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Disturbance, loss of a part of the body, is an important component of life histories. In contrast to plants, sublethal disturbance is not common in animals. Damage to the test of *Mellita* is usually attributed to sublethal predation, but hydrodynamics may be a factor. We found test damage to *Mellita tenuis* on the Florida gulf coast is variable over space and time. Test damage is more frequent in large individuals. This could result from a greater period of time for predation to occur or a decrease in the probability of death from predation. Test damage was variable over space and time, ranging from 0 to >50% of the populations, indicating great variation among locations. Because the test is important in maintenance of position, locomotion, and feeding, damage probably affects the potential for survival, growth, and reproduction.

Damage to the peripheral test of scutellid sand dollars is common and usually ascribed to sublethal predation (Crozier, 1919; Kier and Grant, 1965; MacGinitie and MacGinitie, 1968; Weihe and Gray, 1968; Cocanour, 1969; Merrill and Hobson, 1970; Birkeland and Chia, 1971; Borzone 1992/1993; Nebelsick 1992, 1995, 1999a, 1999b; Nebelsick and Kampfer, 1994; Sonnenholzner and Lawrence, 1998). Sublethal predation indicated by bite marks is recorded even in fossil sand dollars (Zinsmeister, 1980; Nebelsick and Kampfer, 1994; Nebelsick, 1999a). Because the shape and form of the test are adaptive to the ecological conditions in which sand dollars live and for feeding and locomotion (Kier, 1974; Smith, 1984), the loss of test and irregularities in the test can be expected to impair functioning and it could be an important factor affecting growth and reproduction. Vermeij (1987) concluded that injury is a major factor affecting life history characteristics. As a form of disturbance, sublethal damage to the body has been considered an important factor in echinoderm evolution (Lawrence, 1990; Lawrence and Vasquez, 1996). The frequency of test damage also is informative regarding the characteristics of the environment in which populations live.

Harold and Telford (1990) revised the west Atlantic *Mellita*: *Mellita quinquiesperforata* on the coasts of South America, the Caribbean and the western Gulf of Mexico; *Mellita isometra* on the coast of North America; and *Mellita tenuis* on the coast of the eastern Gulf of Mexico. Sublethal predation has been recorded for *Mellita* (*quinquieisperforata*) *isometra* on the coast of North Carolina (Weihe and Gray, 1968) and for *M. quinquiesperforata* on the southern coast of Brazil. Although lethal predation of *M.* (*quinquiesperforata*) *tenuis* has been reported on the Florida gulf coast (Frazer et al., 1991; Kurz, 1995), no record has been made of sublethal predation. Considering its potential importance, we examined *M. tenuis* on the Florida gulf coast for test damage.

MATERIALS AND METHODS

Mellita tenuis were collected from six locations along the Florida gulf coast from Aug. 1995 through Nov. 1998 (Table 1). The anterior–posterior length of each individual was measured. The frequency of individuals with an irregular ambitus was recorded as an indication of damage. The amount of damage was estimated qualitatively (Fig. 1). Level 1 is for intact sand dollars without damage; levels 2–5 are for sand dollars with slight to severe damage.

RESULTS

The frequency of sand dollars in each collection showing test damage is given in Table 2. The frequency of damage varied over space, time, and body size. Fifty-seven percent of the individuals from the collection at the protected St. Joe Bay were damaged, whereas 0 and 1.4% of the individuals from two collections at the exposed Port St. Joe Beach were damaged. The individuals from St. Joe Bay were much larger (82 mm body length) than those from Port St. Joe Beach (19 and 25 mm body length). The frequency of damage at Mullet Key north beach was typically less than that at the nearby Mullet Key east beach. The frequency of damage at Mullet Key north beach

TABLE 1. *Mellita tennuis.* Depth and coordinates of collection sites.

Collection site	Depth (m)	Coordinates
Port St. Joe	3	29°45′N, 58°24′W
St. Joseph Bay	1–1.5	29°40′N, 85°21′W
Mullet Key north beach	2	27°37′N, 82°44′W
Mullet Key east beach	3	27°37′N, 82°44′W
Gulf site	5–6	27°35′N, 82°53′W
Egmont Key	5–6	27°35′N, 82°46′W
Gasparilla Island	2–3	26°46′N, 82°16′W
Naples	1.5–2	26°08′N, 81°47′W

ranged from 3.5% in Aug. 1995 to 30.1% in Nov. 1998. This range was associated with an increase in body size from a mean of 31 mm in 1995 to 53 mm body length in 1998. The frequency of damage of individuals collected the same day approximately 1 km south of the Mullet Key north beach, of the same body length (53 mm), was only 8.1%. However, the very large individuals from nearby Mullet Key east beach (76–84 mm body length) had a high incidence of damage (25–41%). The mean body length and variance of all individuals and of damaged individuals in a collection did not differ.

The percentage of individuals at each level of test damage (1–5) is given in Table 3. No or slight damage (level 2) was most common. The level of damage was low (1–2) in collections with a low frequency of damage (e.g., Port St. Joe, Egmont Key) but high (1–4 or 5) (e.g., St. Joe Bay, Mullet Key, Gulf site) in collections with a high frequency of damage.

DISCUSSION

The frequency of test damage in *M. tenuis* on the Florida gulf coast varied with space, time, and body size, ranging from zero to greater than 50% of the population. Weihe and Gray (1968) reported 9% and >93% test damage to two populations of *M. isometra* on the North Carolina coast, and Borzone (1992/1993) reported 24% test damage to a population of *M. quinquiesperforata* on the coast of southern Brazil.

Both predation and hydrodynamics have been held responsible for test damage to scutellid sand dollars. Crozier (1919) suggested predation by benthic fish is responsible for test damage of *Leodia* (*Mellita*) *sexiesperforata.* MacGinitie and MacGinitie (1968) noted portions of the test of the sand dollar *Dendraster excentricus* were often missing and suggested predation by the spiny lobster *Panulirus interruptus.* Merrill and Hobson (1970) reported the crabs *Loxorhynchus grandis* and *Cancer* sp. feeding on the edges of the test of *D. excentricus.* The frequency of damage may be due to the fragility of the edge of the test or its form that makes it easier for predators, fish or crabs, to break off pieces. Crozier (1919) reported that damage to the test of *L. sexiesperforata* usually was not deep and was restricted to the pos-

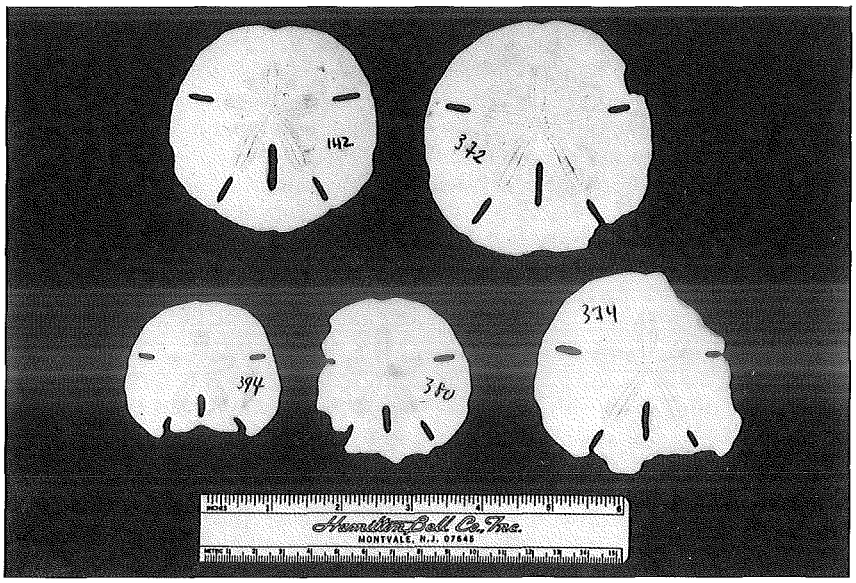

Fig. 1. *Mellita tenuis.* Level of test damage, from 1 (no damage) to 5 (severe damage).

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TABLE 2. *Mellita tenuis*. Frequency of damage of populations on the Florida gulf coast (N in parentheses).

Site	Date	Frequency of damage	Mean body length of all individuals (mm)	Mean body length of damaged individuals (mm)
Port St. Joe	26 May 1997	1.4	18.9 ± 4.1 (65)	—
	5 Oct. 1997	0	25.5 ± 4.4 (27)	—
St. Joe Bay	17 Feb. 1998	57.1	82.4 ± 11.7 (17)	85.8 ± 9.2 (4)
Mullet Key north beach	20 Aug. 1995	3.5	31.4 ± 6.7 (480)	32.6 ± 10.0 (16)
	4 Nov. 1996	7.5	47.3 ± 9.4 (398)	54.4 ± 11.2 (26)[a]
	11 June 1997	9.1	43.9 ± 7.0 (336)	42.0 ± 8.4 (25)
	25 Sep. 1997	8.1	44.7 ± 5.4 (349)	46.8 ± 8.6 (24)
	12 Sep. 1998	18.4	51.6 ± 6.4 (125)	58.0 ± 9.9 (17)
	27 Nov. 1998	30.1	53.1 ± 4.6 (93)	53.1 ± 4.6 (28)
	27 Nov. 1998[b]	8.1	53.0 ± 5.5 (193)	54.3 ± 4.4 (16)
Mullet Key east beach	2 May 1997	25.7	78.5 ± 23.8 (68)	92.9 ± 17.0 (13)[a]
	3 Oct. 1997	41.1	84.9 ± 18.2 (68)	91.2 ± 18.2 (25)
	22 Nov. 1997	36.2	91.8 ± 15.0 (86)	97.8 ± 16.4 (27)
	10 Jan. 1998	28.2	76.5 ± 16.6 (69)	84.2 ± 12.5 (18)
Gulf site	9 March 1997	42.6	111.0 ± 18.6 (38)	118.8 ± 7.7 (19)
	15 Feb. 1998	40.0	99.1 ± 12.9 (25)	97.6 ± 12.5 (7)
Egmont Key	9 March 1997	5.1	52.2 ± 4.5 (306)	53.5 ± 6.6 (13)
	21 Sep. 1997	4.0	55.4 ± 4.4 (173)	56.2 ± 3.0 (6)
	15 Feb. 1998	3.6	55.6 ± 3.7 (138)	57.6 ± 2.9 (5)
	15 Nov. 1998	0	55.6 ± 3.9 (94)	—
Gasparilla Island	14 June 1997	9.2	68.9 ± 9.2 (131)	71.7 ± 8.0 (12)
	1 Oct. 1997	16.5	69.0 ± 7.2 (112)	67.9 ± 6.8 (16)
	31 Jan. 1998	5.6	67.8 ± 7.5 (88)	75.3 ± 0.6 (3)
Naples	5 May 1997	13.2	85.5 ± (38)	82.8 ± 5.1 (5)

[a] Mean body length of damaged individuals was slightly but significantly higher than that of the whole population.
[b] A second collection 1 km south of the usual site on Mullet Key north beach.

terior portion. He suggested this pattern was because the posterior portion was more exposed than the rest of the burrowed body. Damage primarily to the posterior portion of the test has been reported for other sand dollars (*M. isometra*: Weihe and Gray, 1968; *M. quinquiesperforata*: Borzone, 1992/1993; *Echinodiscus auritus*: Nebelsick and Kampfer, 1994; *Encope micropora*: Sonnenholzner and Lawrence, 1998). An alternative explanation for finding only individuals with damage to the ambitus is that damage extending to the coelom results in death. The absence of small individuals with test damage could indicate predation is lethal for them and that scutellid sand dollars have an escape in size from some predators.

Lethal predation on *M. tenuis* has been reported but it takes a much different form. Lethal predation on *M. tenuis* by the gray triggerfish *Balistes capriscus* does not involve the ambitus (Frazer et al., 1991). Instead, the triggerfish inverts the sand dollar and crushes the oral center in order to eat the viscera. Frazer et al. (1991) and Kurz (1995) observed lethal predation of *M. tenuis* by gray triggerfish around artificial reefs. They did not indicate the size of the sand dollars, but their account indicates they were several centimeters in diameter. Both reported an increase in sand dollar density with increased distance from the reefs. Kurz (1995) found that the sand dollar density reached that of a site where gray triggerfish did not occur at 20 m from the reefs. None of the sites sampled in the present study was near refuges of predatory fish. That predation does occur in these habitats is indicated by the observation of Salsman and Tolbert (1965) that *M. tenuis* is nocturnal. Because a diel rhythm of the food of *M. tenuis* is unlikely, their nocturnal rhythm probably is related to predation, most likely from either fish or crabs.

Although Weihe and Gray (1968) suggested that damage to the posterior part of the test of *M. isometra* indicated predation, the extremely high frequency of test damage at an exposed site led them to conclude that hydrodynamics was the primary factor responsible. In our study, the difference in frequency of test damage at the northern and southern ends of Mullet Key is directly correlated with hydrodynamics. However, the frequency and level of test damage were much greater in the protected St. Joe Bay than the exposed Port St. Joe, suggesting that predation was responsible.

TABLE 3. *Mellita tenuis.* Frequency of damage level.

Site	Date	N[a]	n[b]	Frequency of damage level (%)[c]				
				1	2	3	4	5
Port St. Joe	26 May 1997	69	1	98.5	0	0	1.4	0
	5 Oct 1997	30	0	100.0	0	0	0	0
St. Joe Bay	17 Feb 1998	21	12	42.9	23.8	23.8	4.8	4.8
Mullet Key	20 Aug 1995	481	17	96.5	3.1	0.2	0	0.2
north beach	4 Nov 1996	400	30	92.5	6.1	0.6	0.5	0.3
	11 Jun 1997	342	31	90.9	7.3	1.6	0.1	0
	25 Sep 1997	357	29	91.9	5.0	2.1	1.0	0
	12 Sep 1998	125	23	81.6	12.0	4.8	0	1.6
	27 Nov 1998	93	28	69.9	23.7	5.4	1.1	0
	27 Nov 1998[d]	194	17	91.2	6.7	1.5	0.5	0
Mullet Key	2 May 1997	70	18	74.3	19.3	2.1	1.4	2.9
east beach	3 Oct 1997	73	30	58.9	26.0	8.9	6.2	0
	22 Nov 1997	94	34	63.8	27.7	6.4	2.1	0
	10 Jan 1998	71	20	71.8	22.5	2.8	2.8	0
Gulf site	9 Mar 1997	54	23	57.4	34.3	8.3	0	0
	15 Feb 1998	25	10	60.0	32.0	4.0	4.0	0
Egmont Key	9 Mar 1997	336	17	94.9	3.9	1.2	0	0
	21 Sep 1997	177	7	96.0	3.4	0.6	0	0
	15 Feb 1998	138	5	96.4	2.9	0.7	0	0
	15 Nov 1998	94	0	100.0	0	0	0	0
Gasparilla	14 Jun 1997	131	12	90.8	8.4	0.8	0	0
Island	1 Oct 1997	115	19	83.5	13.5	2.2	0.9	0
	31 Jan 1998	90	5	94.4	4.4	0	1.1	0
Naples	5 May 1997	38	5	86.8	13.2	0	0	0

[a] Sample size.
[b] Number of damaged individuals.
[c] 1 = intact individuals without damage; 2–5 individuals with slight to severe damage (see Fig. 2).
[d] A second collection 1 km south of the usual site on Mullet Key north beach.

The frequency of test damage in the population at the northern end of Mullet Key north beach indicates the accumulation of damage over time. Although the frequency of test damage in the population at Mullet Key east beach did not vary over time, the direct relation between the size of the individuals in each collection and frequency of damage suggests an accumulative effect. The very low frequency of test damage at Egmont Key indicates it is a benign environment for *M. tenuis,* in contrast to the nearby Gulf and Mullet Key sites. Whether resulting from predation or hydrodynamics, damage probably affects the potential for survival, growth and reproduction of sand dollars and, consequently, is important in understanding their biology.

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