PRIMARY RESEARCH PAPER

The predatory role of white shrimp (*Litopenaeus setiferus*) in seasonal declines of subtidal macrobenthos

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Abstract The overall purpose of this study was to develop a quantitative model to assess the influence of *L. setiferus* predation on subtidal macrobenthic abundance cycles in an estuarine creek system. Subtidal macrobenthic populations in temperate marine soft-bottom environments are known to undergo seasonal abundance cycles. Although the factors responsible for driving these seasonal shifts in abundance are difficult to identify, both environmental and biological factors have received credit.

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Juvenile white shrimp (*Litopenaeus setiferus*) are seasonally abundant epibenthic predators in the North Inlet estuary that have significant influence upon estuarine macrobenthic densities. Data generated from field and laboratory studies were combined with 20 years of long-term monitoring data to simulate seasonal variations in macrobenthos abundance under different levels of *L. setiferus* predation. Model simulations generated clear reductions in subtidal macrobenthos densities, confirming the role of *L.* setiferus as major consumers of macrobenthos. Model uncertainty was small, and model accuracy increased with shrimp density. In years with low or medium shrimp densities, predicted macrobenthos densities tended to be higher than those observed, yet predicted rates of decline still paralleled long-term observations. Model simulations best matched observed data for the representative high shrimp density year tested. Results indicate that variability in multiple factors, including *L. setiferus* predation, likely control macrobenthos abundance cycles. Predation by earlier-arriving epibenthic feeders may drive initial macrobenthos declines earlier in the year, with *L. setiferus* predation then intensifying and extending these declines throughout the summer and fall. This modeling approach is an important step toward understanding the role of multiple factors driving seasonal macrobenthos dynamics, and the *L. setiferus* population was tractable for examining the importance of epibenthic predation on these organisms.

Introduction

An important characteristic of subtidal benthic population dynamics in temperate marine soft-bottom environments is the occurrence of seasonal abundance cycles that peak in the winter and spring months and drop to low values in the summer and fall (Virnstein, 1977; Coull, 1985; Service & Feller, 1992). The proximate causes driving these seasonal shifts in abundance are difficult to identify, as some factors change predictably throughout the year, while others are associated with short-lived events. Environmental factors such as temperature (Whitlatch, 1977), salinity (Tenore, 1972), dissolved oxygen (Holland, 1985), and sediment characteristics (Sanders, 1958), as well as biological factors such as larval recruitment (Kneib, 1984), competition (Woodin, 1974), food availability or quality (Cheng et al., 1993; Posey et al., 1999), and predation (Virnstein, 1977) have all received credit. Studies of the causes and controls of benthic seasonal abundance cycles are not common, perhaps due to a lack of long-term data needed for detecting such cycles or a temporal mismatch with monitoring schedules.

Predation is an important factor affecting the abundance of benthic organisms in soft sediment communities (Blegvad, 1925; Reise, 1977). Cycles of growth and decline in populations of estuarine benthic invertebrates and their predators exhibit periodicity and overlap at coarse time scales (Virnstein, 1977; Allen et al., 2004; Feller et al., 2004). The seasonal abundance pattern displayed by benthic infauna is often inversely related to the abundance of transient predators such as fish, shrimp, and crabs whose densities peak in the summer and drop in the winter via immigration and emigration. Juvenile penaeid white shrimp, *Litopenaeus setiferus* (Pérez Farfante & Kensley, 1997) and juvenile spot, *Leiostomus xanthurus* (Lacepède, 1802) are among the most common transient epibenthic predators in saltmarsh-dominated estuaries of the southeastern United States. Although both species are important consumers of benthos, penaeid shrimp also consume a wide variety of benthic prey and can have a

profound influence upon estuarine macrobenthos (Mayer, 1985; Hunter & Feller, 1987; Kneib & Knowlton, 1995). Because macrobenthos are an important food source for juvenile *L. setiferus*, which prey upon macrobenthos in a highly seasonal manner, *L. setiferus* predation may be an important factor driving regular seasonal reductions in macrobenthos abundance.

We hypothesized that *L. setiferus* predation is a principal factor influencing the level or severity of seasonal reductions of macrobenthos densities in the North Inlet estuary, South Carolina, USA. The alternative hypothesis suggests that factors other than predation by white shrimp (other predators, food availability or quality, environmental) are the primary drivers. The overall goal of this study was developing a quantitative model to assess the influence of *L. setiferus* predation on subtidal macrobenthic abundance cycles in a subtidal saltmarsh tidal creek ecosystem. A simulation model was designed to connect previously conducted laboratory and field experiments with long-term field monitoring data in an attempt to explain seasonal and long-term variations in *L. setiferus* and macrobenthic populations. The model examined changes in macrobenthos abundance during the 6 months that *L. setiferus* are typically present within estuarine subtidal creeks (Allen et al., 2004). Model initialization utilized average springtime macrobenthos density values derived from the long-term field monitoring data to support model predictions of macrobenthic densities under varying levels of *L. setiferus* predation. Time-series of macrobenthic densities during the 180-day simulation intervals were compared to monthly averages calculated for years of high, medium, and low predator densities from the long-term field monitoring data.

Materials and methods

Long-term monitoring

The North Inlet estuary is 34 km^2 in area, high-salinity (30–34 psu) and well mixed with semidiurnal tides of mean 1.4 m (Fig. 1). The North Inlet system comprises approximately 25 km^2 of intertidal marsh with *Spartina alterniflora* as the dominant vegetation (Haertel-Borer et al., 2004). Sediment types include

Fig. 1 Map of the U.S. Atlantic coast showing South Carolina (SC) with a close-up of the North Inlet estuary and boundary of the North Inlet-Winyah Bay National Estuarine Research Reserve (NI-WB NERR). Long-term seine monitoring for nekton occurred in Crab Haul Creek (CH), long-term cores for macrobenthos monitoring were collected in Bread & Butter Creek (B&B)
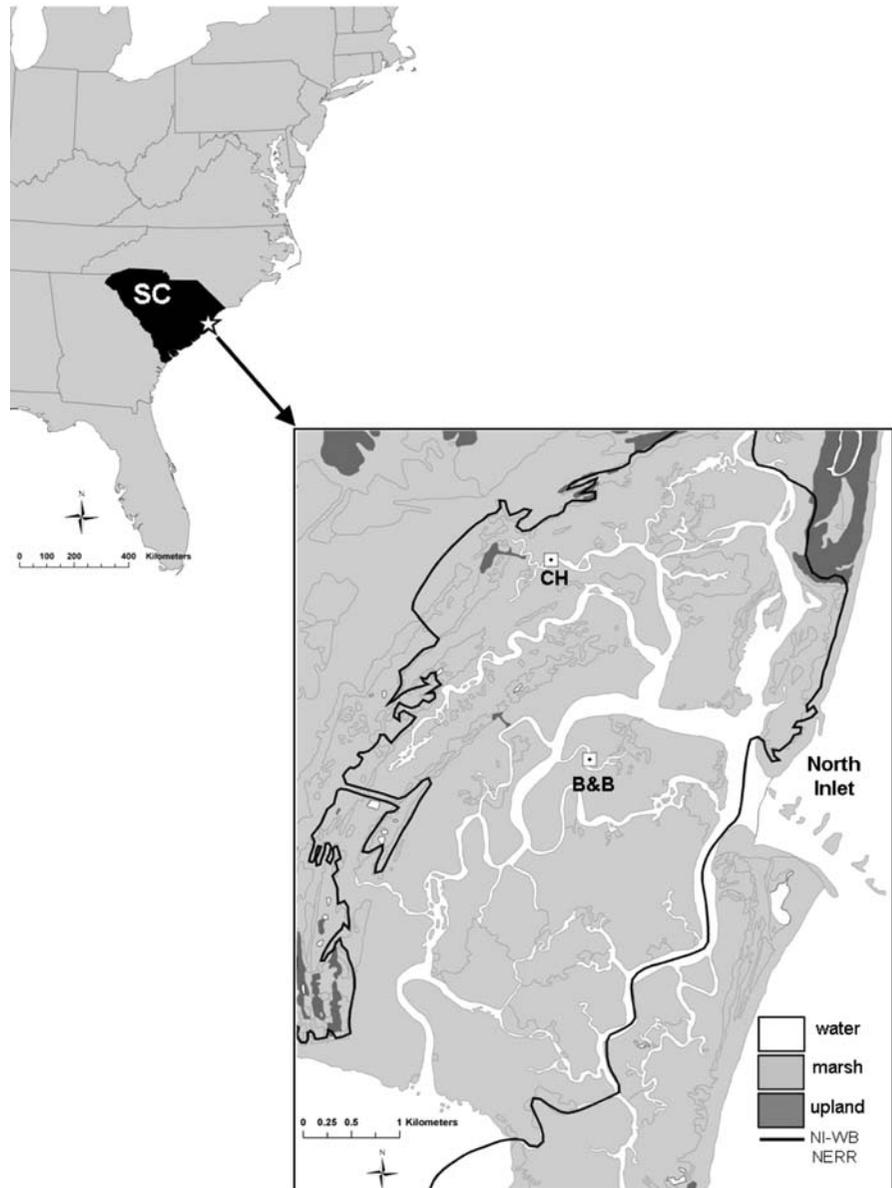
mud and sand with considerable oyster shell hash (Allen et al., 2004; Beseres & Feller, 2007a).

The North Inlet-Winyah Bay National Estuarine Research Reserve (NI-WB NERR) has continued to monitor subtidal macrobenthos in Bread & Butter Creek, North Inlet, SC, from 1981 to present (B&B; Fig. 1; Feller et al., 2004). Eight cores (4.8 cm ID × 5 cm) were collected at biweekly (1981–1991) or quarterly intervals (e.g. seasonally; from 1992 to present) during daytime low tides. The contents of each core were processed separately by

dead sieving sediment core samples on a 0.5-mm mesh screen, and identifying the remaining organisms to the lowest practical taxa using a stereo microscope. Sediment grain size comprised approximately 6% clay, 16% silt, and 77% sand. Final counts of each taxon were converted to number m^{-2} of subtidal sediment derived from the core area (0.0018 m^2).

The NI-WB NERR has also continued to monitor the abundance of nektonic organisms such as juvenile fishes, shrimps, and crabs at biweekly intervals from

1983 to present in Crabhaul Creek (CH; Fig. 1). Nekton are collected using one pass of a 13 m, 6-mm mesh bag seine in an intertidal creek pool (308 m²) with a bottom substrate of mud and scattered oyster shell (Allen et al., 2004). Allen et al. (1992) analyzed seasonal collection efficiencies by conducting 12–14 additional seine hauls during 1984–1988, and found that *L. setiferus* collection efficiency was 25% ± 7% (SE). Densities of *L. setiferus* were therefore adjusted upward by a factor of 4 prior to converting to numbers m⁻² to estimate subtidal *L. setiferus* density for all experimental and modeling efforts. Long-term monitoring data from macrobenthos and *L. setiferus* collections were incorporated for model development.

Experimental approach

Data from previously conducted laboratory and field experiments studying the role of juvenile *L. setiferus* as a benthic predator in the North Inlet estuary were essential for model development. Two 7-d manipulative caging experiments were conducted in the summer of 2003 to determine the effects of juvenile *L. setiferus* predation on ambient subtidal macrobenthic prey (Beseres & Feller, 2007a). The white shrimp densities used (0, 12, and 36 shrimp m⁻²) were well within the range of shrimp densities observed in long-term monitoring collections (Fig. 2B). Total macrobenthos densities in these experiments declined by an average of 40% in cages with 12 shrimp m⁻², and by an average of 60.5% in cages with 36 shrimp m⁻². Results indicated that weekly macrobenthos densities could be reduced up to 673 ind m⁻² d⁻¹ when *L. setiferus* were most abundant (36 shrimp m⁻²), and by 381 ind m⁻² d⁻¹ with fewer shrimp (12 shrimp m⁻²). Four 7-d laboratory experiments were conducted in the summer of 2004 to measure the relative effects of *L. setiferus* predation, sediment disturbance, and macrobenthos emigration on macrobenthos densities (Beseres & Feller, 2007a). These results demonstrated that reductions in total macrobenthos densities were primarily due to *L. setiferus* predation rather than to substrate disturbance or macrobenthos emigration.

In the summer of 2005, laboratory experiments were conducted to determine the density-dependent consumption rates of juvenile *L. setiferus* feeding on macrobenthic bivalve prey *Mercenaria mercenaria* at densities corresponding to 500–20,000 m⁻² (Beseres
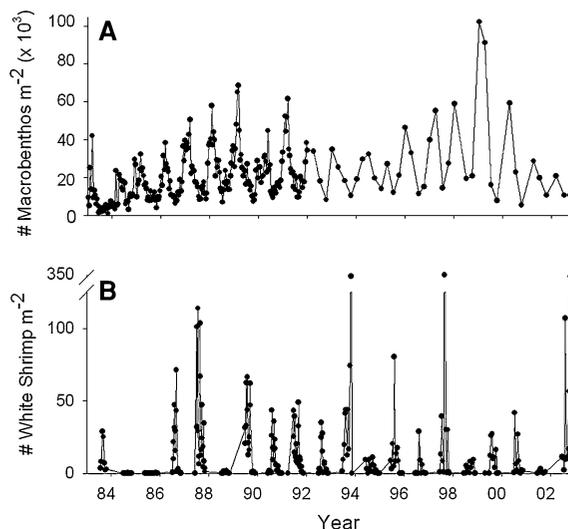
Fig. 2 Long-term monitoring data 1983–2003 of (**A**) average macrobenthos density (m⁻²) from eight replicate cores, and (**B**) *L. setiferus* density (m⁻²) from one standardized seine haul. Ticks on the *x*-axis indicate January 1 of each year. Macrobenthos were collected biweekly until 1992, and quarterly, thereafter

Pollack et al., 2008). The variable consumption rates were best described by a sigmoidal, density-dependent regression model:

$$Y = a \Big/ \left(1 + (X/X_0)^b\right) \qquad (1)$$

where (*a*) is the hourly maximum consumption rate, *X* is the bivalve density, (X_0) is the bivalve density at which the consumption rate was 50% of the maximum, and (*b*) is the width of the sigmoidal curve transition zone. The curve fitting procedure estimated the hourly maximum *L. setiferus* consumption rate (*a*) as 476 bivalves m⁻² consumed per *L. setiferus*, and the bivalve density at which *L. setiferus* consumption is half of the maximum (x_{50}) as 5,455 bivalves m⁻². The results from this set of experiments provided the rate coefficients between the predator (*L. setiferus*) and all-prey (macrobenthos) populations for the model.

Model structure

The model simulation was developed to link previously conducted laboratory and field experiments with long-term field monitoring data in an effort to better explain seasonal and long-term variations in *L.*

setiferus and macrobenthic populations. The model predicted changes in macrobenthos densities in response to variations in gross rates of change in macrobenthos densities and predation by *L. setiferus* for an aggregated 1 m^2 section of ambient subtidal creek sediments that included a full compliment of polychaetes, oligochaetes, and bivalves. Because benthic organisms >0.5 mm are prey for juvenile penaeid shrimp, this size limit was applied to all estimates and formulations (Hunter & Feller, 1987; Dall et al., 1990). Principal processes regulating prey populations include birth, death, growth, immigration, emigration, disturbance, and predation (Wilson & Bossert, 1971). Over the 180-day simulations, populations within the ambient macrobenthic community were assumed to be in steady state (inputs equal outputs) regarding births vs. non-predatory (e.g., age-associated) deaths. Separately, these populations were assumed to be in steady state with regards to immigration versus emigration (Junkins et al., 2006). These two model assumptions were necessary to isolate predation from other population regulatory factors. Laboratory studies indicated that benthic disturbance due to *L. setiferus* foraging and other activities was negligible and thus set as zero for the model (Beseres & Feller, 2007a). Thus, the reduced form of the state equation:

$$\frac{d(MB)}{dt} = G - P \qquad (2)$$

where *MB* is the density of macrobenthos, and *G* represents the maximum daily gross change in macrobenthos density regulated solely by shrimp predation (*P*). The effects of shrimp predation (*P*) were modeled using experimentally derived proportional mortality functions (see Eq. 4).

Nunes & Parsons (2000) reported the minimum average daily percentage change in polychaete abundance in shrimp ponds (*Farfantepenaeus subtilis*) to be 0.5%. We utilized this value as a starting point to parameterize the daily gross rate of change in macrobenthos density (M_G):

$$G = MB \times M_G \qquad (3)$$

Shrimp predation (*P*) was calculated as a function of macrobenthos abundance and the type III (sigmoid) proportional mortality rate (*K*) derived from *L. setiferus* feeding experiments with *Mercenaria mercenaria* (Beseres Pollack et al., 2008). Measured

proportional mortality rates in these experiments were variable and ranged from 0.43 to 0.97 (43–97%). A predator control function (*C*) that varies from 0 to 1 was also included to modulate predation depending upon *L. setiferus* densities.

$$P = MB \times K \times C \qquad (4)$$

Thus, the net growth rate of the macrobenthic community results from the daily gross changes in macrobenthos density and losses from daily predation by *L. setiferus*. The time step was 1 day and an Euler scheme was used for time integration. The model was designed to predict changes in macrobenthos density (# m^{-2}) over the cycle from April through September (6 mo = 180 d) of *L. setiferus* ingress from offshore in to the saltmarsh, consumption and growth while in the estuary, and subsequent seaward emigration that occurs each year.

Model calibration and simulation

Model calibration was conducted to derive optimal values for rate parameters resulting from experiments and to evaluate model tolerance to parameter ranges. Calibration was conducted in a systematic series of model manipulations designed to test responses of macrobenthic densities to different levels of individual and multiple parameter settings. Average annual *L. setiferus* densities from ingress in April to emigration in September were calculated from 1983 to 2003 with each year designated as either low (<5 shrimp m^{-2}), medium (5–15 shrimp m^{-2}), or high (>15 shrimp m^{-2}) in terms of average *L. setiferus* density. Parameters were calibrated for three independent versions of the model based on three single years from the long-term data set representing low shrimp density (1988), medium shrimp density (1990), and high shrimp density (1987; Fig. 2B). Average macrobenthos densities measured in April of each year provided the initial conditions of macrobenthos density (Fig. 2A). The model interpolated between time points to provide a dynamically changing value for predation. Simulated average monthly macrobenthos densities were compared to the long-term monitoring data by calculating the monthly residuals between the observed and predicted values and performing a *t*-test of the null hypothesis that the residual mean = 0.

Given this information, model runs simulated the effects of 1-year of low, medium, or high shrimp density on macrobenthos abundances. Twenty years (1983–2003) of *L. setiferus* density data from the North Inlet estuary were used to generate a time-series of shrimp predator densities that was input into the model. Data from 8 years with the lowest monthly mean *L. setiferus* densities (<5 m^{-2}) were averaged to generate a 6-month time-series representing a season of low shrimp density. The 5 years with the highest monthly mean *L. setiferus* abundances (>15 m^{-2}) were averaged to generate a monthly time-series for high shrimp densities. The remaining 7 years of monthly mean *L. setiferus* densities (5–15 m^{-2}) were averaged to represent medium shrimp density seasons (Fig. 2B).

The 20-year average macrobenthos density for April provided the initial conditions to begin simulation of macrobenthos density ($\sim 32,000$ ind m^{-2}; Fig. 2A). Average monthly macrobenthos densities were calculated from the continuous model output. These discrete values were compared statistically to monthly average macrobenthos densities calculated from the 8 low-density, 7 medium-density, or 5 high-density shrimp years using tests of residuals similarly as in model calibration.

Sensitivity tests

The sensitivity of model output to variations in key parameters was assessed in a series of separate simulations. Sensitivity analyses were conducted on

all model parameters; only parameters with the greatest model sensitivity are discussed. The daily gross change in macrobenthos parameter (M_G) and the disturbance parameter (F_D, assumed to be negligible, 0% day^{-1}, in the base model) were varied systematically from the base model values. While M_G was varied from a base model value of 0.5% day^{-1} by increasing and decreasing by 10% and 25%, F_D was varied from a base model value of 0.0% day^{-1} by increasing and decreasing to 0.1% and 0.25% day^{-1}. The percent change in model output between the expected base model output ($M_{(exp)}$) and the observed sensitivity case ($M_{(obs)}$) was calculated as:

$$\left(\frac{M_{(obs)} - M_{(exp)}}{M_{(exp)}} \right) \times 100 \qquad (5)$$

the average percent change in macrobenthos density over all model time points caused by the given % change in individual parameter values.

Results

Sensitivity tests

The largest amount of variability in simulated macrobenthos densities occurred when increasing or decreasing the disturbance parameter (F_D) from the base model value of 0% day^{-1} to 0.25% day^{-1} (Table 1). Increasing or decreasing the daily gross rate of change in macrobenthos density (M_G) by either 10% or 25%, or varying F_D to 0.10 day^{-1}

Table 1 Sensitivity analysis for the daily gross rate of change in macrobenthos density (M_G) and *L. setiferus* disturbance (F_D) in low, medium, and high density shrimp years (180-day simulation period)

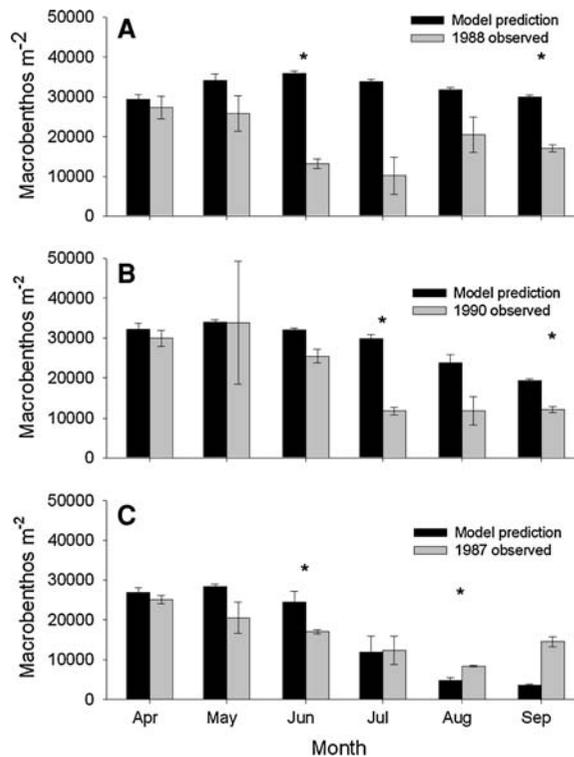| Variable	Parameter (default value)	Sensitivity test value (% day^{-1})	% Change		
			Low shrimp density	Med shrimp density	High shrimp density
MB	M_G (0.5% day^{-1})	0.375	15.4	14.2	11.9
		0.45	5.8	6.1	5.1
		0.55	−4.3	−6.4	−5.6
		0.625	−11.9	−16.8	−15.5
	F_D (0.0% day^{-1})	−0.25	−26.9	−32.5	−37.5
		−0.10	−9.2	−13.3	−12.0
		+0.10	12.3	11.6	9.7
		+0.25	28.2	25.3	21.5

M_G was varied from a base model (default) value of 0.5% day^{-1} by increasing and decreasing this value by 10% and 25%. F_D was varied from a base model (default) value of 0.0% day^{-1} by increasing and decreasing this value to 0.1 and 0.25% day^{-1}

resulted in relatively small variations in model output.
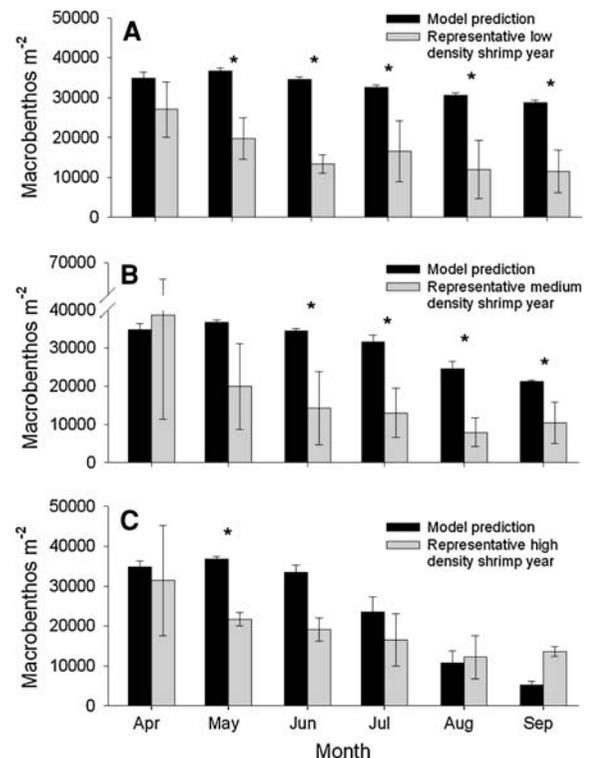
Model calibration and simulation

The calibration model predictions of macrobenthos densities were similar to those observed in 4 of the 6 months for the low (1988), medium (1990), and high (1987) shrimp density years ($P > 0.05$; Fig. 3). Model uncertainty was small; variance around individual mean monthly predictions of macrobenthos density was relatively small compared to the variance around the observed values. In the low shrimp density year (1988), the model predicted only slight declines in macrobenthos density, and values tended to be greater than those observed (Fig. 3A). In the medium shrimp density year (1990), the model predicted an

increased monthly rate of decline in macrobenthos density toward the second half of the simulation period, similar to the pattern observed (Fig. 3B). The greatest declines in macrobenthos abundance—both from model predictions and those observed—occurred in the representative high shrimp density year (1987; Fig. 3C).

Given the calibration results, the model was then used to simulate the effects of one representative year of low, medium, or high shrimp density (calculated from long-term data) on macrobenthos densities. Model uncertainty was again quite small, with the variance around predicted values of macrobenthos density being smaller than the variance around long-term observations (Fig. 4). Model accuracy (agreement between observed and predicted)

Fig. 3 Model calibration results. Monthly average (±SD) macrobenthos densities from model simulations (black bars) and observed data (gray bars) in April through September in a (A) low shrimp density year (1988: <5 shrimp m^{-2}), (B) medium shrimp density year (1990: 5 to 15 shrimp m^{-2}), and (C) high shrimp density year (1987: >15 shrimp m^{-2}). Asterisks indicate calculated monthly residuals (between observed and simulated values) were significantly different from 0 ($P < 0.05$)

Fig 4 Model simulation of the effects of 1-year of low, medium, or high shrimp density on macrobenthos abundances. Monthly average (±SD) macrobenthos densities from model simulations (black bars) and calculated long-term averages from 1983 to 2003 (gray bars) in April through September. The 20-year (1983–2003) calculated average macrobenthos density for April provided the initial macrobenthos density as the starting point for all the three simulations. Asterisks indicate that the calculated monthly residuals (between the observed and simulated values) were significantly different from 0 ($P < 0.05$)

increased with shrimp density. In the representative low shrimp density year, the model predicted minimal declines in macrobenthos densities, which led to values that were significantly and consistently higher than the long-term observations (Fig. 4A). The model predicted greater declines in macrobenthos densities in the representative medium density shrimp year, but the predicted values were still higher than those observed (Fig. 4B). Despite the predictions of higher macrobenthos densities than those occurred in long-term observations, in both the representative low and medium shrimp density years, the predicted rates of macrobenthos decline were nonetheless roughly parallel to those observed. Model simulations best corresponded to the observed data for the representative high shrimp density year (Fig. 4C). Although the model simulation did not capture the initial decline in macrobenthos densities from April to May, model predictions for 5 of the 6 months of simulation were similar to those observed (Fig. 4C).

Discussion

This study developed a benthic community simulation model as a pathway to integrate tidal creek ecological studies conducted across a range of temporal and spatial scales. More specifically, a quantitative model was derived from laboratory and field studies to assess the effects of *L. setiferus* predation on subtidal macrobenthic abundance cycles in a subtidal estuarine creek system. Model inputs of shrimp predation rates and output of macrobenthic densities were calibrated and tested using various predator and prey components accumulated through 20 years of long-term monitoring. This model effectively integrates studies over multiple scales to investigate ecological complexity (McCauley et al., 1993; Wilson et al., 1993; Gentleman, 2002).

Dynamic biological processes such as fluctuations in prey abundances are inherently complicated and involve numerous factors operating over different spatial and temporal scales. However, modeling complex systems necessitates simple models with minimal abstraction (McCauley et al., 1990; Levin, 1992). This ecological modeling effort was customized to determine the capability of a single predator species to modulate seasonal declines in the abundance of their primary prey taxa. Model accuracy

increased at higher shrimp densities. Discrepancies between simulated and observed macrobenthos abundances occurred in part because macrobenthos are eaten by many other species of epibenthic predators (Stehlik & Meise, 2000; Albertoni et al., 2003).

It is very likely that life history attributes of alternative predators are important in the modulation of tidal creek macrobenthos abundances. Early-arriving epibenthic feeders such as spot (*Leiostomus xanthurus*), various juvenile flatfishes, pink and brown shrimp (*Farfantepenaeus duorarum* and *F. aztecus*), and blue crabs (*Callinectes sapidus*) may drive initial macrobenthos declines earlier in the year, with *L. setiferus* predation then intensifying and extending these declines throughout the summer and fall (Ellis & Coull, 1989; Feller & Coull, 1995). Potential interference between *L. setiferus* and other predators may also occur (Kneib, 1987; Mansour & Lipcius, 1991). Posey & Hines (1991) reported strong indirect effects of epibenthic and nektonic predation on benthic infaunal densities and community composition. We did not examine the effects of other resident and transient marine predators in combination with *L. setiferus*, and hence this is an avenue of important future research. Expanding the model framework to include additional predators may help reduce both the variability and discrepancies between simulated and observed results.

The importance of motile predators in controlling patterns of benthic invertebrate abundance has been the subject of many investigations in marine soft-sediments (Woodin, 1974; Reise, 1977; Beukema et al., 1998; and others). Previous studies have shown that *L. setiferus* predation significantly reduces macrobenthic densities in field and laboratory experiments (Service et al., 1992; Zimmerman et al., 2000; Beseres & Feller, 2007a). However, because *L. setiferus* are highly motile within estuarine creek systems, their impact may vary considerably both spatially and temporally (Beseres, 2006). This study was not intended to, nor could it, demonstrate that *L. setiferus* predation alone can account for the annual summer minima of macrobenthos abundances in the North Inlet estuary. However, model simulations generated remarkably clear reductions in subtidal macrobenthos due to this single predator. Such results suggest that *L. setiferus* is likely a major consumer of macrobenthos, particularly when present in high densities.

As the shrimp grow larger in size, *L. setiferus* predation may have a greater role in intensifying and extending macrobenthos declines later in the summer and fall. Changes in the macrobenthic densities were examined at a gross taxonomic level; thus, further analyses by predatory species composition and/or guild may yield a more complete representation of the partial impacts of *L. setiferus* predation on changes in population and community structure. Previous studies of *L. setiferus* and other predators have demonstrated the strongest predation effects on taxa living near the sediment surface compared to deeper burrowing taxa (Virnstein, 1979; Ambrose, 1984; Beseres Pollack et al., 2008). For example, predation by *Carcinus maenas* or *Crangon crangon* shrimp did not affect the overall density of *Corophium* sp., but significant changes in the population structure occurred regardless (Raffaelli et al., 1989).

The potential effect of interannual variability on model simulations was apparent when comparing the calibration and simulation results. The calibration model results tended to agree with the single-year observations of macrobenthos abundance to which they were compared (Fig. 3), whereas the simulation model results were often overestimates of the multi-year (interannual) observations (Fig. 4). The combination of inherent within-year variability in shrimp and macrobenthos abundances, coupled with interannual variability in environmental factors, may have strongly influenced the multi-year model simulations (see also Cloern & Nichols, 1985; Blenckner, 2005). For example, ephemeral spring freshets due to heavy rains can cause large declines in salinity that push shrimp out of the estuary until salinity returns to normal levels; freshets can also produce declines in infaunal predator abundance (Feller, personal observations). Interannual and decadal variability in abiotic and biotic factors have been demonstrated as important regulators of population dynamics in marine systems (Johnson & Wiederholm, 1992; Sugimoto & Tadokoro, 1997; Schwartzlose et al., 1999).

One of the benefits of modeling is its ability to identify important or even missing variables and to generate of new hypotheses based on the results (Christian & Wetzel, 1991). Based upon our sensitivity analyses, it is possible that omitted population regulation factors such as benthic disturbance are in fact non-negligible (Beseres & Feller, 2007a). Some studies have shown significant movements of benthos in response to space competition or sediment disturbance (DeWitt & Levinton, 1984), or by active swimming or passive drift (Commito et al., 1995). The potential effects of disturbance from other environmental (e.g., storms) or biotic (i.e., other consumers) factors are difficult to predict in time and space and should be included in future implementations of the model (Palmer, 1988).

Bivalve proportional mortality rates were used in the simulations as a proxy for actual rates of macrobenthic community mortality (Beseres, 2006). Differences between the predicted and observed macrobenthos densities may be related to the limited data available on mortality rates of other macrobenthic organisms due to predation. The proportional mortality rates of non-bivalve macrobenthic species are unknown but are likely to vary as a function of prey motility, size, defensive behaviors, and other adaptations (Valiela, 1995). Attempts were made to quantify proportional mortality rates of polychaete and oligochaete prey as part of this study, but were hindered by laboratory cultures that could not be successfully maintained. Because *L. setiferus* are known to readily consume multiple types of macrobenthic prey (Mayer, 1985; Hunter & Feller, 1987; McTigue & Zimmerman, 1998), the addition of quantifiable information on prey species-specific mortality rates and behaviors could offer the potential for increased model fit.

The roles of food limitation or quality (bottom-up control) on macrobenthos were not investigated in this study. Previous studies in estuarine habitats have not yielded consistent results, particularly in combination with predator effects. Some experiments have shown negligible effects of food limitation on macrobenthos abundance relative to the effects of predation (Dauer et al., 1982; Wiltse et al., 1984; Posey et al., 1995), whereas others have reported significant results (Seitz & Lipcius, 2001). Interactive effects between fertilization and predator reduction treatments may also be important. In manipulations of two tidal creek ecosystems, infaunal annelid abundance declined with both nutrient enrichment and predator reduction; the response of benthic microalgae to nutrient enrichment was also greatest with predator reduction (Deegan et al., 2007; Fleeger et al., 2008). In smaller-scale field manipulations, haustoriid amphipods demonstrated strong increases in biomass with nutrient additions with predator

removal (Posey et al., 2006). The effects of food quality and not just food availability may also influence macrobenthos abundances. Seasonal variation in sediment nutritive value has been shown to influence growth rates of macrobenthic deposit feeders, with detrital enrichment leading to increased abundances (Levinton & Stewart, 1988; Cheng et al., 1993; Kelaher & Levinton, 2003). Sediment nutrition can be assumed to undergo seasonal changes in the North Inlet estuary as well; however, these changes have not been measured. A general conclusion may be that food supply determines the maximum level of macrobenthos prey population abundances, which is then modified or amplified by predation to the realized level (Renaud et al., 1999; Beukema et al., 2000). Much more study is needed to clarify the relative effects of predation and food variability on estuarine macrobenthic seasonal cycles.

Because of the complexity of estuarine and trophic linkages, with multiple primary producers and consumers, prevalent omnivory, large inter- and intra-annual variability in population densities (Schoener, 1989) and spatial distribution patterns (Beseres & Feller, 2007b) it is likely that multiple factors, nearly all unaccounted for in the current model, interact to control multi-year macrobenthic abundance dynamics. Our relatively simple model simulations generated clear reductions in subtidal macrobenthos due to *L. setiferus* predation thus confirming their impact as major consumers of macrobenthos. The modeling effort also leads to new questions about other factors such as alternative predators or environmental variation (e.g., decreases in salinity from precipitation events), particularly in triggering the initial decline of macrobenthos early in the spring. Modeled rates of macrobenthos decline suggest that *L. setiferus* predation may have greater importance in intensifying and extending the magnitudes or duration of macrobenthos declines later in the summer and fall. This study demonstrates the value of a combined (long-term monitoring, field, and laboratory experiments, modeling) approach for achieving a better understanding of the role of several of many factors on macrobenthos community dynamics as they are influenced by seasonal changes in *L. setiferus* abundance.

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