixula* apparently requires a hard substratum and

Table 3. *Arbacia punctulata* and *Lytechinus variegatus*. Body size (mm horizontal diameter) of dissected individuals and component indices of populations. See Table 1 for site locations and descriptions. (n = 10; mean ± SD).

		Arbacia punctulata				*Lytechinus variegatus*			
	date	site 1	site 3	site 4	site 5	site 2	site 3	site 4	site 5
diameter	Sep 97	—	35.2 ± 3.5	—	41.8 ± 6.6	—	74.2 ± 5.1	—	51.6 ± 3.8
	Feb 98	39.0 ± 3.6	31.6 ± 4.3	33.0 ± 2.9	—	—	69.0 ± 4.6	—	—
	Nov 98	41.8 ± 1.8	33.7 ± 2.3	36.3 ± 1.6	42.6 ± 4.1	66.6 ± 3.7	69.2 ± 2.0	71.0 ± 2.9	64.5 ± 3.6
	Mar 99	42.3 ± 1.9	34.5 ± 3.1	—	37.6 ± 2.9	72.3 ± 1.6	73.0 ± 2.2	73.8 ± 3.5	56.1 ± 3.0
	Oct 99	35.8 ± 9.9	29.5 ± 3.9	—	36.8 ± 3.4	73.7 ± 2.1	71.4 ± 3.1		55.2 ± 4.4
lantern	Sep 97	—	6.5 ± 0.8	—	4.7 ± 0.4	—	—	—	3.2 ± 0.5
	Feb 98	6.8 ± 1.3	9.1 ± 1.2	—	—	—	—	—	—
	Nov 98	5.9 ± 0.6	7.7 ± 1.0	8.5 ± 0.9	5.7 ± 0.4	3.6 ± 0.4	3.4 ± 0.6	3.4 ± 0.6	3.3 ± 0.5
	Mar 99	7.0 ± 0.8	9.7 ± 1.3	7.6 ± 0.9	6.6 ± 0.5	4.0 ± 0.5	4.0 ± 0.5	4.0 ± 0.5	3.4 ± 0.4
	Oct 99	6.2 ± 0.6	7.8 ± 0.8	—	6.2 ± 0.8	3.4 ± 0.3	—	—	3.4 ± 0.3
gonads	Sep 97	—	0.9 ± 0.9	—	1.4 ± 0.8	—	—		3.3 ± 2.0
	Feb 98	3.2 ± 1.8	1.7 ± 1.0	—	—	—	—	—	—
	Nov 98	0.8 ± 0.2	0.5 ± 0.3	0.4 ± 0.2	1.7 ± 0.7	1.8 ± 1.1	1.3 ± 1.1	1.3 ± 1.1	3.4 ± 1.5
	Mar 99	2.4 ± 0.7	1.4 ± 0.3	2.7 ± 1.5	3.9 ± 1.6	2.2 ± 05	2.2 ± 0.9	2.2 ± 0.9	4.5 ± 0.8
	Oct 99	0.9 ± 0.8	0.7 ± 0.3	—	1.2 ± 0.4	2.5 ± 0.7	—	—	2.6 ± 1.2
gut	Sep 97	—	1.6 ± 0.2	—	2.3 ± 0.4	—	—	—	2.5 ± 0.4
	Feb 98	3.9 ± 0.9	4.3 ± 3.0	—	—	—	—	—	
	Nov 98	3.2 ± 0.4	2.6 ± 0.6	2.0 ± 0.6	2.3 ± 0.5	1.4 ± 0.2	1.4 ± 0.2	1.4 ± 0.2	2.2 ± 0.7
	Mar 99	3.2 ± 0.5	2.9 ± 0.4	—	3.8 ± 0.7	1.5 ± 0.2	1.5 ± 0.2	1.5 ± 0.2	2.7 ± 0.2
	Oct 99	2.1 ± 0.3	2.4 ± 0.5	2.9 ± 0.8	2.2 ± 0.2	1.6 ± 0.2	—	—	2.2 ± 0.3
test	Sep 97	—	54.0 ± 3.8	—	53.0 ± 4.4	—	—	—	39.2 ± 2.0
	Feb 98	52.3 ± 5.4	49.6 ± 3.7	—	—	—	—	—	—
	Nov 98	56.3 ± 4.8	57.4 ± 3.3	54.7 ± 3.0	49.8 ± 3.5	38.1 ± 1.7	36.9 ± 1.5	36.9 ± 1.5	40.9 ± 1.9
	Mar 99	54.2 ± 2.2	56.7 ± 3.4	56.1 ± 3.2	57.5 ± 3.0	36.9 ± 2.5	36.7 ± 2.9	36.7 ± 2.9	39.9 ± 2.6
	Oct 99	57.3 ± 5.8	59.7 ± 3.5	—	57.6 ± 1.5	38.0 ± 1.5	—	—	40.4 ± 1.6

can exist at higher hydrodynamic forces than *P. lividus*. *Paracentrotus lividus* is found in seagrass beds in areas of low hydrodynamic forces where *A. lixula* is typically absent.

Sharp & Gray (1962) attributed the greater clinging power of *Arbacia punctulata* than *Lytechinus variegatus* to their larger oral suction discs and concluded this gave it a greater ability to withstand high hydrodynamic forces. This does not explain the microhabitats of *A. punctulata* and *L. variegatus* at the offshore sites. *L. variegatus* can certainly attach to hard substrata and *A. punctulata* is found there on the sand surrounding the rubble at night. The co-occurrence of both species at the shallow nearshore site could be attributed to complete heterogeneity of the habitat and/or more frequent disturbance by hydrodynamic forces.

Arbacia punctulata were smaller at the two offshore sites and the nearshore site where they co-occurred with *Lytechinus variegatus* than at the offshore site where they occurred alone. The sizes of *L. variegatus* co-occurring with *A. punctulata* or occurring alone did not differ. Sea urchin growth is indeterminate, plastic, and asymptotic (Sebens, 1987). Consequently, body size in the field is determined by age and food availability. *Arbacia punctulata* reaches 56 mm in diameter (Harvey, 1956), but its maximum size at the sites here was 10 to 20 mm less than this. The diameters of *L. variegatus* offshore (67 to 74 mm) are at the lower end of the maximum 75 to 90 mm diameter reported for individuals in the field (Watts *et al.*, 2001), and those of inshore individuals (52 to 65 mm) are even smaller. Ebert (1968) showed the importance of a relative shortage of food in limiting growth rate and final size of *Strongylocentrotus purpuratus*. The lack of change in body size of both *A. punctulata* and *L. variegatus* populations over the two years suggests food limitation at both sites.

For both species, the gut index was higher in spring than in fall, indicating seasonal variation in food availability or storage as found for *Strongylocentrotus purpuratus* (Lawrence *et al.*, 1965) and *Lytechinus variegatus* (Beddingfield & McClintock, 2000). The highest gut index found for well-fed *A. punctulata* in the laboratory is 3.3 (Hill, 2000), similar to that of *A. punctulata* at the offshore sites (2.9 to 4.3) in spring, suggesting high food availability from the algae and epibenthic fauna on the rubble.

The highest gut indices reported for well-fed *Lytechinus variegatus* in the laboratory is 2.7 (Hill, 2000) and 2.3 (Bishop & Watts, 1992), greater than that of *L. variegatus* at the offshore sites (1.5 to 1.6) but not the nearshore one (2.7), suggesting food limitation offshore but not nearshore. Offshore individuals are dependent on drift for food as they are found on bare sand and do not ascend the rubble on which algae grow. This is curious, because *L. variegatus* are found on the rubble at the nearshore site. *Lytechinus variegatus* here showed similar seasonal changes in gut index (spring high of near 2.8) to those in sand habitats, *Thalassia testudinum*, and *Syringodium filiformis* in the northeast Gulf of Mexico (Beddingfield & McClintock, 2000).

The highest gonad index found here for *Arbacia punctulata* (3.2) was at the nearshore site, the lowest at offshore site 4 (2.7). The highest gonad index of well-fed *A. punctulata* in the laboratory is 3.2, suggesting that *A. punctulata* on the rubble nearshore had similar food resources. None of the *A. punctulata* populations had an index approaching the level of nearly 15 found for *A. punctulata* in Massachusetts (Sastry, 1975).

Ernest & Blake (1981) found highest gonadal indices for *Lytechinus variegatus* in January to March in the Tampa Bay area, except for one site with a second, smaller peak in midsummer. Beddingfield & McClintock (2000) similarly reported highest gonadal indices for *L. variegatus* in early spring one year in the northeast Gulf of Mexico, but in summer the subsequent year. Both studies found gametogenic activity in spring and in summer that was unrelated to gonad index. The highest of these indices for *L. variegatus* (4.5) also was at the nearshore site and the lowest (2.2) at all offshore sites. The highest values for well-fed *L. variegatus* in the laboratory are 8.5 (Hill, 2000) and 9 (Bishop & Watts, 1992), suggesting that this species does not have abundant food at our sites. The gonad index of *L. variegatus* in the northeast Gulf of Mexico was approximately 22 in beds of *Syringodium filiformis*, 10 in beds of *Thalassia testudinum* and 6 on bare sand (Beddingfield & McClintock, 2000). This indicates the importance of drift food for *L. variegatus.*

The Aristotle's lantern index of *Arbacia punctulata* at the two offshore sites where it co-occurs with *Lytechinus variegatus* is significantly greater than at the offshore site where it occurs alone or at the inshore site. As food availability was not measured, a potential phenotypic response cannot be excluded. The lack of a significant difference in this index of *Lytechinus variegatus* at any of the sites would indicate no difference in food availability or no response of the lantern to food availability as predicted by the phenotypic plasticity hypothesis.

Arbacia punctulata and *Lytechinus variegatus* at the offshore sites were small and had low gut and gonad indices. The lack of change in size in the offshore individuals over two years for both species suggests they are at the size-limit supportable there. These characteristics indicate food limitation and suggest low primary production on the central Florida gulf-coast shelf. The relative decrease in these characteristics of the two species is insufficient to unequivocally demonstrate different response to food limitation. As Hill & Lawrence (1999) found a difference in the response to starvation, the apparent lower food availability at the offshore sites does not stress *A. punctulata* and *L. variegatus* sufficiently to distinguish their response as predicted from life-history theory.

Summary

Despite distinct functional morphologies, *Lytechinus variegatus* and *Arbacia punctulata* co-occur on the Florida gulf-coast shelf in different microhabitats. *Lytechinus variegatus* is found on sand and *A. punctulata* on rock. The small body-size and low amount of gonad production of off-shore individuals indicate low production in this area of the Gulf of Mexico. Despite low production, both species extend their distribution and reproductive potential by their ability to live there.

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