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Mary Carla Curran
curranc@savstate.edu

Randell E. Cross
rcross@fgcu.edu

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Mary Carla Curran[1,2,3] and Randall E. Cross[2,3,4]

[1]Marine Sciences Program
Department of Natural Sciences and Mathematics
P.O. Box 20600
Savannah State University
Savannah, GA 31404, USA
Tel. 912-691-7434
FAX 912-691-7434
email: curranc@savstate.edu

[2]Belle W. Baruch Institute for Marine Biology and Coastal Research
Columbia, SC 29208

[3]University of South Carolina Beaufort
Beaufort, SC 29902

[4]Current address:
Department of Biological Sciences
Florida Gulf Coast University
10501 FGCU Blvd
Fort Myers, FL 33965-6565
Tel. 239-590-7545
FAX 239- 590-7200
email: rcross@fgcu.edu

ABSTRACT

Feeding pits created by rays may directly or indirectly affect the numbers of meiofauna. We examined the recovery rates of meiofauna inside feeding pits in both intertidal and subtidal areas. Cores were taken inside and immediately outside each pit. Numbers of total meiofauna, nematodes, and other meiofauna found within intertidal pits were significantly reduced following pit formation; the numerically dominant nematodes were reduced by 64%. Recovery to background levels occurred by 48 hours. Numbers of meiofauna in subtidal pits were either unaffected by the feeding activity of rays or differences were undetected due to rapid recovery within 24 h. This is the first study in which comparisons have been made concurrently in adjacent subtidal and intertidal areas.

INTRODUCTION

Small benthic organisms such as meiofauna comprise one of the most abundant groups of organisms in soft-bottom communities (1) and have been shown to be important food resources for estuarine fishes and crustaceans (2, 3, 4, 5, 6, 7, 8, 9). The abundance and composition of benthic meiofaunal communities may be affected directly through feeding by higher trophic level organisms or indirectly through disturbance to the sediments that results from feeding activity (10, 11, 12, 13, 14, 15). Physical disturbance from factors such as hydrology affect sediment dynamics and composition, and may also influence the structure of meiofaunal communities (16, 17).

Fishes such as *Leiostomus xanthurus* Lacepede 1802 (spot), *Fundulus heteroclitus* Linnaeus 1766 (mummichog) and *Platichthys stellatus* Pallas 1788 (starry flounder), as well as crustaceans such as *Palaemonetes pugio* Holthuis 1949 (grass shrimp), have been shown to impact benthic meiofaunal communities either through direct feeding or disturbance (5, 7, 11). In fact, disturbance accounted for most of the mortality of nematodes in a study of spot feeding and accounted for over 30% of the mortality of copepods (17). However, predation by juvenile spot has been found to be non-selective and was not a significant source of meiofaunal mortality in some areas (18). Sediment disturbance caused by rays has been documented in various parts of the world (19). *Rhinoptera bonasus* Mitchill 1815 (cownose ray) have been documented to destroy eelgrass beds of *Zostera marina* Linnaeus 1753 replacing that habitat with unstable sand (20). Rays have been shown to reduce harpacticoid copepods in subtidal pits (21) and other meiofauna in intertidal feeding pits (14, 15), despite the fact that the rays are seeking food items such as crabs, other crustaceans (22), and mollusks (22, 23).

Recovery time of meiofauna depends on various factors including location, duration, intensity, and size of disturbance. In repeatedly disturbed large areas, such as dredged sites, recovery could take years (24). Similarly, in large-scale nodule mining areas, meiofaunal numbers were reduced post disturbance (25). Dernie et al. (26) noted that the recovery time of a benthic community significantly increased if disturbance intensity was increased. Vanaverbeke et al. (27) found that nematode communities may be altered due to frequent sand extraction. In areas of small-scale disturbance, previous studies have demonstrated that recovery of benthic organisms was fairly rapid following disturbance, usually within 24 h in many parts of the southeastern United States (16, 21, 28). In a study of subtidal pits formed by the Atlantic stingray *Dasyatis sabina* in Florida, nematodes took about 96 hours to recover (29). In our previous intertidal research, we found that the numbers of nematodes, ostracods, and oligochaetes were reduced in ray feeding pits immediately following feeding pit formation, but they recovered within 48 h (14). However, the timing of feeding pit formation affected recovery time (15). Numbers of meiofauna in pits that were formed earlier in the summer season recovered approximately 24 h faster than pits formed later in the season. This may be the result of the negative cumulative effect of repeated disturbance of the

sediments, which may reduce the population size of possible recolonizers in the area. For polychaetes, Reise (30) noted a significant decrease in numbers after eight days of repeated human disturbance (raking) in a sandy tidal flat. The ability of nematode assemblages to recover from disturbance may also be the result of frequency of disturbance, as noted in a microcosm study by Schratzberger and Warwick (31) who determined that nematode assemblages in mobile sandy sediments were more resilient to physical disturbance than those from sheltered areas comprised of muddy sediments.

There may also be a difference in colonization rates due to differences in the mechanisms available to colonizers in intertidal vs. subtidal areas. Subtidal areas would have constant contact with the water column and therefore organisms, particularly epibenthic copepods, would be able to colonize at any time, although they are more likely to be found in the water column during periods of sediment scour (32, 33). Fleeger et al. (34) determined that copepods were deposited in small depressions in a similar manner to passive particles and could not select areas in environments with moving water. In intertidal areas, pits are only exposed to the water column a few hours a day, limiting recolonization of some meiofauna. However, burrowers such as nematodes and some copepods are thought to have entered artificial depressions via crawling or passively through disturbance-induced suspension in the intertidal and in shallow embayments (35, 36). There is evidence that nematodes, particularly genera represented by small individuals, are able to select their settlement area, indicating that they are not acting entirely as passive particles (37). Savidge and Taghon (38) also noted that meiofaunal colonization occurred concomitantly with erosion from surrounding sediments followed by preferential deposition in depressions. The present study was not conducted to establish species level community responses in the meiofauna, but rather to further elaborate the effects of fish feeding behavior on reductions in meiofaunal numbers in the higher taxonomic groups. Our study is the first to compare the effects of ray feeding on benthic meiofauna in adjacent intertidal and subtidal areas.

MATERIALS & METHODS

Study Area: This study was conducted in the Chowan Creek channel that separates St. Helena Island and Lady's Island, SC (32o 23.6'N; 80o36.8'W). This area experiences semidiurnal tides with some of the greatest tidal amplitudes (> 9 m spring tides) on the east coast of the US south of New England. Maximum surface current velocities are generally in the range of 1-3 knots, as obtained from local tide tables. The study site has an extensive subtidal pool area that holds water at all low tides and an adjacent intertidal sandflat that is approximately 40 m wide. The subtidal ray pits used in the study were in shallow water (10-30 cm deep) and no further than 80 m from the intertidal pits. Utilization of the creek by rays is seasonal, generally late April through October. Ray activity was never observed in the shallow subtidal area at low tide and no rays were ever caught in seine net samples.

The intertidal sand flat was always exposed at low tidal periods for 2-3 h during the study period. We identified newly formed pits in June 2001 by marking all feeding pits in a circumscribed area with flags on the day before sampling. On the subsequent day, any pits not marked were considered newly formed pits and had been created within the previous 24 h. We examined the effects of ray feeding activities in both intertidal and subtidal sediments. The time differences between availability of the two habitat types to rays would be minimal as we have not observed ray feeding in the shallow subtidal area we sampled. Therefore, the maximum difference in time for pit formation between the two habitats would not be more than 1-2 h. We sampled at low tide and collected the top 2 centimeters in newly created pits using a 1.27-cm diameter syringe. In a previous study, we conducted a vertical distribution study of the meiofaunal distribution in an intertidal area with similar sediments down to 14 cm and found that approximately 85% of total meiofauna were found in the top 2 cm (Cross and Curran, unpubl. data). The mean for each set of two cores taken inside and outside each pit was used to represent a replicate "in" or "out" sample in our statistical comparisons. The "out" samples were obtained from undisturbed sediment that was visually distinguishable from disturbed sediment removed from the pits due to ray feeding. The disturbed sediments are piled in mounds outside the pits and have the same lighter color as the disturbed sediments within the pits. A typical ray pit was approximately 250 cm^2. Pits used in the study were not close enough to each other where we would expect disturbed sediments and meiofauna from one feeding pit to settle in another pit used in the study.

Samples were collected at three different times following pit formation. These samples were identified as 24 h, 48 h, and 72 h because they were collected within those respective times from initial pit formation. We sampled five intertidal pits and five subtidal pits, each of which was considered a replicate. Despite the general high variability of meiofauna found in most studies, we have documented statistically significant differences in meiofaunal abundance after sampling relatively few pits (14, 15) using the same core dimensions (15). While samples obtained over time from the same pits may not necessarily be independent, we do not view this as being problematic in this type of study. We consider the usefulness of inferential statistics in following the recolonization dynamics of an experimental unit (feeding pit) as an over-riding factor to any perceived view of non-independence of experimental units over time (39). The design of this study is no different than other studies of disturbance in which investigators return to the same disturbed site over time. Our design enabled us to know the initial disturbance level for each of the pits we followed through time. We did not sample the same organisms or sediment more than once and it was unlikely that our sampling had a measurable effect in the resampled pits since the amount of sediment we collected each day was on average 0.04% of the pit area.

Samples were immediately transported to the laboratory and separated by passing them through a 500-um sieve onto a 63-um sieve while the specimens

were potentially still alive. The material on the 63-um sieve was preserved and stained in 15% buffered formalin/rose bengal solution. The samples were preserved and stained for at least 48 h. We used a standard decantation method for which the supernatant with organisms was decanted and observed under a microscope at 20x. Meiofauna were counted and categorized into the taxonomic and functional groups: nematodes; copepods; nauplii; ostracods; polychaetes; and oligochaetes. Data are presented as total number of meiofauna, nematodes, and "other" meiofauna (all meiofauna except nematodes) because few meiofauna other than nematodes were collected. In the figure, we show nematodes and not total meiofauna since the nematodes dominated the samples. Densities of meiofauna were expressed per 10 cm^2.

Statistics

A 2-way analysis of variance (ANOVA) was used to compare numbers of meiofauna for the two main factors: tidal location (subtidal vs. intertidal) and pit location (inside vs. outside pits) for each time of collection. All data except the 72-h data for total meiofauna and nematodes met the assumptions of homogeneous variances and normal distributions for ANOVA. The 72-h data that exhibited unequal variances were transformed using a natural log function to achieve homoscedasticity. The null hypothesis was that there were no differences in the number of organisms found inside and outside pits, regardless of the elapsed time after pit formation and regardless of whether the pits were formed in the intertidal or subtidal areas. Tukey's multiple comparison procedures were used to assess significant differences of meiofaunal numbers in the 4 sample types (intertidal inside pits, intertidal outside pits, subtidal inside pits, and subtidal outside pits). All statistical analyses were conducted using SigmaStat Statistical Software (40).
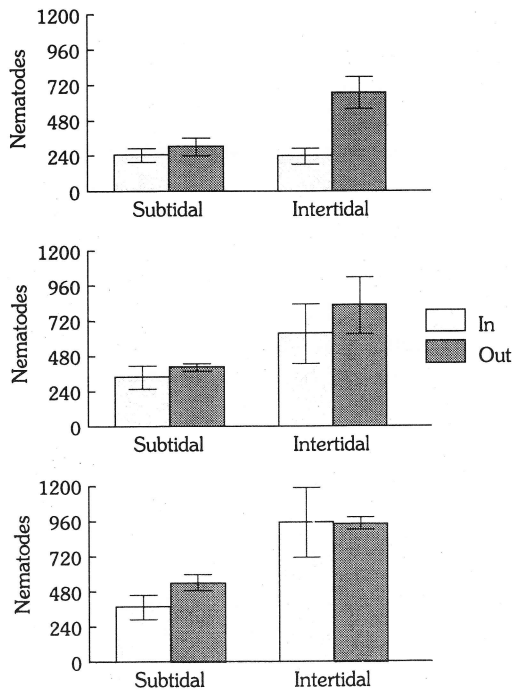
RESULTS

For the intertidal area, there were fewer total meiofauna, nematodes, and other meiofauna inside feeding pits compared to numbers found in the undisturbed sediments outside the feeding pits ($p < 0.05$) at 24 h (2 tidal cycles) (Table I, Fig. 1). There were no significant differences ($p > 0.05$) for the three categories of meiofauna inside and outside feeding pits at 48 h (4 tidal cycles) or 72 h (6 tidal cycles) (Table I, Fig. 1). Nematodes were 64% lower inside feeding pits (241.0 individuals per 10 cm^2) than outside pits (666.8 individuals per 10 cm^2) after 24 h (2 tidal cycles). Nematodes comprised 94.7% of the initial meiofauna in undisturbed areas. Other meiofaunal densities were low in the intertidal and never exceeded 42 individuals per 10 cm^2.

Table I. Mean number of total meiofauna and nematodes (per 10 cm^2) inside and outside of intertidal and subtidal pits.

Location	Mean Total Meiofauna		Mean Nematodes		Mean "Other" Meiofauna	
	In	Out	In	Out	In	Out
Intertidal						
24 h (2 tidal cycles)	253.6	703.9	241.0	666.8	12.6	37.1
48 h (4 tidal cycles)	672.3	858.7	636.0	827.1	38.7	31.6
72 h (6 tidal cycles)	995.4	979.6	953.5	944.8	41.9	34.8
Subtidal						
24 h (2 tidal cycles)	272.6	332.6	249.6	304.9	22.9	27.7
48 h (4 tidal cycles)	379.2	462.2	338.1	406.1	41.1	56.1
72 h (6 tidal cycles)	424.2	594.9	376.0	543.5	48.2	51.4

Figure 1. Mean numbers of nematodes per 10 cm^2 at 24 (2 tidal cycles), 48 (4 tidal cycles), and 72 h (6 tidal cycles) after pit formation. Error bars are ± S.E. (intertidal in vs. intertidal out at 24 h, $p < 0.001$) (subtidal out vs. intertidal out 24, 48, and 72 h; $p < 0.05$)

For the subtidal area, there were no statistically significant differences between total meiofauna, nematodes, and other meiofauna found inside feeding pits and outside feeding pits ($p > 0.05$) for any of the sample times (Table I, Fig. 1). There was only an 18% reduction in number, from 332.6 to 272.6 individuals per 10 cm^2. Nematodes comprised 91.7% of the initial meiofauna in undisturbed areas. Other meiofaunal densities were low in the subtidal and never exceeded 57 individuals per 10 cm^2.

In the undisturbed sediments found outside the feeding pits, the numbers of total meiofauna and nematodes were significantly greater ($p < 0.05$) in the intertidal compared to the subtidal area at 24 h (2 tidal cycles) and 72 h (6 tidal cycles) (Table I, Fig. 1). The initial mean intertidal value for total nematodes was 703.9 individuals per 10 cm2, which is 212% more than the 332.6 individuals per 10 cm2 found in the subtidal. There was not a statistically significant difference ($p > 0.05$) between the 48 h (4 tidal cycles) samples (Fig. 1), although the intertidal samples contained more nematodes. There were no significant differences ($p > 0.05$) for the other meiofauna category for any of the sampling times.

DISCUSSION

The extent to which rays disturb the sediment surface depends on the location and time of year. We found that up to 19% of the sediment surface in the intertidal creek area was disturbed at any time during the summer months (15). Furthermore, feeding pit coverage was underestimated because we did not take into account the area disturbed by the excavated sediment that collects near the periphery of the pits. VanBlaricom (41) found that that amount of disturbed area increased during periods of warm water for subtidal pits created by *Urolophus halleri* Cooper 1863 (round stingray) and *Myliobatis californica* Gill 1865 (bat ray). In Florida, Sherman et al. (29) estimated that approximately 1% of the area was disturbed by new pits per day. Sediment may be disturbed for at least a meter down current from the feeding depression (22). Disturbance by rays reduced nematode numbers in feeding pits by at least 64% (15), or up to 80% as found by Sherman et al. (29).

There were fewer total meiofauna and nematodes inside feeding pits compared to numbers found outside of feeding pits in the intertidal area after 24 hours. This initial difference in numbers inside compared to outside feeding pits in the intertidal area is corroborated in earlier studies (14, 15) and appears to be the result of initial disturbance. However, no differences were detected in meiofaunal numbers found inside versus outside feeding pits in the subtidal area after disturbance. However, Reidenauer and Thistle (21) found a reduced number of copepods in subtidal pits along the Florida gulf coast. In a study of subtidal pits formed by *D. sabina* in Florida, nematodes took about 96 hours to recover (29).

The numbers of total meiofauna and nematodes in the subtidal area were consistently lower than the numbers of meiofauna found in the intertidal, although these values are only statistically significant at 24 and 72 h. There

were 47.2% fewer total meiofauna in the subtidal area than the intertidal. Lower numbers of meiofauna in the subtidal may be due to the longer time period this area is exposed to predators or disturbers of meiofauna. Such low subtidal values may make it more difficult to detect a difference in the subtidal area where background levels of meiofauna are relatively low. We found more copepods in our intertidal samples, and this finding was supported by Palmer and Brandt (32).

The faster recovery time in our study than in studies conducted in other areas may be due in part to the semidiurnal tides and higher water velocity. One reason that Sherman et al. (29) noted slower recovery rates in some areas (e.g., Florida) than in others (e.g., South Carolina, 15) was a slower current speed to transport meiofauna. The faster recovery time in the subtidal area because of the continuous water supply and presumed source of meiofauna transported to the disturbed areas, whereas intertidal pits are only exposed to a new supply of meiofauna for a few hours before, during, and after high tide. The "other" meiofauna in our study rarely exhibited any statistically significant differences. This may have been due to the small number of copepods, nauplii, ostracods, polychaetes, and oligochaetes collected (mean value less than 57 individuals/10 cm^2, Table I). Even though our copepod numbers were low, we were actually sampling at a time (low tide) when we would expect peak copepod numbers in the sediment (32, 42). Nematodes comprised approximately 92-94.7% of the initial meiofauna in undisturbed areas. The position of nematodes as the dominant (17, 43) or codominant (44) taxa in marine sediments has been well established.

We believe that there are many factors that account for the variability in recolonization rates of meiofauna following disturbance and/or predation and that the timing and placement of pits (intertidal vs. subtidal) may also play a role in the recovery of meiofauna in intertidal feeding pits (15). Numbers of meiofauna in intertidal pits that were formed earlier in the season recovered faster than pits formed later in the season (15). This may be the result of a negative cumulative effect of repeated disturbance of the sediments, which may reduce the population size of possible recolonizers available to the intertidal area. Subtidal areas had fewer meiofauna but took less time to recover presumably because of more continuous recolonization via the water column. Our study was the first to compare intertidal and subtidal pits synchronously and sets the stage for future studies to elucidate differences in disturbance and recolonization between these areas.

ACKNOWLEDGMENTS

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