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Role of a natural disturbance in an assemblage of marine free-living nematodes

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ABSTRACT: One of the predictions of theoretical treatments of soft-bottom benthos is: if disturbance were responsible for the persistence of a species in a community, that species should become disproportionately abundant in recently disturbed patches. We investigated this prediction using marine free-living nematode species in subtidal (2 to 3 m depth) sediments off the Florida panhandle (29°54.55'N, 84°31.45'W), frequently disturbed by stingrays *(Dasyatis sabina)*. In disturbed sediments nematode densities gradually increased over 4 d until they exceeded abundances in background sediments 96 h after the initial disturbance. None of the species examined responded to disturbance in the manner expected. We conclude that small-scale natural disturbances are not important in the maintenance of nematode species in this community.

INTRODUCTION

The role of disturbances (disasters *sensu* Harper, 1977) in the organization of ecological communities has occupied the thoughts of ecologists for almost a century (e. g. Clements, 1916). Several contemporary ecologists have concluded that natural disturbances play an important role in structuring a variety of communities (Platt, 1975: terrestrial plants; Cairns et al., 1976: freshwater protozoans), in particular communities of sessile marine organisms on hard bottoms (Dayton, 1971, 1973; Osman, 1977; Connell, 1978; Paine, 1979; Sousa, 1979).

The importance of disturbance in the organization of soft-bottom communities is less established. Grassle and Sanders (1973; see also Johnson, 1970) have presented a model in which disturbances create a mosaic of patches of different ages. Species that are inferior resource competitors persist in the community by locating and exploiting the early portion of the recovery of disturbed patches, where their competitors are reduced or absent. One would expect that species that are maintained in the community by disturbance will become disproportionately abundant early in the recolonization of a patch. This prediction has been tested in soft-bottom communities but with inconsistent results (VanBlaricom, 1978, 1982; Thistle, 1980; Reidenauer and Thistle, 1981).

In this study of soft-bottom disturbance, we investigated the response of marine free-living nematode species to a natural disturbance in the form of feeding pits created by the Atlantic stingray *Dasyatis sabina* (LeSeur) as it searched for macro-infaunal prey. The goals of the study were to (1) see if nematode abundances were reduced in ray pits; (2) discover how long such reduced abundances persist; and (3) examine the recovering assemblage at the species level to determine whether any nematode species became disproportionately abundant in disturbed patches thereby testing the prediction of the Grassle and Sanders (1973) model.

MATERIALS AND METHODS

We selected a study area at 2 m depth in St. George Sound 300 m off the coast of the Florida panhandle (29°54.55'N, 84°31.45'W) The site is adjacent to a seagrass meadow, and the bottom is a fine sand (2.2 ∅ graphic mean) with a 2 to 3 mm flocculent layer. During a 24-h period, current velocities measured at 20 cm above bottom averaged 4.3 cm s^{-1}. There is little wave action in the absence of storms. Oxidized sediments extend to 1 to 3 cm depth. Ray pits are dug in this area between March and November.

A 60-m^2 area that experienced frequent disturbance

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by rays was permanently marked with 3 parallel, 10-m transect lines placed 3 m from one another. The lines were tagged at 10-cm intervals. A 3-m cross line, also tagged at 10-cm intervals, was used by SCUBA divers to form a set of Cartesian coordinates that allowed accurate mapping of ray pit positions.

The area was mapped 7, 6, 5, 3, 1, and 0 d prior to sampling. Fresh feeding pits were recognizable for 3 d before they became indistinguishable from the background topography. These daily mappings were used to (1) calculate the percent of the study site disturbed by the rays; (2) locate areas undisturbed for at least 10 d in which to take background samples; (3) identify pits made the night before the first sampling time.

The study involved sampling a pit over time so that accurate relocation was required. Accordingly, a removable 3-m steel rod was positioned horizontally above a pit. The pit center was marked on the rod, and PVC stakes were placed at each end. Pits were relocated by positioning the rod on the appropriate stakes and finding the correct center mark. Relocation was accurate to 1 cm. A background site was selected 50 cm away from each pit and at the same distance from the transect line as the pit and located using the same technique. (Rays dig pits in such a way that the excavated sediment is expelled in one direction. Control sites were chosen to avoid this side of the pit and were placed on sites that were visually indistinguishable from the sediment surface further from the pit.) A plexiglass template was placed over the positioning rod to divide the pit and background sites into 4 quadrants that were randomly chosen to be sampled, one at each of the 4 sampling times (Hours 0, 24, 48, 69). Two of 6 possible core positions within each quadrant (also chosen randomly) were sampled with 3.5-cm diameter cores. This procedure was used to sample each of 3 replicate natural pits and their paired controls.

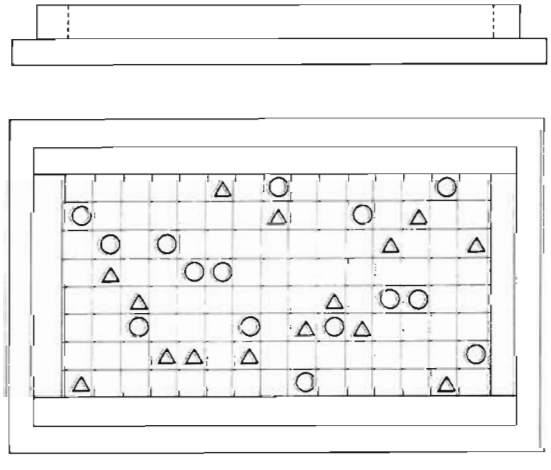

Fig. 1. Lateral and vertical schematic views of the sampling tray with a hypothetical symbol arrangement

The ray pits were made sometime during the night before Hour 0, but their precise ages could not be determined. To investigate the early stages of recolonization, and to determine a more accurate age of the natural pits, SCUBA divers created replicate artificial pits by digging holes with a bucket to equal the dimensions of natural pits. The 2 artificial pits were sampled over a shorter time scale (Hours 0, 5, 24, 29 – short-term pits) using the techniques described above.

For all cores the overlying water and top 1-cm layer were preserved with 4 % formaldehyde. Ten 14-cm cores were taken in background areas and sliced into 1-cm layers. In these cores, 62 % of the nematodes were in the top 1-cm layer. All of the numerically dominant nematode species had their abundance maximum in the 0–1 cm layer.

Nematodes were separated from sediment using the Barnett sorting trough (Barnett, 1968; mean efficiency 99 %, N = 15), retained on a 50 µm sieve, and stained with rose bengal before sorting under a dissecting microscope. The harpacticoid copepods from these samples have been reported on elsewhere (Reidenauer and Thistle, 1981). Because nematodes were 10 times more abundant than harpacticoids, a technique was devised that allowed all of the harpacticoids to be sampled and only a fraction (we chose 1/4) of the nematodes to be collected without bias. Our procedure used a clear plexiglass sorting tray with well dimensions 9.5 cm by 5 cm by 1 cm (Fig. 1). The grid on the bottom of the tray divided the interior into 120 cells (8 rows by 15 columns). We attached a paper sheet to the underside of the tray with 2 different symbols arranged to fall beneath 30 of the cells. We used a stratified random arrangement of symbols; one of each symbol type was placed in cells of each of the 15 columns. Cells without such symbols were not sorted for nematodes. Nematodes that fell completely within the boundaries of cells with 1 symbol type were picked. Nematodes that fell completely or partially within a cell of the second symbol type were also picked. (In using this method, the operator did not need to decide whether a nematode was half in or half out of a cell.) The sample was spread as evenly as possible in a sorting tray that contained a 0.4 % solution of tap water and Calgon® (added to prevent the nematodes from floating) and scanned under the dissecting microscope.

The statistical model used to test for differences in total nematode abundance between pit and background samples at each time was a treatment by block, two-way ANOVA, with the treatment factor (disturbed versus background) fixed, and the blocking factor (between-pit differences) random (mixed model; Sokal and Rohlf, 1969). Each species was tested for disproportionate abundance using the Mantel-Haenszel test as described in Snedecor and Cochran (1976). For each

pair of pit and background samples, one can construct a 2 × 2 contingency table and calculate the probability that a species occurs in the same proportion in background and pit samples. The Mantel-Haenszel test allows these contingency tables to be combined into a single test (in this case 3 pairs of pit and background samples). The 5 % significance level was used in all statistical comparisons.

RESULTS

The efficiency of the subsampling procedure is demonstrated in Table 1. The table shows that the procedure permits one to pick 1/4 of the nematodes ± 1 %. We used linear regression to test for dependence of subsampling efficiency (y) on abundance (x). The regression equation ($Y = -1.35 + .0016\ X$) was used to test the null hypothesis β (slope) = 0 versus the 2-sided alternative $\beta \neq 0$. An ANOVA for simple linear regression was unable to reject this hypothesis ($F = 4.96$, $p > 0.05$); therefore, subsampling efficiency appears to be independent of nematode density. However, when the number of nematodes in the subsample was less than 50, the error increased greatly (range 23.39 % to 27.60 %). Consequently, we completely sorted nematodes when the number of nematodes in the subsample was less than 50 (~200 total nematodes).

Table 1. Efficiency data for subsampling procedure. The expected percent in the sample was 25 %

Total nematodes	Number in subsample	Percent in subsample
1002	251	25.05
649	161	24.81
959	244	25.44
388	94	24.23
957	244	25.50
811	209	25.77
904	218	24.12
505	124	24.55
390	94	24.10

To investigate the performance of the sorting technique at the species level, we identified the 20 most abundant nematode species in the subsample and in the remainder from 4 samples. We used these data in a 2-celled χ^2 test that the binomial probability of any species being included in the subsample was 1/4 (Table 2). No species departed from expectation. We concluded that (1) the technique gave an unbiased and precise subsample of the total number of nematodes in a sample; (2) sampling was independent of species-specific properties.

Ray disturbance was a prominent feature of the study site during the experiment (see Reidenauer and Thistle, 1981, Table 1). The average dimensions of the pits, as well as the total area covered by pits, varied little over the course of the experiment. From the 3 available estimates of percent of area disturbed by new pits per day, a 75 % distribution-free confidence interval (Conover, 1971) is 0.71 % to 1.04 %. Assuming that

Table 2. Rank order abundance and percent composition for the 20 most dominant nematode species and a 2-celled χ^2 test of subsampling accuracy averaged over 4 samples ($\chi^2.05$, 4df = 9.488)

Species	Rank	% of Total	Cumulative %	$\Sigma_1^4\chi^2$
Theristus sp. a	1	16.6	16.6	1.00
Chromaspirina sp. a	2	9.4	26.0	5.82
Metachromadora (Metachromadoroides) sp. a	3	7.7	33.7	1.26
Viscosia brachylaimoides	4	6.3	40.0	2.93
Monoposthia sp.	5	5.7	45.7	6.20
Theristus sp. b	6	5.0	50.7	2.01
Chromadorella sp.	7	4.6	55.3	0.55
Metachromadora (M.) sp. b	8	4.1	59.4	0.30
Innocuonema sp. a	9	3.2	62.6	2.18
Microlaimus sp.	10	2.8	65.4	1.18
Innocuonema sp. b	11	2.4	67.8	2.11
Desmodora sp.	12	2.2	70.0	0.40
Sabatieria sp.	13	2.0	72.0	1.04
Metachromadora (M.) sp. c	14	2.0	74.0	1.87
Chromaspirina sp. b	15	1.8	75.8	2.81
Theristus sp. c	16	1.8	77.6	0.65
Innocuonema sp. c	17	1.5	79.1	0.89
Oncholaimus sp.	18	1.4	80.5	0.96
Tricordorina sp.	19	1.3	81.8	3.33
Metachromadora (M.) sp. d	20	1.3	83.1	2.20

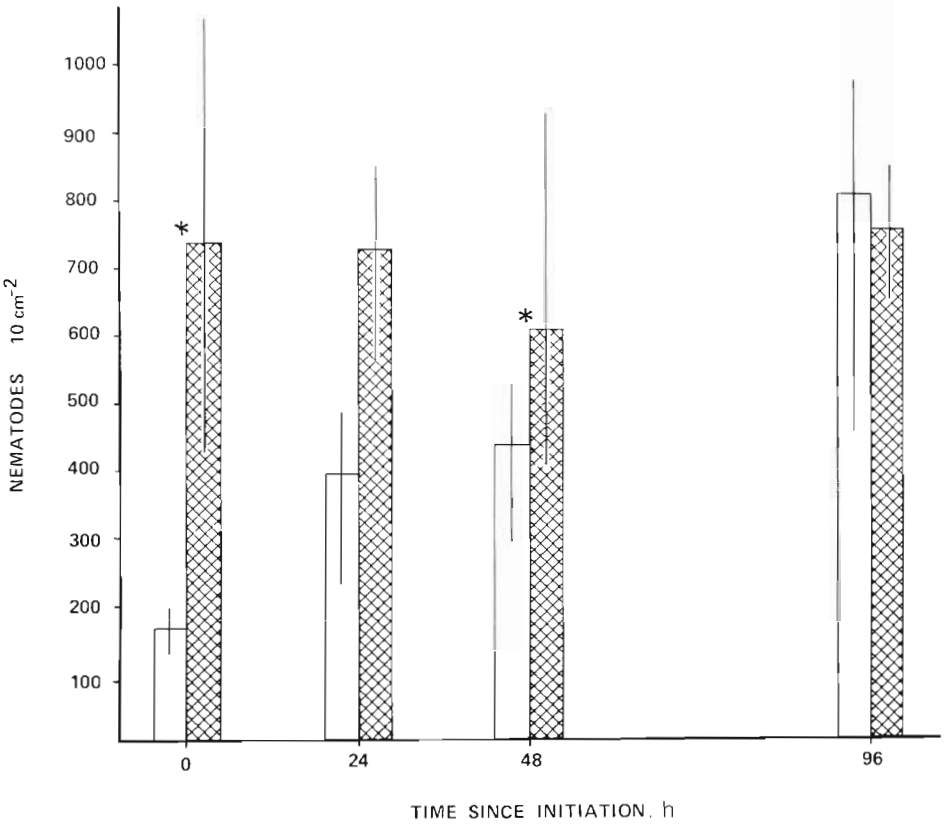

Fig. 2. Mean nematode abundances in the 3 natural pits (clear) and the background samples (hatched), at the 4 recovery times. Bars: overall mean; error lines: range. Significant differences between means marked with an asterisk (*)

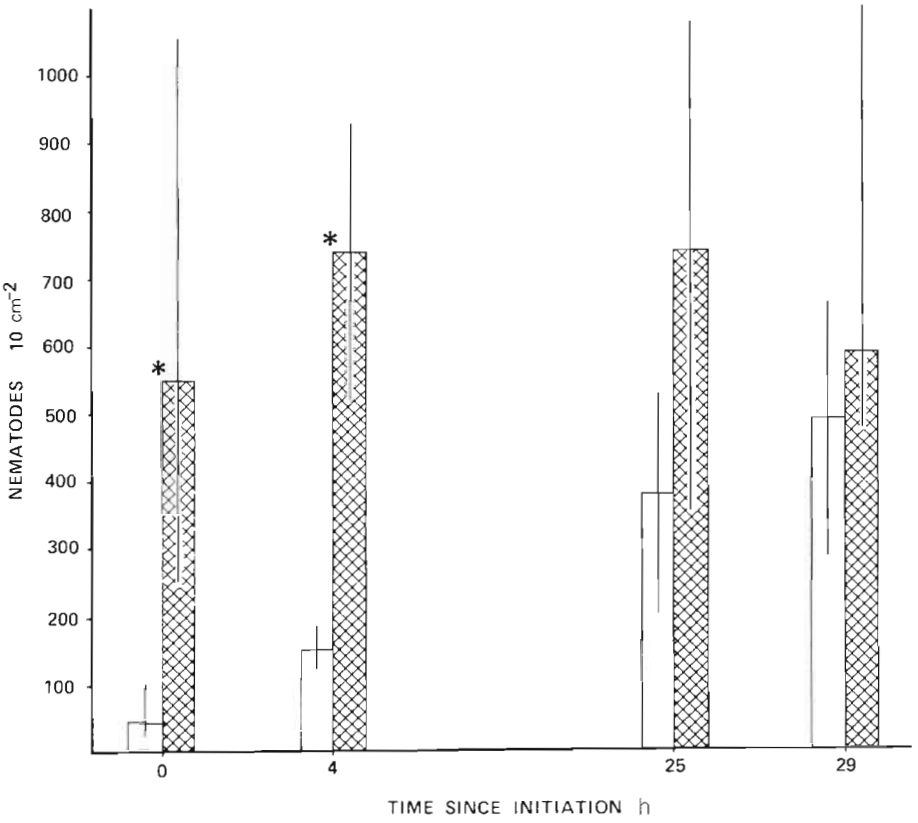

Fig. 3. Mean nematode abundances in the 2 artifical pits (clear) and the background samples (hatched) at the 4 recovery times. Bars: overall mean; error lines: range. Significant differences between means marked with an asterisk (*)

new pits never overlap old ones and using the higher estimate yields 50/1.04 = 48 d to disturb 50 % of the area. Alternatively, assuming that new pits are placed randomly with respect to old ones and using the lower estimate, we find that $(1 - 0.0071)^n = 0.5$ is solved by n = 97 d to disturb 50 % of the area. In either case, ray disturbance could be expected to have significant impact on the study site.

Table 3. Abundances (numbers 9.6 cm^{-2}) of dominant nematode species in the first half of the data 1 from pit (P) and background samples (B) at 4 recovery times. For consistency of presentation, nematode abundances obtained using the subsampler were multiplied by 4

	Hour 0						Hour 24					
Species	P• [1]	B	P• [2]	B	P• [3]	B	P [1]	B	P [2]	B	P [3]	B
Theristus sp. a	19	224	4	20	46	192	104	116	52	40	60	108
Chromaspirina sp. a	8	100	38	64	6	32	12	76	24	80	8	48
Metachromadora (Metachromadoroides) sp. a	18	68	38	56	12	24	60	40	68	44	24	60
Viscosia brachylaimoides	8	92	12	32	11	24	28	16	20	20	16	44
Monoposthia sp.	12	56	15	52	4	24	44	40	0	40	28	24
Theristus sp. b	14	12	14	12	8	8	12	4	12	24	16	28
Chromadorella sp.	7	92	7	12	0	88	4	28	20	8	24	60
Metachromadora (M.) sp. b	5	56	10	48	0	20	28	16	8	32	4	8
Innocuonema sp. a	9	20	6	8	1	12	8	24	16	16	4	16
Microlaimus sp.	2	20	8	12	10	8	12	44	8	28	8	24
Innocuonema sp. b	12	16	5	4	20	24	16	4	20	20	4	12
Desmodora sp.	8	28	10	16	2	4	12	24	44	28	12	12
Sabatieria sp.	1	40	2	0	0	12	8	40	16	4	0	8
Metachromadora (M.) sp. c	0	0	3	16	1	8	0	0	0	4	0	0
Chromaspirina sp. b	3	28	3	12	0	0	4	40	8	4	8	28
Theristus sp. c	4	28	0	0	1	4	16	36	0	12	12	16
Innocuonema sp. c	1	0	1	4	11	8	0	0	0	8	0	8
Oncholaimus sp.	1	4	4	4	3	0	0	16	8	8	0	4
Tricordorina sp.	10	16	0	0	0	0	8	16	8	12	0	12
Metachromadora (M.) sp. d	0	0	5	0	18	8	0	0	16	36	0	4
Total (all species)	159	1184	196	428	192	576	480	764	432	560	236	668

	Hour 48						Hour 96					
	P [1]	B	P [2]	B	P [3]	B	P [1]	B	P [2]	B	P [3]	B
Theristus sp. a	80	172	56	120	32	60	120	228	176	192	224	60
Chromaspirina sp. a	48	132	52	88	28	144	28	48	64	40	84	84
Metachromadora (Metachromadoroides) sp. a	76	56	44	36	92	60	16	20	32	56	64	60
Viscosia brachylaimoides	28	56	36	76	4	24	44	64	44	76	52	36
Monoposthia sp.	48	36	64	36	12	32	32	36	60	60	60	72
Theristus sp. b	24	24	60	16	28	8	16	8	28	40	8	40
Chromadorella sp.	4	64	8	12	0	16	8	20	116	28	32	28
Metachromadora (M.) sp. b	36	44	24	36	36	16	16	32	44	40	80	52
Innocuonema sp. a	24	32	48	12	36	0	12	0	4	36	0	8
Microlaimus sp.	0	16	8	12	4	8	0	4	56	0	16	4
Innocuonema sp. b	20	4	20	8	12	20	8	8	8	32	32	36
Desmodora sp.	16	8	12	4	4	24	4	28	24	0	16	12
Sabatieria sp.	4	40	0	8	4	8	0	0	24	8	16	24
Metachromadora (M.) sp. c	0	0	0	0	0	36	0	0	16	12	12	48
Chromaspirina sp. b	0	16	0	8	0	16	36	56	16	16	16	64
Theristus sp. c	8	28	0	8	0	4	36	36	16	32	20	8
Tricordorina sp.	0	0	0	8	4	24	0	4	0	12	28	40
Oncholaimus sp.	0	32	4	8	0	8	4	16	24	8	20	4
Innocuonema sp. d	0	0	12	12	8	0	0	0	0	4	0	0
Metachromadora (M.) sp. d	16	4	12	4	12	0	0	4	8	12	0	0
Total (all species)	488	924	524	584	364	592	456	788	932	816	996	740

• Samples where nematode abundances were so low that subsampling procedure could not be used

Figs. 2 and 3 show the response of nematode abundances to natural ray disturbance (3 pit-and-control pairs) and short-term disturbance (2 pit-and-control pairs). Two-way analysis of variance at each sampling date detected significant differences between pit (clear) and background (hatched) areas on the first and third sampling dates of the experiment. On the second sampling date, the mean of the background samples was almost twice the mean of the pit samples, but the difference was not significant ($p = 0.65$). By the fourth sampling date, the average densities of nematodes in the pits exceeded the background values.

The short-term artificial pits were tested in a less powerful 2-way ANOVA because only 2 pits were studied. Significant differences between pit and background samples were detected up to 5 h after their formation. Because the densities of nematodes in the natural pits at 0 h were approximately the same as densities at 5 h in the short-term pits, it was concluded that the natural pits were on the average about 5-h old when first sampled.

We collected 116 nematode species during the study. The 12 dominant species comprised 70 % of the total fauna, and the addition of the next 8 most abundant species increased the cumulative total to 83 % (Table 2). Voucher collections of these species were deposited in the British Museum of Natural History and at the Smithsonian Institution. We restricted the remaining analyses to these relatively abundant species.

If a nematode species were exploiting conditions resulting from the reduced nematode densities in ray pits, it should have become disproportionately abundant in pit as compared to background samples. To test

Table 4. Data used in the second set of Mantel-Haenszel tests. Only species-time combinations that were significant in the first half of the data are shown (P = pit, B = background). For consistency of presentation, numbers obtained by using the subsampler were multiplied by 4

	Hour 0						Hour 24					
Species	P• [1]	B	P• [2]	B	P• [3]	B	P [1]	B	P [2]	B	P [3]	B
Theristus sp. a							80	196	56	208	52	164
Metachromadora (Metachromadoroides) sp. a	17	116	23	48	7	48	40	48	16	16	20	44
Monoposthia sp.												
Theristus sp. b	6	60	7	32	10	36						
Chromadorella sp.												
Innocuonema sp. a												
Microlaimus sp.												
Innocuonema sp. b	5	36	3	4	9	32						
Innocuonema sp. c	1	0	4	8	6	16						
Oncholaimus sp.	0	4	1	4	1	4						
Innocuonema sp. d	3	8	2	0	3	4						
Metachromadora (M.) sp. d	0	0	0	8	2	0						
Total (all species)	125	1012	158	604	156	712	392	672	704	844	356	836

	Hour 48						Hour 96					
	P [1]	B	P [2]	B	P [3]	B	P [1]	B	P [2]	B	P [3]	B
Theristus sp. a												
Metachromadora (Metachromadoroides) sp. a	44	28	24	56	16	32						
Monoposthia sp.	20	20	12	60	12	24						
Theristus sp. b	16	12	12	20	4	12						
Chromadorella sp.							196	16	8	4	16	8
Innocuonema sp. a	8	16	28	48	0	28						
Microlaimus sp.							4	24	8	48	40	8
Innocuonema sp. b							12	4	0	16	4	20
Innocuonema sp. c												
Oncholaimus sp.												
Innocuonema sp. d	8	4	4	24	0	0						
Metachromadora (M.) sp. d												
Total (all species)	488	640	467	556	292	404	656	704	944	832	872	648

• Samples where nematode abundances were so low that the subsampling procedure could not be used

this hypothesis, we first randomly chose 1 of the 2 replicate cores from each pit at each sampling time to test each species for disproportionate abundance using the Mantel-Haenszel test and then repeated the procedure on the second half of the data. We used this technique to control the inflation of Type-I error (the probability of rejecting a true null hypothesis) caused by multiple testing by insisting that significant disproportionate abundance be detected in both halves of the data. The family-wide error rate can be estimated under these circumstances as the product of the significance level used in the first test and that used in the second, multiplied by the number of tests performed. In our case $0.05 \times 0.05 \times 20$ equals 0.05. Despite the fact that we tested 20 species on each day, the probability of a rejection of a true null hypothesis remained 0.05.

A total (over all times) of 17 tests showed significant disproportionate abundance of a species in the pit cores in the first half of the data (Table 3): *Theristus* sp. a., *Innocuonema* spp. b, c, d, *Oncholaimus* sp., and *Metachromadora* spp. a, d at Hour 0; *Theristus* sp. a and *Metachromadora* sp. a, at Hour 24; *Theristus* sp. b, *Innocuonema* spp. a, b, d, *Metachromadora* sp. a and *Monspothia* sp. at Hour 48; and *Microlaimus* sp. and *Chromadorella* sp. at Hour 96. Only *Chromadorella* sp. at Hour 96 was significant when tested in the second half of the data (Table 4).

DISCUSSION

Sediment disturbance by rays was intense (an average of 0.91 % of the area reworked d^{-1}) and persistent (seasons lasting ~270 d), suggesting that only a relatively small proportion of the study site is free from disturbance for an entire year. The disturbance had a great effect on the nematodes, reducing densities by at least 80 %. For 3 d after disturbance, nematode densities in the pits were below background levels. These facts suggest that a nematode species might profitably exploit the disturbed patches. However, although a seemingly important disturbance is present in this community, only one nematode species becomes disproportionately abundant during the recovery. The response pattern of this species requires examination. Its dispersion was markedly pitchy in both pit and control samples over all times. The fact that at Hour 0 this species was as disproportionally abundant in control as it was at Hour 96 in the treatment (Table 3) suggests that it was not responding to ray-pit disturbance. In sum, the result expected under the Grassle and Sanders (1973) model was not obtained.

Disturbance does not appear to be structuring this community by permitting competitively subordinate species to numerically exploit conditions in a disturbed patch during the early portion of patch recovery. However, disturbance may be important to the organization of this community in ways our experiment could not detect, e.g. a species could gain a necessary advantage from disturbed patches without increasing its proportional abundance in them (Thistle, 1981). Also, disturbances may keep species' abundances generally below levels where competitive exclusion occurs (Dayton and Hessler, 1972) and thereby be fundamentally important to the persistence of competitively subordinate species.

Reidenauer and Thistle (1981) came to the same conclusion in their study of the harpacticoid copepods from these samples. In contrast, Thistle (1980) found that 2 harpacticoid species responded to a smaller disturbance in this habitat made by an acorn worm, and VanBlaricom (1978, 1982) reported that several macrofaunal species responded to subtidal ray-pit disturbance off California. The heterogeneity of these results suggests that the effect of disturbance is both site and species dependent.

An explanation of our findings that no nematode species responds to ray pits may come from an investigation of dispersal rates of nematode species. Nematode species may be unable to respond to disturbance because they lack sufficient dispersal capabilities to arrive consistently at newly opened space. This inability could explain why none of these nematode species has been able to develop a consistent numerical response associated with disturbance.

The rate of recolonization reported here, over 48 h to repopulate a 0.7 m^2 area, is much slower than that in the intertidal region of South Carolina (12 h for a 9-m^2 man-made disturbance; Sherman and Coull, 1980). However, the results are consistent with current speeds measured at the 2 areas, 15.5 cm s^{-1} in South Carolina and 4.3 cm s^{-1} in the Gulf of Mexico. Also, bedload transport associated with the intertidal study appears to be much less important at our subtidal site. Reidenauer and Thistle (1981) found complete recolonization by harpacticoids after 24 h, indicating that in this subtidal site there may be important differences in locomotion and current dispersal rates between nematodes and harpacticoids as suggested by Bell and Sherman (1980) for an intertidal soft bottom.

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