

Changes in the Spatial Distribution of Subtidal Macrobenthos Due to Predation by White Shrimp (*Litopenaeus setiferus*)

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ABSTRACT: Manipulative caging experiments were conducted in North Inlet, South Carolina, to measure the predatory effect of juvenile penaeid white shrimp, *Litopenaeus setiferus*, on their subtidal macrobenthic prey. We used the natural neighbor interpolation procedure within a Geographic Information System (GIS) to map macrobenthos distributions at both the start and end of the cage deployments. Moran's I, a commonly used index of spatial autocorrelation, provided a quantitative metric for evaluating the statistical significance of the observed changes. We tested the hypothesis that juvenile white shrimp are optimal foragers by assessing whether their predatory behavior was targeted at higher density macrobenthos patches inside the enclosures, resulting in a more homogeneous distribution of prey after seven days. Since large changes in patchiness could occur over seven days without incurring a significant change in index value, we treated each index as a continuous measure of patchiness, and examined whether the value increased or decreased consistently among treatment replicates. Using Moran's I, the abundance and spatial distribution of macrobenthos inside control, partial, open, and shrimp inclusion treatments varied in their response. After seven days, decreased patchiness was consistently observed in the high density shrimp treatment replicates, and increased patchiness in the open plots. The GIS natural neighbor interpolation created a succinct visual representation of dramatic changes in prey spatial distribution and prey densities throughout each cage. The GIS interpolation conveyed the dynamic nature of the spatial variability that would not have been evident by calculation of Moran's I alone. Although we could only weakly support our hypothesis, the combination of visual interpolation methods with index calculations has great potential for gaining further insights into the role of different factors as they affect changes in spatial distribution of benthic infauna.

Introduction

Soft-sediment benthic organisms have important structural and functional roles in marine and estuarine communities. These organisms maintain ecosystem processes and services by sustaining fisheries at the base of the benthic food web, creating biogenic structure, and processing nutrients and sequestering contaminants (Thrush and Dayton 2002). Benthic communities are spatially heterogeneous, especially in estuarine soft-sediments where individuals from different age classes and functional groups regularly interact (Barry and Dayton 1991; McIntosh 1991). This spatial heterogeneity or patchiness can be affected by numerous factors, including disturbance and predation (Flint and Younk 1983; Thrush and Dayton 2002), sediment characteristics (Bernstein et al. 1978; Hogue and Miller 1981; Langton et al. 1990), organism feeding mode (Wilson 1976; Reise 1979), and physiological responses to fluctuations

in environmental variables (Bernstein et al. 1978; Holland et al. 1987; Decho and Fleeger 1988; Drake et al. 2002). Physical processes are believed responsible for large-scale spatial variability, whereas smaller-scale spatial heterogeneity is likely due to multiple abiotic and biotic factors including predation (Thorson 1957; Findlay 1981; Barry and Dayton 1991). Understanding the spatial distribution of organisms is important and widely applicable for designing appropriate sampling regimes for commercially and recreationally important species, prey items, and pests (Taylor 1984), and may also provide information on interspecific or intraspecific biological interactions (Botton 1984).

Optimal foraging theory, originating principally from the ideas of Emlen (1966) and MacArthur and Pianka (1966), states that foraging behaviors that maximize energy intake per unit time present a selective advantage. Charnov (1976) extended this idea, predicting that motile predators in a heterogeneous environment will focus their feeding efforts on the most dense prey patches, leaving only when the net rate of energy intake in that patch falls to the average net rate of energy intake for the habitat. Optimal foraging predators should cause more homogeneous prey densities

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(decreased patchiness) by reducing prey abundance in patches where prey are numerous, diminishing variation among patches (Schneider 1978; Botton 1984). Alternatively, when the spatial and temporal extent of a disturbance is small relative to the colonization potential of the prey community, prey patchiness will persist (Thrush and Dayton 2002).

Macrobenthic invertebrates are important prey for many resident and transient consumer populations in estuarine ecosystems. Juvenile white shrimp *Litopenaeus setiferus* (Pérez Farfante and Kensley 1997) are seasonally abundant consumers that help regulate subtidal macrobenthic abundances (Mayer 1985; Hunter and Feller 1987; McTigue and Zimmerman 1991; Pape-Lindstrom et al. 1997). This study examined the spatial dynamics of subtidal macrobenthos subjected to varying levels of predation by juvenile white shrimp. In previous experiments, reduced macrobenthos abundances were observed inside shrimp inclusion cages over seven days (Beseres and Feller 2007). Dispersion indices suggested that significant changes in macrobenthos spatial distribution had also occurred (Beseres 2006). Global positioning coordinates were used to map macrobenthos core sample locations and associated macrobenthos densities within each cage. These data were used to examine changes in macrobenthos spatial distribution by combining the use of Moran's I, a commonly used index of spatial autocorrelation, with the relational spatial graphic capabilities of a Geographic Information System (GIS). Moran's I provides an objective, quantitative measure of the significance of observed spatial changes, while the GIS approach allows a rich visual assessment of spatial dynamics that is not possible using indices of dispersion alone. The combination of these methods allowed us to test the hypothesis, based on optimal foraging theory, that juvenile white shrimp predation reduces the patchiness of their subtidal macrobenthic prey by targeting high-density prey patches and consequently homogenizing prey densities (decreasing patchiness) throughout the caged area.

Materials and Methods

Two 7-day manipulative field experiments were conducted from July 12 to 19 (Expt I) and from July 24 to 31 (Expt II), 2003, in Crabhaul Creek (33°20'N, 79°10'W), located in the North Inlet-Winyah Bay National Estuarine Research Reserve near Georgetown, South Carolina, USA. This warm temperate estuary is 34 km² in area, has a high salinity, and is well mixed with semidiurnal tides of mean range 1.4 m. Crabhaul Creek in particular is adjacent to forested uplands and is subject to depressed salinities after major rainfalls. The North Inlet system comprises approximately 25 km² of

tidal marsh, with *Spartina alterniflora* as the dominant intertidal marsh vegetation (Haertel-Borer et al. 2004). The surface sediments of Crabhaul Creek ranged from clay to very coarse sand, with a mean sediment diameter (\pm standard error [SE]) of 302.7 \pm 119.0 μ m (medium sand); total organic matter (% by dry weight) ranged from 0.53% to 2.79%, with a mean (\pm standard error [SE]) of 0.92 \pm 0.20%.

Experimental cages were constructed using 1 \times 1 \times 0.5 m PVC frames covered with 0.6 cm mesh galvanized steel hardware cloth on top and sides. Five replicates of five experimental cage treatments (25 total) were used: IX, shrimp inclusion treatment (12 shrimp m⁻²); 3X, shrimp inclusion treatment (36 shrimp m⁻²); CC, shrimp exclusion treatment; HC, partial cage with mesh covering half of the top and sides; and OP, open cage with no mesh. For the shrimp inclusion treatments, juvenile white shrimp were collected using seine and cast nets at low tide in a nearby subtidal creek. Prior to use in the experiments, shrimp were held (and fed daily) in continuously-circulating seawater tanks for not longer than four days.

On day 1 of each experiment, the 25 treatment cages were assigned randomly to subtidal positions within Crabhaul Creek, emplaced approximately 1–2 m apart. To sample within a cage, a 10 \times 10 grid was used and the location of a core was determined using two numbers (x, y) from a random number table; only one core (5.75 cm inside diameter, 25.95 cm² surface area) could be collected per cell. Grid locations directly adjacent (within one core diameter) to the cage edge were excluded from sampling. Six core samples were collected from the upper 2 cm of sediment within each cage; the remaining holes were filled with defaunated sediment. For the shrimp inclusion treatments, shrimp total length (tip of rostrum to end of uropod) of a subsample (25 of 250 shrimp) was measured such that shrimp within a similar size range were used in both experiments. Shrimp were placed into the inclusion treatment cages using dip nets after all of the cores were collected.

On day 7 of each experiment, six additional macrobenthic core samples were collected at random from previously unsampled locations within each cage. Cores were held in coolers until sampling was complete (ca. two to three hours), then taken to the laboratory for processing. Samples were fixed with 10% buffered seawater formalin with Rose Bengal stain, stirred gently, and equilibrated for a minimum of 48 h before gently sieving through a 500- μ m screen. After fixation, most cores were held 6–18 mo prior to sieving. Macrobenthic organisms retained on the screen were sorted and identified to family level (for polychaetes) or major

taxon using a stereo microscope at 25–50X magnification. A complete description of the cage sampling methods is reported in Beseres and Feller (2007).

Concurrent with the experiments, water temperature (°C) was measured at 10-min intervals using an Onset StowAway Tidbit Temperature Logger, which was secured to the mesh side of one cage near the center of the experimental array. Surface salinity was measured daily at slack low tide using an optical, temperature-compensated refractometer. Positional coordinates of each experimental cage and several nearby reference points were measured using a Garmin Global Positioning System (Garmin GPS 12Map). Subsequent georeferencing provided accurate data for cage and core sample locations within Crabhaul Creek.

One cage from each experiment had to be removed from the analysis. In Expt I, replicate cage CC-1 was lost due to a storm. In Expt II, a large predatory pinfish (*Lagodon rhomboides*) was discovered inside replicate cage 1X-2 on day 7.

CHANGES IN ABUNDANCE

The mean density of macrobenthos (m^{-2}) was compared in each treatment cage on day 7 to the initial mean density on day 1 to determine whether overall reductions in prey density had occurred. Despite data transformations, densities did not meet the assumptions of parametric statistics; Mann-Whitney Rank Sum tests ($\alpha = 0.05$) were used in lieu of *t*-tests (Hollander and Wolfe 1999). A statistical comparison of the average change in macrobenthos abundance between treatments was unsuccessful due to low statistical power ($p = 0.165$).

CHANGES IN SPATIAL DISTRIBUTION

Input data for the spatial analysis were number of macrobenthos per core. The spatial autocorrelation of macrobenthic organisms within each cage was computed using Moran's I:

$$I = \frac{n \sum \delta_{ij} (x_i - \bar{x})(x_j - \bar{x})}{(\sum \delta_{ij}) \sum_i (x_i - \bar{x})^2}$$

where x_1, \dots, x_n are numbers of macrobenthic organisms in n core samples from each cage, and δ_{ij} is a weighting function based on core location (Ripley 2004). Weights were ascribed using inverse distances, such that the effect of one core sample on another decreases with distance.

Moran's I measures the spatial autocorrelation of features based simultaneously on their locations and values (Goodchild 1986; Griffith 1987). The index evaluates whether the pattern expressed by the

feature (number of macrobenthos) is clustered, dispersed, or random. Index values range from +1 to -1; values larger than 0 indicate positive spatial distribution (clustering or patchiness), values smaller than 0 indicate negative spatial distribution (dispersion), and values near 0 indicate random spatial distribution. The significance of the departure from randomness is evaluated by calculating a z-score (Griffith 2003). Moran's I is a more appropriate measure of spatial autocorrelation than commonly used indices of dispersion (Morisita's I_δ , variance to mean ratio), which do not consider spatial location (Jumars et al. 1977). Moran's I also has been used frequently in studies of marine benthos (Hogue and Miller 1981; Jumars and Eckman 1983; Decho and Fleeger 1988; Fleeger et al. 1990; Sun and Fleeger 1991).

Visual analysis of changes in macrobenthos spatial distribution was conducted using the natural neighbor procedure within a GIS (ArcGIS 9.2, ESRI). Natural neighbor interpolation calculates values in unsampled locations as a weighted moving average of sampled nearest neighbor values (number macrobenthos $core^{-1}$; Mitas and Mitasova 1999; Sárközy 1999; Childs 2004). This technique uses geometric relationships to weight nearby points as a function of the distance from the input and output locations; the greater the distance between points, the less influence on the output value (Childs 2004). This procedure uses a standard Voronoi diagram that partitions the input set of spatial data points into cells. When interpolating the value at a new site (placed among these cells), the neighboring cells are called the natural neighbors of this new site (Park et al. 2006). Macrobenthos abundances from the nearest core samples were given the most weight when interpolating abundances for unsampled areas within each cage.

To implement the natural neighbor interpolation procedure, macrobenthos densities at each core sample location were input into the GIS. These data were then used to interpolate additional macrobenthos densities (cell size 6.25 cm^2) throughout the remainder of the cage area. The interpolation produced contours for graphically displaying the data; colors were used to identify density classes. These spatial data layers for day 1 and day 7 were linked independently for Expt I and Expt II. Interpolations of macrobenthos abundance were excluded from areas where the values were unrealistic (i.e., outside the boundaries of the experimental cages). These graphical data representations allowed for visual comparisons of spatial changes in macrobenthos abundance within the different experimental cage treatment types. Calculations of the percent change in macrobenthos abundance within each experimental cage over

seven days were made for comparisons between treatments and experiments. Within the GIS, cages could also be virtually removed from their actual spatial orientations and rearranged according to treatment and replicate number in order to compare prey spatial distribution patterns as a function of treatment type.

Results

Shrimp total length was similar in both experiments, ranging from 49 to 74 mm (mean \pm SE: 61.4 \pm 1.5 mm) in Expt I and 45 to 77 mm (mean \pm SE: 56.6 \pm 1.6 mm) in Expt II. Water temperature for Expts I and II ranged from 22.0°C to 32.3°C and 23.2°C to 33.7°C, and salinity (psu) ranged from 16.5 to 36.0 and from 5.6 to 35.5, respectively.

CHANGES IN ABUNDANCE

In both Expts I and II, macrobenthos density significantly decreased in the majority of high-density shrimp inclusion cages (3X; Tables 1, 2). In Expt II, significant declines in macrobenthos density also occurred in some of the control cages (CC; Table 2). Macrobenthos densities in the normal-density shrimp cages (1X) and the other treatments decreased with less statistical significance and consistency between the two experiments (Tables 1, 2).

CHANGES IN SPATIAL DISTRIBUTION

On day 1, calculations of Moran's I indicated that macrobenthos were randomly distributed throughout the cage array for both experiments (Tables 1, 2). The natural neighbor interpolation presented graphical predictions of macrobenthos patchiness on day 1 for both experiments (Fig. 1). The densities of macrobenthos in individual patches were noticeably lower on day 1 of Expt II despite being conducted just a week later in a separate, contiguous area. Note that the natural neighbor procedure did not interpolate macrobenthos densities where insufficient neighboring data were available (e.g., outer edges of the 25-cage array).

After seven days, calculations of Moran's I indicated that changes in macrobenthos spatial distribution had occurred. Since large changes in patchiness could occur over seven days without incurring a significant change in index value, we treated each index as a continuous measure of patchiness, and examined whether the value increased or decreased consistently among treatment replicates. In Expt I, macrobenthos patchiness consistently decreased in the high-density (3X) shrimp treatment replicates (Table 1). Patchiness tended to increase in the 1X, CC, HC, and OP treatment replicates. In Expt II, patchiness again

consistently decreased in the 3X treatment and increased in the OP treatment (Table 2). Contrary to Expt I, patchiness consistently decreased in the CC and HC treatments. No consistent pattern was observed in the 1X replicates.

The natural neighbor interpolation graphically demonstrated the loss of high and medium-high density macrobenthos patches after seven days in both Expts I and II (Fig. 1). There was no consistent pattern for the direction or magnitude of change based on cage location. In support of the Moran's I results, the GIS interpolation illustrated consistent reductions in prey patchiness in the 3X treatment replicates for both experiments. In Expt I, patches with the greatest reductions in macrobenthos (76–100%) occurred in shrimp inclusion treatment replicates (1X, 3X) and were observed on a smaller scale in OP, HC, and CC cages (Fig. 2). In Expt II, the greatest declines (76–100%) were again observed in several 3X and 1X cages, but also in one HC cage (Fig. 2). None of the medium-density and high-density prey patches remained in the 3X treatment cages after seven days and very few were present in 1X and OP for both experiments (Fig. 2).

Discussion

The patchy distribution displayed by the natural neighbor GIS interpolation on day 1 of both experiments is consistent with results for estuarine and marine polychaete species (Jumars et al. 1977), and for multispecies benthic communities in marine, freshwater, shallow, and deep habitats (Gage and Geekie 1973; Minshall and Minshall 1977; Scheibling 1980; Volckaert 1987). Although the mechanisms responsible for these prey spatial distributions on day 1 are unknown, they may include small-scale disturbances such as the biological activities of organisms or uneven distribution of food resources (Decho and Fleeger 1988; Thrush and Dayton 2002).

Optimally foraging predators should target high-density prey patches, eventually homogenizing prey densities amongst patches (Hughes 1980a; Jumars and Eckman 1983). In our experiments, the value of Moran's I consistently decreased, indicating a trend toward more homogeneous distributions over seven days in the 3X treatment replicates. The natural neighbor GIS interpolation provided visual evidence of these changes. Similar results have been reported for bivalves; individuals inside predator exclusion cages maintained their patchy distributions, while patchiness decreased for those exposed to predation (Botton 1984). In our experiments, consistent changes in the index value were not observed in cages with normal densities of shrimp (1X). Significant effects may be limited to areas with

TABLE 1. Changes in macrobenthos abundances and Moran's I calculations for field Expt I. Bold abundances indicate a significant change over seven days. Departure from random distribution for macrobenthos was evaluated for each replicate on day 1 and again on day 7 of the experiment using Moran's I index; asterisks indicate significance. Arrows indicate the directional change in patchiness over seven days based on Moran's I.

Treatment — Replicate #	Experiment I					
	Mean # Macrobenthos (m ⁻²)		Percent Reduction	Moran's I		Directional Change in Patchiness
	Day 1	Day 7		Day 1	Day 7	
IX						
1	5,262	5,326	-1	-0.25	-0.13	↑
2	8,983	3,144	65	-0.37	-0.20	↑
3	6,820	4,428	35	-0.34*	-0.22	↑
4	7,764	5,518	29	-0.27	-0.29	↓
5	7,443	5,583	25	-0.10*	-0.38*	↓
3X						
1	8,213	2,567	69	-0.02*	-0.21	↓
2	7,058	2,374	66	-0.11	-0.15	↓
3	8,278	3,575	57	-0.21	-0.25	↓
4	8,278	1,027	88	0.06*	-0.08*	↓
5	5,159	4,107	20	-0.35*	-0.34*	↑
CC						
1	—	—	—	—	—	—
2	9,818	3,914	60	-0.29	-0.33	↓
3	8,021	7,443	7	-0.28	-0.04	↑
4	6,288	6,738	-7	-0.07*	-0.02*	↑
5	8,406	4,492	47	-0.20	-0.18	↑
HC						
1	2,805	6,353	-126	-0.12	-0.28*	↓
2	11,037	3,401	69	-0.45*	-0.11*	↑
3	8,415	5,903	30	-0.39*	-0.05*	↑
4	9,561	10,203	-7	-0.19	-0.31	↓
5	8,085	5,583	31	-0.20	0.02*	↑
OP						
1	5,262	3,401	35	-0.23	-0.27	↓
2	8,663	7,700	11	-0.29	-0.34	↓
3	5,262	4,748	10	-0.34	-0.08	↑
4	9,946	3,337	66	-0.09	-0.01*	↑
5	9,176	5,500	40	-0.07	0.03*	↑

high shrimp densities, such as at low tide in subtidal creeks and isolated pools. The effect of normal density shrimp predation may be small relative to the redistribution potential of the prey community (Thrush and Dayton 2002).

The mechanisms responsible for consistent increases in patchiness in the OP cages are not known. These open plots offered unrestricted access to a diverse suite of potential predators and disturbers that may have affected macrobenthos spatial distribution, including: grass shrimp (*Palaeomonetes pugio*), spot larger than 50 mm (*Leiostomus xanthurus*), various juvenile flatfish, pink and brown shrimp (*Farfantepenaeus duorarum* and *F. aztecus*), and blue crabs (*Callinectes sapidus*; Service et al. 1992).

Significant effects of predation on benthos spatial distribution have been demonstrated for several avian and fish predators. O'Connor and Brown (1977) demonstrated how oystercatchers concentrated their foraging on cockles *Cerastoderma edule* within high-density (and most profitable yield)

patches until the higher-than-average yield for the area was consumed, making it more profitable to move into less dense and previously less-profitable patches. Migratory shorebirds have been reported to reduce the patchiness of both estuarine infaunal macrobenthic prey on mudflats in Massachusetts (Schneider 1978) and urchins on a reef flat in Panama (Schneider 1985). Wellenreuther and Connell (2002) reported that the predatory reef fish (*Cheilodactylus nigripes*) attacked invertebrate prey at a higher rate within high-density prey patches. Our application of optimal patch use theory to juvenile white shrimp adds to a relatively new and promising area of research using invertebrate predators (Hughes 1980a).

Moran's I is one of the most commonly used tests of spatial autocorrelation (Sun and Fleeger 1991; Dubin 1998). Using the index to evaluate macrobenthos spatial distribution both pretreatment and post-treatment was advantageous due to its objective, quantitative foundation. The natural neighbor GIS interpolation complemented the index values

TABLE 2. Changes in macrobenthos abundances and Moran's I calculations for field Expt II. Bold abundances indicate a significant change over seven days. Departure from random distribution for macrobenthos was evaluated for each replicate on day 1 and again on day 7 of the experiment using Moran's I index; asterisks indicate significance. Arrows indicate the directional change in patchiness over seven days based on Moran's I.

Treatment — Replicate #	Experiment II					
	Mean # Macrobenthos (m ⁻²)		Percent Reduction	Moran's I		Directional Change in Patchiness
	Day 1	Day 7		Day 1	Day 7	
IX						
1	5,968	3,529	41	-0.11	-0.01*	↑
2	—	—	—	—	—	—
3	5,467	2,310	58	-0.19	-0.27	↓
4	7,443	6,032	19	-0.27	-0.25	↑
5	5,069	1,476	71	-0.33	-0.36*	↓
3X						
1	4,620	2,759	40	-0.04*	-0.17	↓
2	4,043	1,219	70	-0.16	-0.11	↑
3	3,978	1,283	68	-0.01*	-0.03	↓
4	7,187	1,540	79	-0.09*	0.05*	↑
5	6,160	4,043	34	-0.15	-0.22	↓
CC						
1	5,005	6,417	-28	-0.05*	-0.42*	↓
2	6,994	3,850	45	-0.21	-0.15	↑
3	4,748	2,631	45	-0.06*	-0.11	↓
4	4,107	1,604	61	-0.45*	-0.50*	↓
5	2,695	1,412	48	-0.10	-0.18	↓
HC						
1	4,697	2,823	40	-0.18	-0.16	↑
2	3,529	1,476	58	-0.14	-0.27	↓
3	5,262	5,518	-5	-0.13	-0.13	=
4	5,711	3,529	38	-0.05*	-0.28	↓
5	5,005	2,246	55	-0.14	-0.42*	↓
OP						
1	5,198	2,246	57	-0.13	-0.31	↓
2	6,096	4,299	29	-0.60*	-0.12	↑
3	6,353	8,213	-29	-0.36	-0.17	↑
4	6,032	5,198	14	-0.15	-0.37*	↓
5	4,363	4,235	3	-0.34	-0.06*	↑

by conveying the dynamic nature of macrobenthos spatial distributions. Both procedures use information on sample densities and locations, but the GIS spatial interpolation allowed for the simultaneous visualization of changes in prey abundance and spatial distribution through time. Coupling interpolation procedures with the index calculations helped improve our analysis of optimal foraging theory (*sensu* Charnov 1976; Hughes 1980a,b), in this case for an invertebrate predator.

The ability of the GIS to handle and process geographically-referenced data distinguishes it from other spreadsheet packages that produce traditional contour plots and three-dimensional graphical representations (Chang 2004). The spatial interpolation procedure in particular translates point data into surface data that can then be linked with other surfaces for spatial analysis and modeling (Chang 2004). As more data are collected (e.g., sediment characteristics, water quality, meteorological measurements) existing data layers can easily be linked and interpolations modified using the spatial re-

lational capabilities of the GIS. When combined with in situ sampling, GIS is a powerful tool for utilization in ecological studies (Little et al. 1997), meeting the need described by Hunsaker et al. (1993) for spatial marine ecosystem models that quantify predator-prey and interspecies interactions. Applications of this technology can also easily extend beyond investigations of predator-prey dynamics, such as in comparing predicted versus observed habitat distributions (Lathrop et al. 2001; Höök et al. 2003) and determining whether an perturbed area has recovered to its pre-perturbation condition (Olesen et al. 2004).

All of the Moran's I values calculated in this study were very near 0, indicating that the spatial distributions diverged only to a small degree from being random. The consistently low index values also suggest that the macrobenthos patch size was smaller than one which would include adjacent samples, and that these small patches were not clustered on the scale of core sampling (Jumars et al. 1977). Similarly low degrees of spatial autocor-

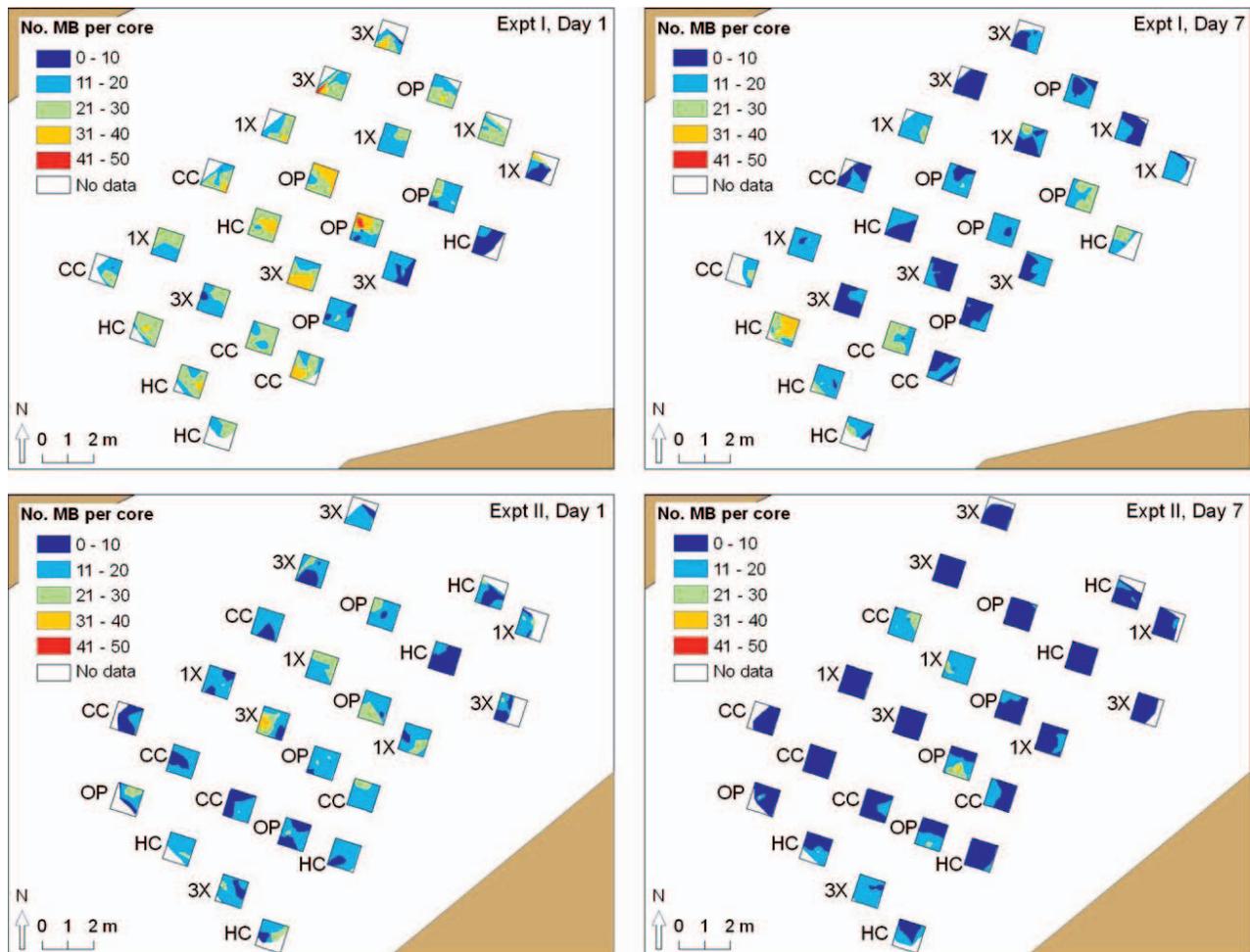


Fig. 1. GIS natural neighbor interpolation of macrobenthos abundance (number of macrobenthic organisms core⁻¹) within experimental cages in Crabhaul Creek, SC for: (upper two panels) Expt I, day 1 and day 7; (bottom two panels) Expt II, day 1 and day 7. Note: CC replicate 1 missing in Expt I, 1X replicate 2 missing in Expt II.

relation have been reported for amphipods (*Dogielinotus loquax*) using irregularly spaced samples (Jumars et al. 1977). Further research is warranted using the GIS natural neighbor interpolation procedure for better association with Moran's index calculations when assessing changes in spatial distribution. For instance, what actually happens to the spatial distribution of organisms when their index changes from -0.2 to $+0.2$?

We did not originally design our cage sampling strategy with spatial analysis in mind, as our initial goal was exclusively to examine changes in prey abundance. In the future, increasing the number of core samples per sample area would decrease the variance around Moran's I calculations and potentially reveal stronger patterns of spatial distribution. Using a uniform grid sampling approach rather than randomly-selected core locations would im-

prove the accuracy of both Moran's I and the natural neighbor GIS interpolation.

The spatial distribution or patchiness of individuals enhances the complexity of community structure (Whittaker and Levin 1977). By advancing our knowledge of the role of predation in shaping prey spatial distribution, we can also improve our understanding of changes in community structure. This study is novel in its application of the natural neighbor interpolation procedure within a GIS to generate graphical representations of prey spatial distribution, providing a unique picture of changes through time that would not have been detected by spatial autocorrelation. The concurrent use of an index such as Moran's I provides a quantitative metric for evaluating the significance of the observed changes. Although the field caging experiment was initially designed to assess short-term

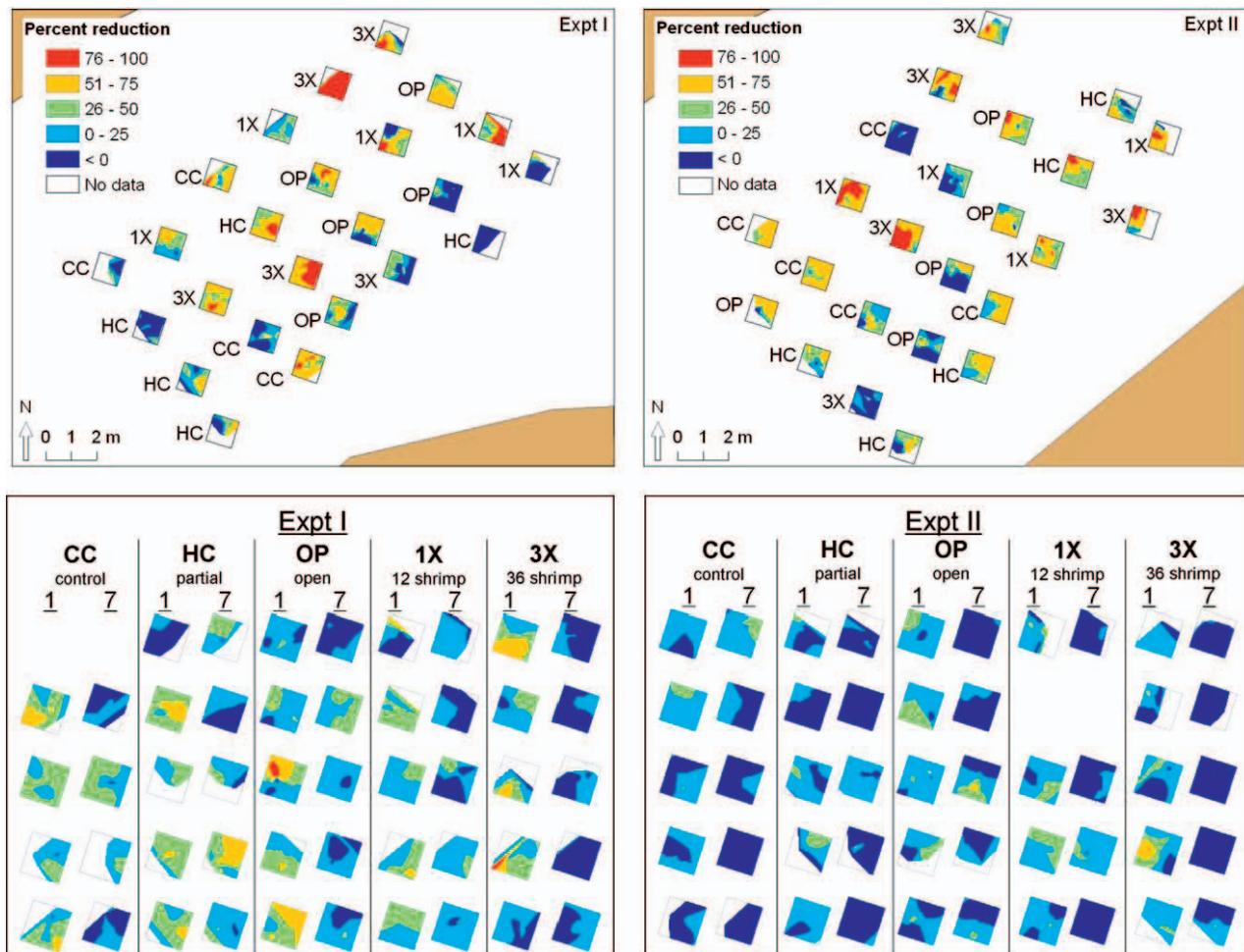


Fig. 2. Upper two panels: percent reduction in macrobenthos abundance in experimental cages over 7 d in Expt I; Expt II. Bottom two panels: GIS natural neighbor interpolation of macrobenthos abundance on day 1 and day 7 for Expt I and Expt II; cages have been virtually removed from their spatial orientation within the creek in order to compare changes within the same replicate cage from day 1 to day 7. Columns indicate experimental treatments, rows indicate the treatment replicates. For example, the 2 cages in the bottom left corner represent the macrobenthos abundances in replicate cage 5 of the CC treatment on day 1 and in the same cage on day 7.

temporal changes in prey abundance, the spatial analyses helped to further our understanding of the overall effects of predation on benthic prey. Designing studies with use of GIS in mind provides a powerful tool for detecting temporal changes in spatial distribution that can extend beyond investigations of predator-prey dynamics and interspecies interactions.

ACKNOWLEDGMENTS

This research was conducted under a Graduate Research Fellowship award for the North Inlet-Winyah Bay National Estuarine Research Reserve (NERR) to J. J. Beseres from the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanic and Atmospheric Administration. We thank two anonymous reviewers for their insightful comments. We appreciate the comments and advice of Drs. D. M. Allen, R. T. Kneib, S. E. Stancyk, and S. A. Woodin during experimental design and

manuscript review. Many thanks also to L. Schmidt for assistance with GIS and to C. Buzzelli for help with GPS measurements and the map of North Inlet. We are grateful to the Baruch Marine Field Laboratory and the North Inlet-Winyah Bay NERR for the use of their facilities and general support. Cage construction would not have been possible without assistance from S. Forehand and R. Matthews. Thanks also to the many field assistants for their important contributions to the North Inlet caging experiments: M. Behum, M. Beseres, K. Bretsch, T. Buck, K. Butler, L. Elder, S. Foose, J. Friedmann, M. Hankins, J. Heidenreich, M. Henry, J. Keesee, M. Lynch, J. Pollack, S. Villanueva, K. Washburn, and J. Yeager. This study partially fulfills the requirements of J. J. Beseres's PhD program. This is Contribution No. 1454 from the Belle W. Baruch Institute of Marine and Coastal Sciences.

LITERATURE CITED

BARRY, J. P. AND P. K. DAYTON. 1991. Physical heterogeneity and the organization of marine communities, p. 270-320. *In* J. Kolasa and S. T. A. Pickett (eds.), *Ecological Heterogeneity*, Volume 86. Springer-Verlag, New York.

- BERNSTEIN, B. B., R. R. HESSLER, R. SMITH, AND P. A. JUMARS. 1978. Spatial dispersion of benthic Foraminifera in the abyssal central North Pacific. *Limnology and Oceanography* 23:401–416.
- BESERES, J. J. 2006. Ecological impacts of predation by white shrimp (*Litopenaeus setiferus*) on subtidal macrobenthos in North Inlet, SC, deduced from field, laboratory, and modeling studies. PhD dissertation, University of South Carolina, Columbia, South Carolina.
- BESERES, J. J. AND R. J. FELLER. 2007. Importance of predation by white shrimp *Litopenaeus setiferus* on estuarine subtidal macrobenthos. *Journal of Experimental Marine Biology and Ecology* 344: 193–205.
- BOTTON, M. L. 1984. Spatial distribution of three species of bivalves on an intertidal flat: The interaction of life-history strategy with predation and disturbance. *Veliger* 26:282–287.
- CHANG, K. 2004. Introduction to Geographic Information Systems, Volume 2. McGraw-Hill, New York.
- CHARNOV, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129–136.
- DECHO, A. W. AND J. W. FLEEGER. 1988. Microscale dispersion of meiobenthic copepods in response to food-resource patchiness. *Journal of Experimental Marine Biology and Ecology* 118:229–244.
- DRAKE, P., A. M. ARIAS, F. BALDO, J. A. CUESTA, A. RODRIGUEZ, A. SILVA-GARCIA, I. SOBRINO, D. GARCIA-GONZALEZ, AND C. FERNANDEZ-DELGADO. 2002. Spatial and temporal variation of the nekton and hyperbenthos from a temperate European estuary with regulated freshwater inflow. *Estuaries* 25:451–468.
- DUBIN, R. A. 1998. Spatial autocorrelation: A primer. *Journal of Housing Economics* 7:304–327.
- EMLEN, J. M. 1966. The role of time and energy in food preference. *The American Naturalist* 100:611–617.
- FINDLAY, S. E. G. 1981. Small-scale spatial distribution of meiofauna on a mudflat and sandflat. *Estuarine, Coastal and Shelf Science* 12:471–484.
- FLEEGER, J. W., M. A. PALMER, AND E. B. MOSER. 1990. On the scale of aggregation of meiobenthic copepods on a tidal mudflat. *P.S.Z.N.I: Marine Ecology* 11:227–237.
- FLINT, R. W. AND J. A. YOUNG. 1983. Estuarine benthos - Long-term community structure variations, Corpus Christi Bay, Texas. *Estuaries* 6:126–141.
- GAGE, J. AND A. GEEKIE. 1973. Community structure of the benthos in Scottish Sea-Lochs. III. Further studies on patchiness. *Marine Biology* 20:89–100.
- GOODCHILD, M. F. 1986. Spatial autocorrelation. Concepts and Techniques in Modern Geography, Volume 47. Geo Books, Norwich, U.K.
- GRIFFITH, D. A. 1987. Spatial autocorrelation: A primer. Resource Publications in Geography. Association of American Geographers, State College, Pennsylvania.
- GRIFFITH, D. A. 2003. Spatial Autocorrelation and Spatial Filtering. Springer-Verlag, Berlin, Germany.
- HAERTEL-BORER, S. S., D. M. ALLEN, AND R. F. DAME. 2004. Fishes and shrimps are significant sources of dissolved inorganic nutrients in intertidal salt marsh creeks. *Journal of Experimental Marine Biology and Ecology* 311:79–99.
- HOGUE, E. W. AND C. B. MILLER. 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology* 53:181–191.
- HOLLAND, A. F., A. T. SHAUGHNESSY, AND M. H. HIEGEL. 1987. Long-term variation in mesohaline Chesapeake Bay macrobenthos: Spatial and temporal patterns. *Estuaries* 10:227–245.
- HOLLANDER, M. AND D. A. WOLFE. 1999. Nonparametric Statistical Methods, Volume 2. Wiley-Interscience, New York.
- HÖÖK, T. O., E. S. RUTHERFORD, S. J. BRINES, D. M. MASON, D. J. SCHWAB, M. J. McCORMICK, G. W. FLEISCHER, AND T. J. DESORCIE. 2003. Spatially explicit measures of production of young alewives in Lake Michigan: Linkage between essential fish habitat and recruitment. *Estuaries* 26:21–29.
- HUGHES, R. N. 1980a. Predation and community structure, p. 699–728. In J. H. Price, D. E. G. Irvine, and W. F. Farnham (eds.), *The Shore Environment*, Volume 2. Academic Press, London, U.K.
- HUGHES, R. N. 1980b. Optimal foraging theory in the marine context. *Oceanography and Marine Biology: An Annual Review* 18: 423–481.
- HUNSAKER, C. T., R. A. NISBET, D. C. L. LAM, J. A. BROWDER, W. L. BAKER, M. G. TURNER, AND D. B. BOTKIN. 1993. Spatial models of ecological systems and processes: The role of GIS, p. 248–264. In M. Goodchild, B. Parks, and L. Steyaert (eds.), *Environmental Modeling with GIS*. Oxford University Press, New York.
- HUNTER, J. AND R. J. FELLER. 1987. Immunological dietary analysis of 2 penaeid shrimp species from a South Carolina tidal creek. *Journal of Experimental Marine Biology and Ecology* 107:61–70.
- JUMARS, P. A. AND J. E. ECKMAN. 1983. Spatial structure within deep-sea benthic communities, p. 399–451. In G. Rowe (ed.), *Deep-sea Biology*, Volume 8. Wiley, New York.
- JUMARS, P. A., D. THISTLE, AND M. L. JONES. 1977. Detecting two-dimensional spatial structure in biological data. *Oecologia* 28: 109–123.
- LANGTON, R., E. LANGTON, R. THEROUX, AND J. UZMANN. 1990. Distribution, behavior and abundance of sea pens, *Pennatulaculata*, in the Gulf of Maine. *Marine Biology* 107:463–469.
- LATHROP, R. G., R. M. STYLES, S. P. SEITZINGER, AND J. A. BOGNAR. 2001. Use of GIS mapping and modeling approaches to examine the spatial distribution of seagrasses in Barnegat Bay, New Jersey. *Estuaries* 24:904–916.
- LITTLE, L. S., D. EDWARDS, AND D. E. PORTER. 1997. Kriging in estuaries: As the crow flies, or as the fish swims? *Journal of Experimental Marine Biology and Ecology* 213:1–11.
- MACARTHUR, R. H. AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *The American Naturalist* 100:603–609.
- MAYER, M. A. 1985. Ecology of juvenile white shrimp, *Penaeus setiferus* Linnaeus, in the salt marsh habitat. M.S. Thesis, Georgia Institute of Technology, Atlanta, Georgia.
- MCINTOSH, R. P. 1991. Concept and terminology of homogeneity and heterogeneity in ecology, p. 24–46. In J. Kolasa and S. T. A. Pickett (eds.), *Ecological Heterogeneity*. Springer-Verlag, New York.
- McTIGUE, T. A. AND R. J. ZIMMERMAN. 1991. Carnivory vs. herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives). *Journal of Experimental Marine Biology and Ecology* 151:1–16.
- MINSHALL, G. W. AND J. N. MINSHALL. 1977. Microdistribution of benthic invertebrates in a rocky mountain (USA) stream. *Hydrobiologia* 55:231–249.
- MITAS, L. AND H. MITASOVA. 1999. Spatial interpolation, p. 481–492. In P. Longley, M. Goodchild, D. Maguire, and D. Rhind (eds.), *Geographical Information Systems: Principles, Techniques, Management and Applications*, Volume 1. GeoInformation International, Wiley, New York.
- O'CONNOR, R. J. AND R. A. BROWN. 1977. Prey depletion and foraging strategy in oystercatcher *Haematopus ostralegus*. *Oecologia* 27:75–92.
- OLESEN, B., N. MARBÀ, C. M. DUARTE, R. S. SVELA, AND M. D. FORTES. 2004. Recolonization dynamics in a mixed seagrass meadow: The role of clonal versus sexual processes. *Estuaries* 27: 770–780.
- PAPE-LINDSTROM, P. A., R. J. FELLER, S. E. STANCYK, AND S. A. WOODIN. 1997. Sublethal predation: Field measurements of arm tissue loss from the ophiuroid *Microphiopholis gracillima* and immunochemical identification of its predators in North Inlet, SC, USA. *Marine Ecology Progress Series* 156:131–140.
- PARK, S. W., L. LINSEN, O. KREYLOS, J. D. OWENS, AND B. HAMANN. 2006. Discrete Sibson interpolation. *IEEE Transactions on Visualization and Computer Graphics* 12:243–253.
- PÉREZ FARFANTE, I. AND B. KENSLEY. 1997. Penaeid and sergestoid shrimps and prawns of the world; keys and diagnoses for the families and genera. *Memoires du Museum National d'Histoire Naturelle* (Fr), Paris, France.

- REISE, K. 1979. Spatial configurations generated by motile benthic polychaetes. *Helgoland Marine Research* 32:55–72.
- RIPLEY, B. D. 2004. *Spatial Statistics*, Volume 1. John Wiley and Sons, Hoboken, New Jersey.
- SÁRKÓZY, F. 1999. GIS functions - interpolation. *Periodica Polytechnica Civil Engineering* 43:63–86.
- SCHEIBLING, R. 1980. Abundance, spatial distribution and size structure of populations of *Oreaster reticulatus* (Echinodermata: Asteroidea) on sand bottoms. *Marine Biology* 57:107–119.
- SCHNEIDER, D. 1978. Equalization of prey numbers by migratory shorebirds. *Nature* 271:353–354.
- SCHNEIDER, D. C. 1985. Predation on the urchin *Echinometra lucunter* (Linnaeus) by migratory shorebirds on a tropical reef flat. *Journal of Experimental Marine Biology and Ecology* 92:19–27.
- SERVICE, S. K., R. J. FELLER, B. C. COULL, AND R. WOODS. 1992. Predation effect of three fish species and a shrimp on macrobenthos and meiobenthos in microcosms. *Estuarine, Coastal and Shelf Science* 34:277–293.
- SUN, B. AND J. W. FLEEGER. 1991. Spatial and temporal patterns of dispersion in meiobenthic copepods. *Marine Ecology Progress Series* 71:1–11.
- TAYLOR, L. R. 1984. Assessing and interpreting the spatial distributions of insect populations. *Annual Review of Entomology* 29:321–357.
- THORSON, G. 1957. Bottom communities (sublittoral of shallow shelf). In G. Hedgpeth (ed.), *Treatise on Marine and Palaeoecology*, Volume 1. *Memoirs of the Geological Society of America* 67:461–534.
- THRUSH, S. F. AND P. K. DAYTON. 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Annual Review of Ecology and Systematics* 33:449–473.
- VOLCKAERT, F. 1987. Spatial pattern of soft-bottom Polychaeta off Nova-Scotia, Canada. *Marine Biology* 93:627–639.
- WELLENREUTHER, M. AND S. D. CONNELL. 2002. Response of predators to prey abundance: Separating the effects of prey density and patch size. *Journal of Experimental Marine Biology and Ecology* 273:61–71.
- WHITTAKER, R. H. AND S. A. LEVIN. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12:117–139.
- WILSON, J. G. 1976. Dispersion of *Tellina tenuis* from Kames Bay, Millport, Scotland. *Marine Biology* 37:371–376.

SOURCE OF UNPUBLISHED MATERIALS

- CHILDS, C. 2004. Interpolating surfaces in ArcGIS spatial analyst. ArcUser, July–September. <http://www.esri.com>.

Received, October 26, 2006

Revised, April 9, 2007

Accepted, May 8, 2007