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The Population Dynamics of the Brittlestar *Ophioderma brevispinum* in Near- and Farshore Seagrass Habitats of Port Saint Joseph Bay, Florida

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The population dynamics of the brittlestar *Ophioderma brevispinum* were followed monthly from Jan. 1995 to March 1996 in a near- and farshore seagrass bed in Saint Joseph Bay, FL. Abiotic (sea water temperature and salinity) and biotic (seagrass cover and sublethal predation) factors that could influence populations were also measured. Densities of individuals at both sites peaked in winter and spring, then declined dramatically in early summer months, and increased once again in the early fall at the offshore site and in the late fall at the nearshore site. Mean monthly disc diameters of individuals did not reveal any evidence of juvenile recruitment, suggesting seasonal migrations of adults into and out of near- and farshore seagrass beds. Seagrass cover at both sites varied substantially with season, with the highest cover in the summer months when brittlestar densities were lowest. Sublethal predation, as measured indirectly by counting the numbers of arm tips regenerating in individuals, did not differ significantly between sites except for the month of Feb. 1995, when levels of arm tip regeneration were higher among individuals at the nearshore site. The high overall incidence of individuals with regenerating arms at both sites suggests that predators exert persistent sublethal predatory pressure and may contribute to mortality. Individuals may migrate into deeper water during summer months to avoid thermal stress, hypoxia, or high levels of ultraviolet radiation and to avoid predation when predator densities are likely to be highest.

B rittlestars are numerically dominant and therefore trophically and ecologically important members of a wide diversity of marine benthic communities (Hyman, 1955; Fell, 1966; Bowmer and Keegan, 1983; O'Connor et al., 1983; Valentine, 1991; Clements et al., 1994). Their dominance is so marked that they are often used to designate discrete community types (Thorson, 1957). Nonetheless, few studies have been done to determine factors affecting the abundance and distribution of brittlestars, particularly subtropical species.

Population dynamics in brittlestars vary depending on habitat type and reproductive mode (Fell, 1966; Hendler, 1975). Exposure to wide fluctuations in environmental factors in nearshore environments may determine the survival rate of juvenile recruits or adults (Nilsson and Skold, 1996; Johnson and Kier, 1998). Predation on individuals can be considerable, and the use of sublethal arm damage as a measure of predation pressure has been employed by investigators of both extant and fossilized brittlestars (Bowmer and Keegan, 1983; Duineveld and vanNoort, 1986; Aronson, 1987, 1991).

Ophioderma brevispinum is a moderately sized brittlestar, with adults attaining a maximum of 1.5 cm disk diameter and arms that are up to 7.5 cm in length (Hendler et al., 1995). This species is common in shallow-water habitats from Massachusetts to Florida, the Gulf of Mexico, and the Caribbean (Hendler et al., 1995). *Ophioderma brevispinum* has been described by Stancyk (1970) and Hendler (1982) to feed on detritus, crustaceans, polychaetes, sponges, and algae and also to display opportunistic scavenging behaviors. In Saint Joseph Bay, FL, *O. brevispinum* inhabits seagrass (*Thalassia testudinum*) flats. Grave (1900) and Hendler (1975) described *O. brevispinum* as having an abbreviated form of lecithotrophic vitellaria larvae. The reproductive cycle of *O. brevispinum* in Waquoit Bay, MA, is characterized by midsummer spawning, followed by gametogenesis and gradual gonadal growth during the winter, and then greatly accelerated gonadal growth from May to June (Hendler and Tyler, 1986). Stancyk (1970, 1974a) found a similar reproductive pattern for *O. brevispinum* in Cedar Key, FL.

The present study examined and compared population dynamics of *O. brevispinum* in near- (90 m offshore) and farshore (170 m offshore) subtidal *T. testudinum* seagrass sites in Saint Joseph Bay, FL. Although both near- and farshore sites had similar fine-grained sand substrates and similar water depths (average 1–1.5 m), they exhibited distinct faunal differences, indicating that differences in abiotic or biotic
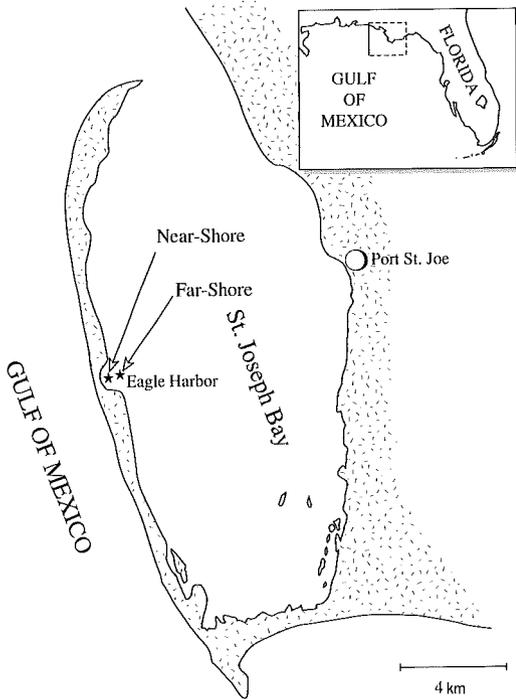
Fig. 1.   Map of Saint Joseph Bay, FL, showing the locations of the near- and farshore seagrass study sites.

factors may be affecting the two sites. For example, the common regular sea urchin *Lytechinus variegatus* is found consistently in abundance at the farshore seagrass site but occurs only in very low numbers at the nearshore site (C. Leonard, pers. obs.; Beddingfield, 1997). To examine both environmental and biotic factors that may be important in regulating the population dynamics of *O. brevispinum,* seawater temperature, salinity, seagrass density, and sublethal predation were measured seasonally at both seagrass sites.

MATERIALS AND METHODS

Port Saint Joseph Bay is a shallow bay on the western Florida Panhandle measuring approximately 12 km in width and 24 km in length (Fig. 1). Vegetation within the bay consists primarily of the seagrasses *T. testudinum* and *Syringodium filiforme,* and extensive areas of sand flats are interspersed within seagrass beds (Valentine and Heck, 1991; Beddingfield, 1997; Beddingfield and McClintock, 1999).

Ophioderma brevispinum were sampled monthly within the near- and farshore seagrass sites (Fig. 1) between Jan. 1995 and March 1996 (no monthly sample was collected in Jan.

1996). Seawater temperature and salinity were measured monthly at each subtidal site with a hand held thermometer and a refractometer. Tidal ranges and water depths were not measured at each site each month, but to the best our knowledge, neither site experienced aerial exposure during the study period. Six 1-m² quadrats were haphazardly positioned within each seagrass site and methodically searched by hand for all brittlestars. Individuals with 2-mm disk diameters measured approximately 3–4 cm from arm tip to arm tip, making them easily visible and detectable when searching by hand in the field. Smaller juvenile individuals (<2 mm disc diameter) could not be completely accounted for by this method of collection. Density estimates, disk diameter measurements, and measures of sublethal predation (incidence of arm tip regeneration) were therefore restricted to individuals with disk diameters 2 mm or greater.

Individuals were placed into a large plastic bag containing fresh seawater as they were collected. Once all individuals from each quadrat were collected, calipers were employed to measure the disk diameter of each individual. Arm tips undergoing regeneration were also counted and the numbers were recorded. Broken arm tips that showed no sign of regeneration were not counted because of the possibility that they were broken during the collection process. However, arm breakage due to collection was minimal. After being measured, all individuals were released back into the quadrat from which they had been collected. Moreover, every month between April 1995 and Feb. 1996 (except Jan. 1996), a point contact technique was used to calculate the percentage of seagrass cover at each site. This was accomplished by sectioning a 1-m² quadrat into 25 cross points with twine. Percentage of cover was determined by counting the number of cross points that contacted a blade of living seagrass (*T. testudinum*). Ten quadrats haphazardly placed within each seagrass bed were counted at each site each month.

Statistical analysis.—A two-way ANOVA and Friedman analysis were employed to test for significant differences in densities between the two sites and between months. A Bartlett's test for homogeneity of variances was not homogeneous; therefore, a nonparametric Friedman analysis was performed to test for differences between the two sites and between months. Analysis of the proportion of individuals having one or more arm tips regenerating over the year was accomplished with R × C contin-
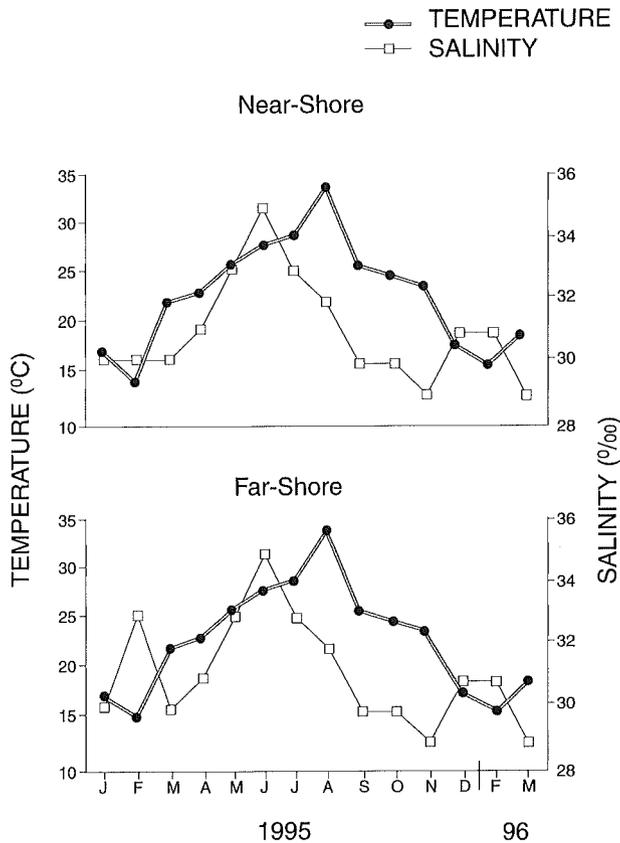
Fig. 2.   Seawater temperatures and salinities at near- and farshore seagrass sites in Port Saint Joseph Bay, FL, between Jan. 1995 and March 1996.

gency tables (Sokal and Rohlf, 1981). Differences in seagrass density were compared between sites by an ANOVA.

RESULTS

Seawater temperatures from Jan. 1995 to March 1996 were similar at the two seagrass sites except for the month of Feb. 1995, when seawater temperature at the farshore site was 2 degrees higher than at the nearshore site. Near- and farshore seawater temperatures ranged from 13 C in Feb. to 34 C in Aug. and from 15 C in Feb. to 34 C in Aug., respectively (Fig. 2). Salinities were also similar at the two sites throughout the year with the exception of Feb. 1995, when salinity at the nearshore site was 3 ppt lower than that measured at the farshore site (30 vs 33 ppt). Salinities at both sites ranged from a high of 34 ppt in June 1995 to a low of 29 ppt in Nov. 1995 (Fig. 2).

Densities of *O. brevispinum* ranged from 0.5 individuals/m² in June 1995 to 17.5 individuals/m² in March 1995 at the nearshore seagrass

site and from 0.6 individuals/m² in May 1995 to 23.3 individuals/m² in Feb. 1995 at the farshore seagrass site. Peak densities at the nearshore site occurred 1 month later than at the farshore site, with both sites showing a decline in densities throughout the summer months. Densities began to rise again at the farshore site in Aug. 1995 but not until Nov. 1995 at the nearshore site. Densities at the two sites were not significantly different from one another over the year ($P = 0.08$; Fig. 3). Nonetheless, with the exception of March and April 1995, consistently higher mean numbers of individuals were found at the farshore site.

The mean disk diameters for individuals at the nearshore site ranged from 10.1 mm in June 1995 to 6.3 mm in Nov. 1995. Mean disk diameters at the farshore site ranged from 11.6 mm in June 1995 to 6.6 mm in Jan. 1996. At both sites, individuals sampled in the months of May, June, and July 1995 had mean disk diameters approximately 2–3 mm larger than during the rest of the year; however, during these months, densities of individuals were
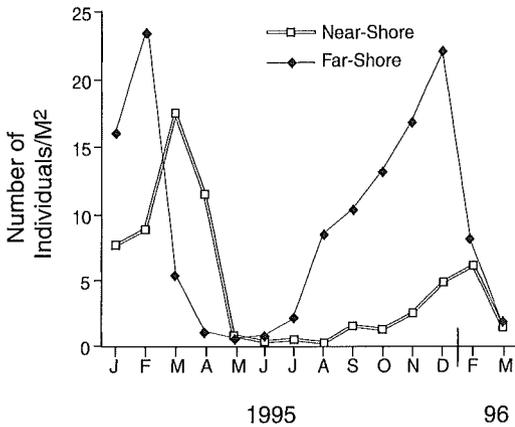
Fig. 3. Mean densities of *Ophioderma brevispinum* at near- and farshore seagrass sites in Port Saint Joseph Bay, FL, between Jan. 1995 and March 1996. No sample was collected in Jan. 1996.
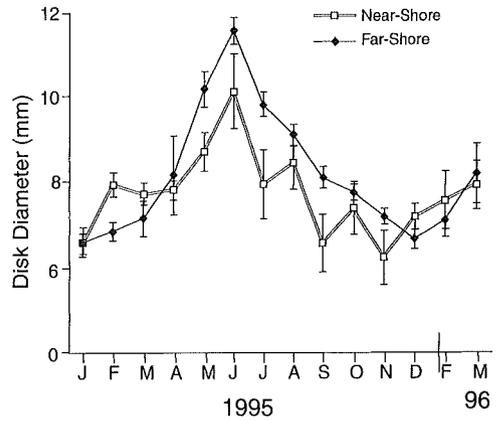

Fig. 4. Mean disc diameters of *Ophioderma brevispinum* at near- and farshore sites in Port Saint Joseph Bay, FL, between Jan. 1995 and March 1996. Sample sizes are 10 or greater with the exception of the nearshore site in Aug. (n = 3) and Oct. (n = 9) and the farshore site in April (n = 7).

very low, with only the larger individuals remaining in the seagrass beds. A significant difference in mean disk diameter was detected between the two sites in February 1995 (P = 0.002), with individuals at the nearshore site having larger mean disk diameters. No overall significant difference was found in sizes of individuals between the two sites over the year (P = 0.25; Fig. 4). Individuals from both near- and farshore seagrass sites revealed high levels of arm tip regeneration throughout the study (22–75% of the individuals sampled had at least one arm tip regenerating). No significant differences in percentages of individuals with or without one or more arm tips regenerating were detected between sites except for the month of Feb. 1995, when arm tip regeneration levels were higher at the nearshore site (P < 0.001; Fig. 5).

Seagrass density did not differ significantly between near- and farshore sites throughout the study (P = 0.247; Fig. 6). A clear annual pattern of changes in sea grass density with season was found, with lowest densities occurring during winter months and highest densities present during summer months. Mean point contact values ranged from lows of 0.4 blades/25 points at the farshore site and 0.9 blades/25 points at the nearshore site in Feb. 1996 to 24.5 blades/25 points at the farshore site and 24.6 blades/25 points at the nearshore site in July 1995. Seagrass density at both sites increased two to three-fold between April and May 1995. Densities remained high from May to Sep. 1995, then decreased steadily from Oct. 1995 to extremely low levels in Feb. 1996.

DISCUSSION

As has been shown for other species of brittlestars in soft-bottom bay environments of the northern Gulf of Mexico (Valentine, 1991), densities of *O. brevispinum* in Saint Joseph Bay showed marked seasonal fluctuations in both near- and farshore seagrass beds. Brittlestars were approximately eight times more abundant in the winter than in the summer months at both seagrass sites. This finding is in contrast to the findings of Stancyk (1974a), who found that *O. brevispinum* in Cedar Key, FL, had higher densities in summer than in the winter months. Moreover, the annual variation in densities observed by Stancyk (1974a) was less marked (31–42 individual/m^2) than that found at Saint Joseph Bay (0.5–23 individuals/m^2). Monthly mean disc diameter determinations indicated that both near- and farshore sites sustained populations of individuals of similar adult body sizes (generally 6–12 mm disk diameter) over the course of the study period; only in Feb. were individuals at the nearshore site larger than those at the farshore site. Although individuals with disc diameters as small as 2 mm could be confidently collected, very few juvenile individuals were detected over the course of the study. Seasonal increases and decreases in densities of large adult individuals at both the near- and farshore seagrass sites suggest that *O. brevispinum* in Saint Joseph Bay are migrating out of shallow-water seagrass habitats in Feb. and March. That these adult individuals buried during time periods of recorded low densities is unlikely because re-
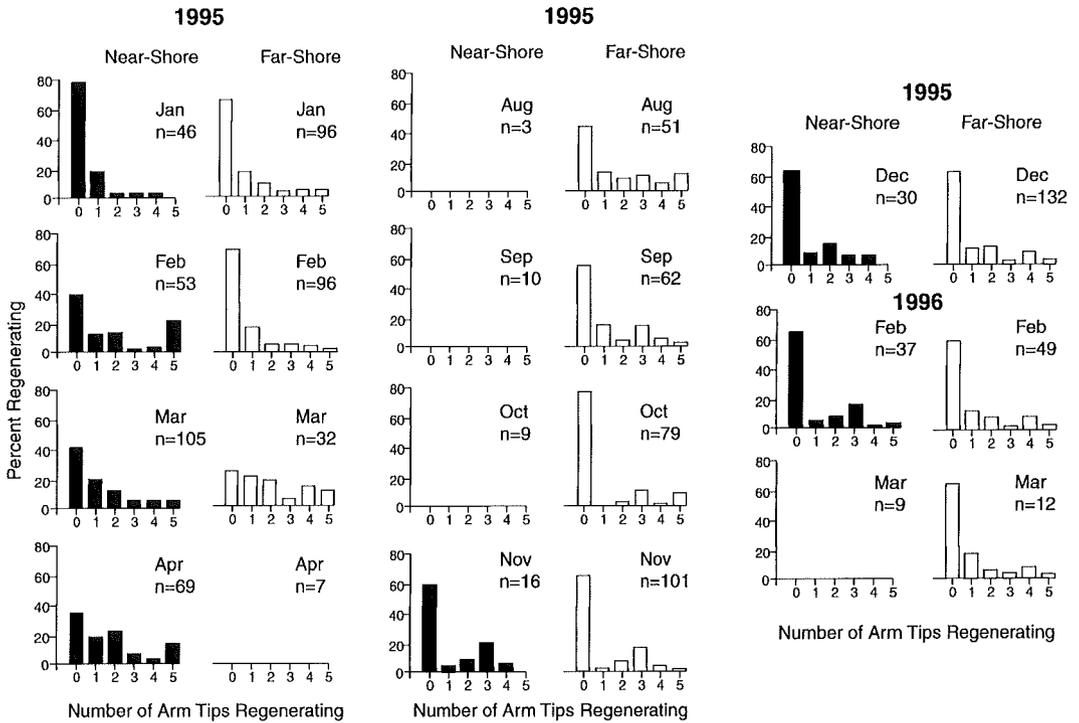
Fig. 5. Percentages of individuals with one to five arm tips regenerating for *Ophioderma brevispinum* at near- (shaded bars) and farshore (open bars) sites in Port Saint Joseph Bay, FL. Distributions are presented only for those months when sample size was >10 at a minimum of one site. When sample sizes were <10 at both sites in a given month, no data are presented.
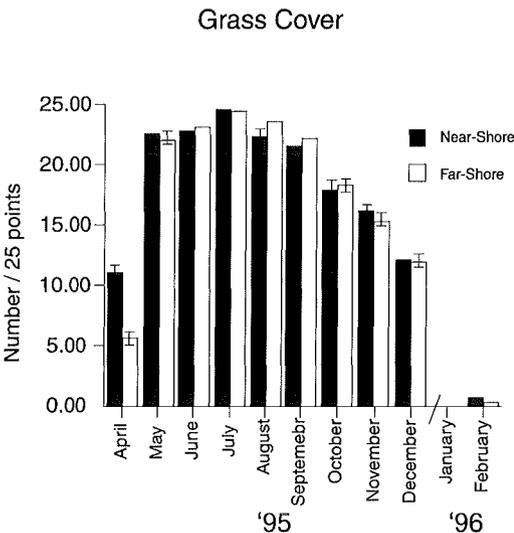

Fig. 6. Frequency of point contact for the seagrass *Thalassia testudinum* at near- and farshore seagrass sites in Port Saint Joseph Bay, FL, between April 1995 and Feb. 1996. Shown is the mean number of times that 25 evenly spaced points within a 1-m quadrat contacted seagrass (n = 10 quadrats per site per month). No sample was collected for Jan. 1996.

peated monthly searches of the substratum failed to yield buried individuals (C. Leonard, pers. obs.). Migration back into farshore seagrass beds appears to begin in Aug., with nearshore seagrass habitats being recolonized by Dec.

Both abiotic and biotic factors may be influencing seasonal patterns of abundance of this ophiuroid in Port Saint Joseph Bay. Salinities documented in the present study displayed moderate annual fluctuations, with consistently higher salinities measured at both sites during summer months. A moderate decline of 5 ppt occurred during the winter months. Fluctuations in salinity were likely attributable to differences in seasonal precipitation patterns. Nonetheless, salinities ranged well within levels determined to be tolerable to *O. brevispinum* (Stancyk, 1974a) and are therefore unlikely to influence the population dynamics of *O. brevispinum*. In contrast, seawater temperatures at both seagrass sites varied dramatically, steadily increasing from March to Aug. 1995, reaching a high of 34 C, then declining until reaching a low in Feb. (13 C). Importantly, summer seawater temperatures measured at both study

sites were substantially higher than Stancyk (1974a) found to be lethal to *O. brevispinum* (>30 C caused mortality). These temperatures could be expected to be even higher when coupled with shallow water depths associated with low tides at midday. Therefore, seawater temperature is likely a significant factor influencing seasonal fluctuations in population densities of *O. brevispinum*. Brittlestars may be migrating out of the seagrass beds to avoid exposure to high seawater temperatures or suffering outright mortality due to exposure to lethal temperatures. Episodic winter storms moving from the north have been known to force waters out of the bay, resulting in extremely low seawater temperatures and low seawater levels (Beddingfield and McClintock, 1994). When coupled with low tides, such winter events can result in temporary aerial exposure of shallow sand flats and seagrass beds, causing significant mortality among nearshore marine invertebrates (e.g., the sea urchin *Lytechinus variegatus*; Beddingfield and McClintock, 1994). Although no such event occurred during the 1995–96 winter of the present study, populations of *O. brevispinum,* particularly those in nearshore seagrass beds, would be negatively impacted by these episodic weather events.

Biotic factors that may be affecting the population dynamics of *O. brevispinum* include, among other factors, the degree of structural biotic refuge (seagrass cover) and the potential for predation. *Thalassia testudinum* densities did not differ significantly between the two seagrass sites throughout the year. However, seagrass densities were highest in the summer, then declined in the fall, and became extremely low in the winter (see also Valentine and Heck, 1991). *Ophioderma brevispinum* may live at the base of seagrass blades to gain protection from predators and to prevent desiccation during extreme tidal conditions (Stancyk, 1974a). If the presence of structural refugia (seagrass) was responsible for seasonal patterns of brittlestar abundance, then one would expect population densities of *O. brevispinum* to increase in the summer when seagrass densities are maximal. The opposite pattern was observed, indicating that, although increased seagrass structure may indeed provide refuge from predators (Orth et al., 1984; Heck and Wilson, 1987), it is not directly driving patterns of brittlestar abundance.

Ophioderma brevispinum has been documented as prey of the sea stars *Luidia clathrata* and *Luidia alternata* (Stancyk, 1974b) and is likely to be consumed also by fish and crabs (Bow-

mer and Keegan, 1983; Duineveld and van-Noort, 1986). Measurements of numbers of arm tips regenerating is a well established method of determining predation levels in brittlestars (Aronson, 1987, 1991). One or more arm tips regenerating on an individual may or may not represent more than one predation event. However, determining the numbers of individuals with one or more arm tips regenerating provides information on relative levels of predation. Sublethal predation levels, on the basis of arm tip removal, were similar at both seagrass sites and were generally high, indicating that even within seagrass beds, where structural refugia might be expected to be high, sublethal predation is an important factor that influences energy budgets (Stancyk et al., 1994) and may be a significant determinant of population dynamics in *O. brevispinum*. Hendler et al. (1995) noted that this species displays very little disposition to lose arm tips with handling stress, and thus the prevalence of *O. brevispinum* with regenerating arms is likely due to sublethal predation. Nonetheless, some arm tip loss may also be related to temperature or hypoxic stress. Low densities of individuals in summer and fall months precluded a comparative site-specific analysis of patterns of sublethal predation during these seasons. Increased predation pressure because of higher densities of predators (fish and crabs) that occur when summer and early fall seagrass densities are high (Orth et al., 1984) may act in concert with high summer seawater temperatures to influence seasonally low densities of *O. brevispinum* in both near- and far-shore seagrass habitats in Port Saint Joseph Bay.

Additional factors that might contribute to the seasonal movements of *O. brevispinum* out of shallow warm waters in Saint Joseph Bay include hypoxia and exposure to ultraviolet radiation. Hypoxia can influence production, population dynamics, spawning, and demography in shallow-water populations of the brittlestar *Amphiura filiformis* (Skold et al., 1994; Nilsson and Skold, 1996; Skold and Gunnarsson, 1996). Moreover, Johnson and Kier (1998) recently documented significant damage resulting from exposure to solar ultraviolet radiation in *O. brevispinum*. We made no direct measurements of oxygen concentrations or ultraviolet radiation levels in Saint Joseph Bay, but shallow subtidal grass flats at our study sites likely are subject to both hypoxic events and exposure to elevated ultraviolet radiation during summer and fall months when ophiuroids appear to migrate away from these habitats.

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