

JUVENILE WHITE SHRIMP *LITOPENAEUS SETIFERUS* PREDATION ON MACROBENTHIC AND ZOOPLANKTONIC PREY

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ABSTRACT An important part of quantifying predator-prey dynamics is to understand the contribution of various prey types to the predator diet. Although the role of juvenile penaeid shrimp as benthic predators is well established, recent research has indicated that penaeids are also capable of utilizing the energy available in zooplanktonic form. Yet the relative role of juvenile penaeids as direct zooplankton predators, capturing and consuming zooplankton from the water column—as compared with their role as benthic predators of animals that live on, or have fallen to, the bottom remains unknown. Two separate sets of laboratory experiments were conducted to determine the density-dependent predation rates of juvenile *Litopenaeus setiferus* feeding directly on (1) zooplanktonic prey *Artemia salina* in the water column and (2) benthic prey *Mercenaria mercenaria* in sediment. The average proportional mortalities for *M. mercenaria* (43% to 97%) were much higher than for *A. salina* (–10% to 28%). At low prey densities, proportional prey mortality increased with increasing prey densities for both *M. mercenaria* and *A. salina*, indicating a type III functional response by *L. setiferus*. A maximum consumption rate of 476 *M. mercenaria*/*L. setiferus*/hr was estimated in the benthic feeding experiments, whereas predator satiation was not observed even at the highest *A. salina* densities. High proportional *M. mercenaria* mortalities across moderate densities (1,000–2,500 m⁻²) suggest the potential for *L. setiferus* regulation of *Mercenaria* populations. Negative proportional *A. salina* mortalities at low and moderate densities suggest that *L. setiferus* are not efficient zooplankton predators. The variable consumption rates displayed by *L. setiferus* feeding on different prey types are a demonstration of their dietary plasticity as omnivores. Although *L. setiferus* are more effective as benthic predators, their ability to capture and consume prey from the water column suggests that zooplankton may be a viable alternative prey source when benthos are unavailable or inaccessible.

KEY WORDS: functional response, *Litopenaeus setiferus*, macrobenthos, predator-prey, shrimp, zooplankton

INTRODUCTION

An important part of quantifying predator-prey dynamics is to understand the contribution of diverse prey types to the diet and the role of predation in regulating different prey communities. Penaeid shrimp, and in particular the white shrimp (*Litopenaeus setiferus* Linnaeus, 1767), have been well documented as epibenthic predators on a wide variety of prey including small crustaceans, bivalve molluscs such as the hard clam *Mercenaria mercenaria*, and polychaete and oligochaete worms (Mayer 1985, Hunter & Feller 1987, Dall et al. 1990, McTigue & Zimmerman 1998, Beseres & Feller 2007a). Although the role of penaeids as benthic predators has been well established, penaeid gut contents are often finely macerated and difficult to identify under the microscope (Williams 1955). As such, penaeids are generally not placed into a single trophic category (Moriarty 1977), but instead are described as omnivores, with a diet reflecting the general food availability in the environment, including not only benthic, but also planktonic, and free-swimming prey (Cockcroft & McLachlan 1986, Dall et al. 1990). Although previous research has demonstrated that zooplankton clearly contribute to the diet of postlarval penaeid shrimp (Coman et al. 2003), the capacity of juvenile penaeid shrimp to be direct predators on zooplankton remains unknown. To our knowledge, no studies exist that have

examined the dual role of juvenile penaeid shrimp as both a benthic predator and a direct predator on zooplankton.

Previous studies (e.g., Rubright et al. 1981, Chen & Chen 1992, Martinez-Cordova et al. 1998) have implied that juvenile penaeid shrimp are capable of utilizing the energy available in zooplanktonic form, yet they have not been able to distinguish between zooplankton capture from the water column and ingestion of those that have fallen to or live on the bottom. This is an important distinction, because it is unknown whether penaeids are able to obtain sufficient energy when their usual benthic food items are scarce, unavailable, or inaccessible. Significant temporal variations in zooplankton and benthos abundances have been reported from shrimp pond studies; coupled with gut content analysis, the changes in abundance of both prey types was attributed to active grazing by shrimp *Penaeus vannamei* (Martinez-Cordova et al. 1998). Similarly, in shrimp ponds (*Penaeus stylirostris*) supplemented with inorganic fertilizer, increases in chlorophyll, planktonic copepod production, and shrimp growth were reported (Rubright et al. 1981). It was not specified, however, whether the increased shrimp growth was because of capture of zooplankton out of the water column, from increased benthic input from fallen zooplankton, or their fecal material. In laboratory experiments, *Penaeus monodon* was capable of capturing and consuming live zooplankton, but again it was not distinguished whether the shrimp were capturing zooplankton out of the water column or picking them off the bottom of the experimental chamber (Chen & Chen 1992).

In the current study, we sought to examine and compare the role of juvenile white shrimp *Litopenaeus setiferus* as predators

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on benthos in sediment and on zooplankton swimming in the water column. Two different sets of laboratory feeding experiments were conducted to examine the density-dependent predation rates of *L. setiferus* feeding directly on (1) recently settled hard clams *Mercenaria mercenaria* in sediment and (2) zooplanktonic *Artemia salina* swimming in the water column. For each prey type, we determined the functional response (FR) relationship, defined as the quantity of prey consumed per predator per prey density, which typically assumes one of three forms: type I (linear, density independent), type II (hyperbolic, inversely density dependent), and type III (sigmoid, density dependent) (Holling 1965, Murdoch & Oaten 1975, Hassell et al. 1977). Although it can be difficult to distinguish between a type II and type III FR, the types can be differentiated by expressing the number of prey consumed in terms of proportional prey mortality. At low prey densities, proportional prey mortalities decrease with increasing prey densities for the type II FR, and increase with increasing prey densities for the type III (Gotelli 2001). The type I FR is generally uncommon for motile predators that actively search for prey (Hassell 1979). Quantifying the FR of *L. setiferus* on different prey types is important for understanding the contribution of multiple prey sources to the shrimp diet, the capacity for *L. setiferus* predation to regulate different prey communities, and the creation of models to investigate ecological dynamics for ecologically and economically important populations (Beseres Pollack et al. submitted).

MATERIALS AND METHODS

Benthos Feeding Experiments

The role of *L. setiferus* as a benthic predator was examined using recently settled bivalves *Mercenaria mercenaria* as prey. Long-term biweekly (1981–1991) and now quarterly (1992 to present) monitoring of subtidal macrobenthos in the North Inlet estuary has shown average quarterly subtidal macrobenthos densities ranging from $1.3 \times 10^4 \text{ m}^{-2}$ (summer) to $3.3 \times 10^4 \text{ m}^{-2}$ (winter; 1983–2003), with bivalves constituting between 5% and 20% of the total macrobenthos community (Feller et al. 2004).

Laboratory feeding experiments were conducted at the Baruch Marine Field Laboratory in Georgetown, SC, using filtered seawater delivered continuously from the North Inlet estuary (33°20'N, 79°10'W). Experiments occurred from July through September 2005 using round, clear plastic tanks (25 cm ID \times 20 cm H). Consumption rates of *L. setiferus* were determined at nine *M. mercenaria* densities matching 500–20,000 bivalves m^{-2} (25–1,000 bivalves tank^{-1}), simulating (and exceeding) a natural range of macrobenthos densities measured in the long-term monitoring data (Feller et al. 2004). Recently settled *M. mercenaria* spat were obtained fresh weekly, sieved gently through a 600- μm onto a 500- μm mesh screen, and held for 24 h in flowing, filtered seawater. Juvenile white shrimp were collected with seine nets from the North Inlet estuary. Six individual shrimp of total length (TL) 67–79 mm were placed into holding tanks and acclimated to feeding on *M. mercenaria* spat for 12 h prior to each experiment. Six bivalve density treatments were conducted per experiment. Six tanks were filled with 3 cm of defaunated subtidal sediment that had been sieved through a 500- μm screen, frozen for a week, and

rinsed with filtered seawater. Three liters of filtered seawater were then added to each tank and aerated under ambient outdoor conditions. Individual live *M. mercenaria* were counted under a stereo microscope at $\times 40$ magnification and then added evenly at selected densities to each of the tanks. After a 2-h acclimation period to allow bivalves to burrow into the sediment, an individual *L. setiferus* was added to each of the tanks. The area available to each shrimp for foraging corresponded to that for a density of 20 shrimp m^{-2} , a midrange value from long-term monitoring data (Allen et al. 2004). Experiments were conducted for 24-h; on completion, the shrimp, sediment, and bivalves were preserved in Rose Bengal with 10% buffered formalin. The remaining bivalves were counted under a stereo-microscope and subtracted from the initial nominal abundance to calculate number of prey consumed. Experiments were replicated for each prey density.

The relationship between *L. setiferus* consumption rates and *M. mercenaria* densities was examined by determining the best-fit nonlinear regression model for the raw data. The models were fit to the data using the Regression Wizard in SigmaPlot 10.0 (Systat Software Inc., 2006), which uses the Marquardt-Levenberg algorithm to find parameter estimates of the independent variables that give the best fit between the equation and the data.

Feeding Depth Experiments

Because benthic prey are able to burrow into the sediment, two 12-h laboratory experiments (one daytime, one nighttime) were conducted in the summer of 2005 to quantify the depth at which *L. setiferus* are able to access prey items in subtidal creek sediments. Eight tanks (same as used in the feeding experiments) were filled with seawater from Crabhaul Creek (23°C, 32 psu; in the North Inlet estuary), and aerated from above. Five 1 cm-thick layers of artificially colored sediment (Kaleidoscope Colored Play Sand, TX Agri Products, Conroe, TX) were carefully poured through the water and allowed to settle onto the bottom of each tank. Care was taken not to cause extra turbulence in the water. Approximately 500 *Mercenaria mercenaria* spat (500–600 μm) were used as prey. One hundred spat were placed between each uniquely-colored layer of sediment as well as onto the sediment surface (Fig. 1).

Two feeding depth experiments were conducted: one during the daylight hours (0800–2000), and one through the night (2000–0800). At the initiation of each experiment, tanks each were assigned randomly to either *L. setiferus* or control treatments, to control for benthic disturbance of the colored sediments. Six *L. setiferus* treatments contained one *L. setiferus* tank^{-1} (68–79 mm TL), whereas two control treatments contained prey only. The experiments lasted 12 h, after which the experiment was ended and the sediment color from the deepest layer that was now present on the sediment surface was qualitatively observed as a proxy for the maximum depth of predation/disturbance by *L. setiferus*.

Zooplankton Feeding Experiments

The role of *L. setiferus* as a zooplankton predator was examined using freshly hatched *Artemia salina* nauplii. Long-term biweekly (1981–1991) and now quarterly (1992 to present) monitoring of water-column mesozooplankton in the

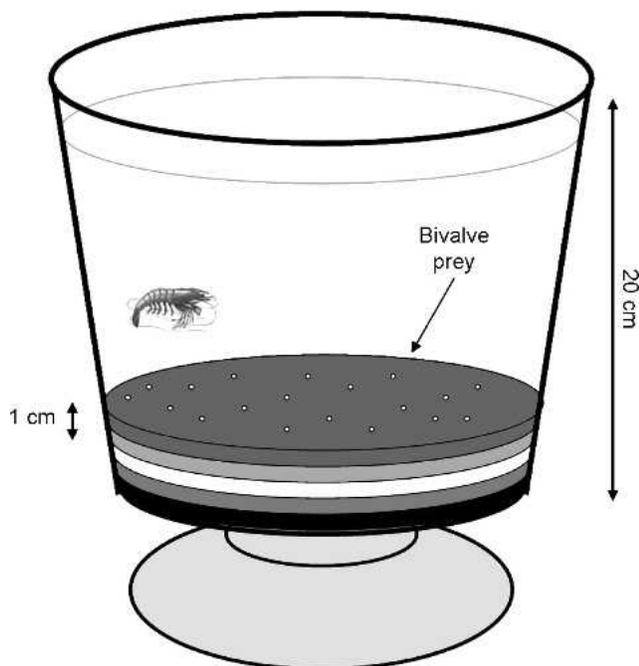


Figure 1. Tank setup for Feeding Depth experiments. Round, clear tanks were filled with 1 cm each of 5 different colored sediments and 12 cm seawater. Approximately 100 *Mercenaria mercenaria* spat were placed between each layer of sediment; *L. setiferus* treatments contained 1 *L. setiferus* tank⁻¹, controls contained no shrimp.

North Inlet estuary has shown average quarterly mesozooplankton densities ranging from $5.1 \times 10^3 \text{ m}^{-2}$ (winter) to $2.6 \times 10^4 \text{ m}^{-3}$ (summer; 1981–2003; Allen et al. 2007).

Laboratory feeding experiments were conducted using juvenile *L. setiferus* collected from the North Inlet estuary and transported in aerated coolers to the University of South Carolina seawater laboratory in Columbia, SC. The shrimp were maintained in aquaria at constant salinity (25 psu) and temperature (20°C) whereas being fed twice daily with pelleted feed. A stock culture of *Artemia salina* was prepared by aerating dry, vacuum-sealed, previously refrigerated cysts in filtered seawater continuously for 4 d inside inverted 2 L bottles to induce hatching. This yielded a stock concentration of approximately 720 individuals per ml ($7.2 \times 10^8 \text{ m}^{-3}$). The stock culture was diluted with filtered seawater to the following concentrations relative to the original stock for use in the experiments: 0.5%, 1.5%, 2.8%, 4.2%, 5.5%, and 7.0%. The initial specific concentration of *Artemia* was determined for each dilution.

Experiments were conducted in November 2002. Prior to each experiment, three *L. setiferus* of similar total length (TL, from tip of rostrum to end of telson; 72–94 mm) were placed into separate holding tanks and acclimated for 2 h. Four round clear plastic tanks (same as for the benthos feeding experiments) were fitted with a “false-bottom” platform constructed of 500 µm plastic mesh elevated 2 cm from the bottom. Tanks were filled with 3 L of filtered seawater and the selected density of *A. salina*. An individual *L. setiferus* was introduced to each of three experimental tanks to prevent intraspecific or crowding effects, and all tanks were placed in the dark (to prevent any response of *A. salina* to differential lighting) for 1 h. Upon completion, the

water and remaining *A. salina* from each tank were poured onto a 62-µm screen, and the retained organisms were diluted up to 100 mL using 90 mL of filtered seawater and 10 mL of 10% buffered formalin.

To quantify the number of *A. salina* consumed, a 1-mL subsample was removed from the homogeneously stirred 100 mL beaker using a Stempel pipet and placed into a gridded Petri dish. Individual nauplii in the 1 mL subsample were counted under a dissecting microscope at $\times 40$ magnification. This counting process was repeated, without replacement, in triplicate for each experimental tank. The resulting mean number of *A. salina* in each dish was multiplied by the dilution volume to determine the mean number of prey in each tank at the end of the experiment. The mean number of *A. salina* remaining in each tank was subtracted from the initial specific concentration of *Artemia* determined for each dilution to give the mean number of prey consumed. The relationship between *L. setiferus* consumption rates and *A. salina* densities was examined using the initial specific concentration of *Artemia* determined for each dilution and similar methods as described for the benthos feeding experiments.

RESULTS

Benthos Feeding Experiments

Consumption rates of *L. setiferus* feeding on *M. mercenaria* increased over the lower range of prey densities, saturating at $\sim 10,000$ bivalves m^{-2} (Fig. 2A). Observations of shrimp foraging as well as microscopic examination of *L. setiferus* gut contents after the experiments confirmed that *M. mercenaria* had been consumed. The variable consumption rates were best described by a sigmoidal, density-dependent regression model ($r^2 = 0.92$, $P < 0.0001$), indicating a type III FR relationship:

$$Y = a/[1 + (X/X_0)^b]$$

where (a) is the hourly maximum consumption rate, (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 (Table 1). 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 where *L. setiferus* consumption is $\frac{1}{2}$ of the maximum (x_{50}) as 5,455 bivalves m^{-2} . The average proportional bivalve mortalities ranged from 0.43–0.97 (43–97%) with reduced mortalities at low and high prey densities and higher mortalities over intermediate prey densities (Fig. 2B). At low prey densities, the pattern of increasing proportional mortalities with increasing densities confirms the observation of a type III FR for *L. setiferus* feeding on *M. mercenaria*.

Feeding Depth Experiments

Using qualitative measurements, all six *L. setiferus* treatments in the daytime feeding experiment exhibited feeding/disturbance depths of < 2 cm, and one of the six displayed a feeding/disturbance depth of < 1 cm. Similarly, in the nighttime feeding experiment, all six *L. setiferus* treatments exhibited feeding/disturbance depths of < 2 cm, with two of the six displaying feeding/disturbance depths of < 1 cm. Shrimp were observed feeding and digging shallow burrow pits within the

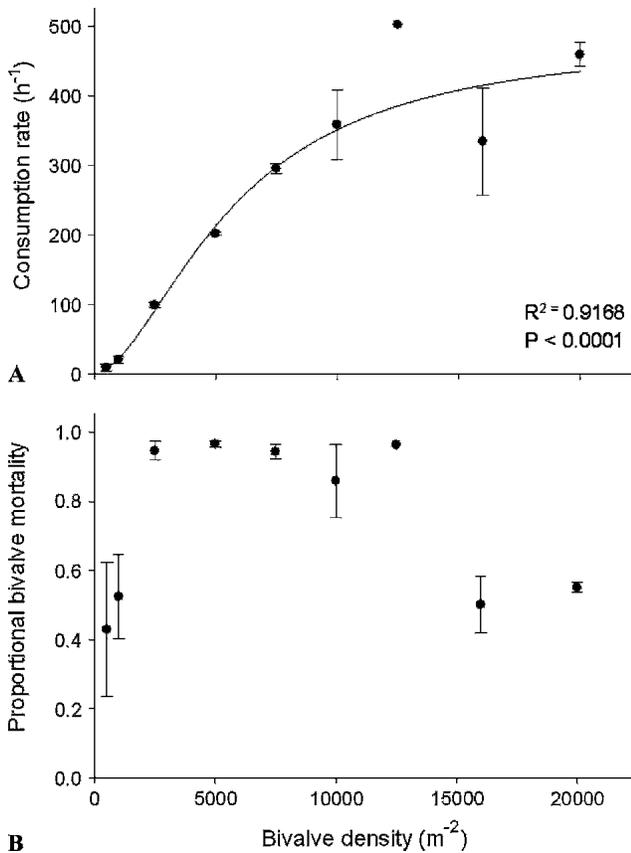


Figure 2. (A) Mean number (\pm SE) and (B) proportion of *M. mercenaria* spat consumed per *L. setiferus* in 1 h in relation to nine nominal bivalve densities (m^{-2}). Line is fit with a sigmoidal, density-dependent regression model (Table 1).

tanks during the daytime and nighttime experiments. No significant disturbance caused by the presence of prey items was shown in the prey only treatments; surface sediment remained at the surface after 12 h and was not contaminated by deeper sediments. Bivalves were observed to burrow down only a few mm; all sediment layers remained intact.

Individual *L. setiferus* were videotaped in dark and light conditions (4 h each) to determine whether they displayed differential behaviors when feeding in the light (benthos feeding experiments) versus the dark (zooplankton feeding experi-

ments). Regardless of light regime, shrimp were observed to display similar behaviors (e.g., swimming, picking, searching, digging, burrowing) for similar proportions of time.

Zooplankton Feeding Experiments

Consumption rates of *L. setiferus* feeding on *A. salina* increased exponentially and did not reach saturation across the full range of prey densities offered (Fig. 3A). Observations of shrimp feeding in the water column as well as microscopic visual examination of *L. setiferus* gut contents after the experiments confirmed that zooplankton had been consumed. The variable consumption rates were best described by a two-parameter exponential growth curve ($r^2 = 0.56$, $P < 0.0001$), indicating the lower portion of a type III FR relationship where consumption rates are accelerating with increases in prey density:

$$Y = y_0 + \log(a) \times a^X$$

where (a) is the intrinsic rate of increase of prey consumption, and (y_0) is the minimum consumption rate (Table 2). The curve fitting procedure estimated the intrinsic rate of increase of prey consumption (a) as 1.12 *A. salina* mL^{-1} consumed per *L. setiferus*, and the minimum consumption rate (y_0) as -1.72 *A. salina* mL^{-1} . The negative value indicates that *L. setiferus* was an ineffective predator at low densities of *A. salina*. The maximum *L. setiferus* consumption rate could not be estimated because of the lack of predator saturation across this range of prey densities. The average proportional zooplankton mortalities ranged from -0.10 – 0.28 (-7% – 28% ; Fig. 3B). The observed pattern of increasing proportional prey mortality with increases in prey density is again indicative of a type III FR relationship.

DISCUSSION

In contrast to the general understanding that white shrimp are primarily epibenthic feeders after the postlarval stage, this study demonstrates that juvenile *L. setiferus* are also able to catch and consume live swimming zooplankton directly from the water column. Average prey mortalities were much lower for *A. salina* than for *M. mercenaria*, suggesting that although *L. setiferus* may be capable of utilizing zooplankton as an alternative food source, they are more effective as benthic predators. The relative inefficiency of *L. setiferus* as water-column feeders may also contribute to the lack of information in the literature describing direct zooplankton predation by juvenile penaeid shrimp. Zooplankton have generally been considered as valuable to *L. setiferus* as a food source only after they have entered the more accessible benthic food web as detritus (Rubright et al. 1981). The direct contribution of zooplankton to the natural *L. setiferus* diet is difficult to quantify because of the relative inefficiency of water-column feeding by *L. setiferus*. Under conditions with low densities of benthic prey such as in temperate estuaries during the summer months, white shrimp may seek alternative zooplankton prey that they would not normally need to consider. Similar conditions may also occur in *L. setiferus* culture ponds, where benthic prey can become depleted and zooplankton may provide a viable source of alternative prey. However, the generally high turbidities of estuarine creeks may limit *L. setiferus* feeding

TABLE 1.

ANOVA results and parameter estimates for sigmoidal, density-dependent regression model of *L. setiferus* consumption rates on various concentrations of bivalves *M. mercenaria*.

Source	DF	SS	MS	F	P
Regression	2	862,782.74	431,391.37	192.81	<0.0001
Residual	35	78,308.41	2,237.38		
Total	37	941,091.16	25,434.90		
Parameter	Coefficient	Std. Error	T		P
a	475.89	90.47	5.26		0.0019
b	-1.99	0.92	-2.16		0.0741
x0	5,455.29	1,580.04	3.45		0.0136

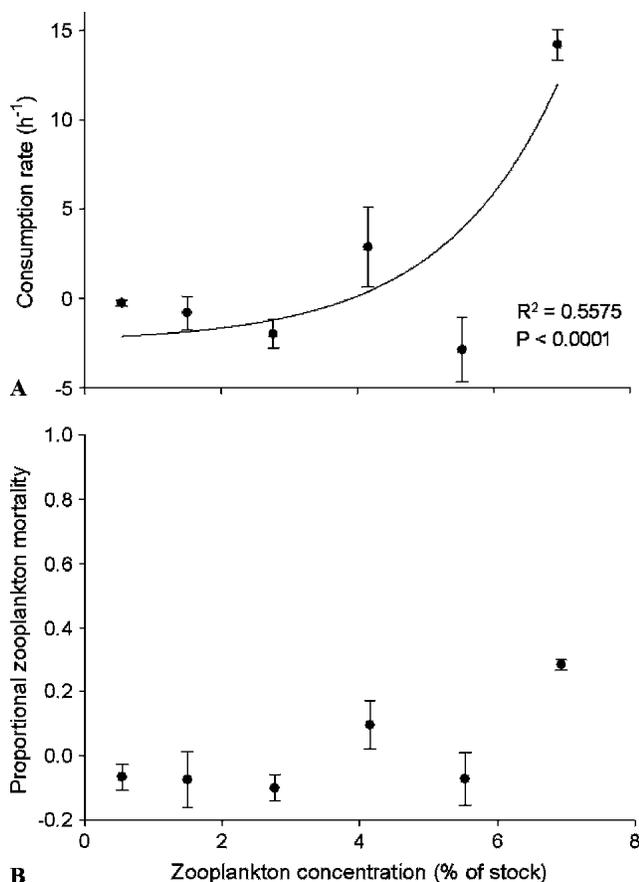


Figure 3. (A) Mean number (\pm SE) and (B) proportion of *A. salina* consumed per *L. setiferus* in 1 h in relation to six zooplankton concentrations (% of stock culture). Line is fit with a 2-parameter exponential growth model (Table 2).

on zooplanktonic prey *in situ*, as may the increased exposure risk to nektonic predators when feeding in the water column.

Quantifying the FR of *L. setiferus* on distinct prey types is an important step in understanding the contribution of multiple prey sources to the *L. setiferus* diet and the role of predation in regulating different prey communities. Juvenile *L. setiferus* consuming young bivalve spat exhibited a type III FR, a result that has been previously shown for other invertebrate predators such as sand shrimp *Crangon septemspinosa* (Wennhage 2002, Taylor & Collie 2003) and blue crab *Callinectes sapidus* (Lipcius

& Hines 1986, Mansour & Lipcius 1991, Eggleston et al. 1992). The type III response has the greatest potential for predator regulation of prey numbers because of the negative feedback of predation on prey density (Valiela 1995). The proportion of *M. mercenaria* consumed by *L. setiferus* increased with density over moderate prey densities (1,000–2,500 m⁻²), and thus *L. setiferus* may have the potential to regulate bivalve populations within this range (Holling 1965, Hassell et al. 1977). In addition, the ability of shrimp to forage within 0–2 cm sediment depth allows them to access the highest densities of *in situ* macrobenthic prey, both bivalve and other taxa (Beseres & Feller 2007a)

Consumption rates increased exponentially for *L. setiferus* feeding on *A. salina*, indicating the lower portion of a type III FR with density-dependent mortality. Despite our direct visual observations of *L. setiferus* ingesting *A. salina* at rates exceeding 2–5 per second, predator satiation was not reached over the range of zooplankton densities offered (exceeding those measured during long-term monitoring of North Inlet, SC). Similar results have been reported for juvenile *Penaeus monodon* feeding on zooplankton (Chen & Chen 1992), and for copepods feeding on particulate matter (Mayzaud & Poulet 1978). Regardless, the relatively low proportional prey mortalities of *A. salina* indicate that *L. setiferus* predation is unlikely to have significant impacts on zooplankton *in situ*. The exponentially increasing portion of the type III FR demonstrated in the zooplankton feeding experiments cannot continue indefinitely; predators eventually reach satiation (regardless of FR type) or become limited by the handling time needed to capture and consume individual prey (Gotelli 2001). Results indicate that the satiation point for *L. setiferus* feeding on zooplankton must occur at higher densities of zooplankton than are regularly encountered by *L. setiferus* in nature.

At low prey densities, proportional prey mortalities decrease with decreasing prey densities for the type III FR, creating a low density refuge for prey and helping to stabilize prey populations (Murdoch & Oaten 1975, Valiela, 1995). In the benthos feeding experiments, the lowest proportional mortalities for *M. mercenaria* occurred at the lowest densities. Long-term monitoring data suggest that a low-density refuge may also exist for the *in situ* macrobenthic community in North Inlet, SC; macrobenthos in subtidal creeks have consistently declined to ~1,000 m⁻² in August and September (Feller et al. 2004). Similar examples of low density refuges have been demonstrated in other marine benthic systems. Infaunal bivalves *Mya arenaria* demonstrate a low density refuge from predation by blue crabs *Callinectes sapidus* in Chesapeake Bay sandy habitats (Lipcius & Hines 1986), as do thin shelled clams *Macoma balthica* in sandy and muddy habitats (Seitz et al. 2001). Polychaete and amphipod communities in commercial *L. setiferus* ponds have been observed to decline from densities of 45,000 m⁻² and 5,000 m⁻² respectively, to stabilize at densities ~10 m⁻² (Hopkins et al. 1995).

Numerous biological mechanisms may be responsible for a low-density refuge, including predator switching to alternative prey, reduced predator reinforcement of successful prey selection, or reduction in foraging activities (Murdoch 1969, Real 1979, Abrams 1982, Lipcius & Hines 1986, Dunbrack & Giguère 1987). Optimal foraging theory further predicts that motile predators in a heterogeneous environment will focus their feeding efforts on the most dense prey patches, moving on

TABLE 2.

ANOVA results and parameter estimates for nonlinear, exponential regression model of *L. setiferus* consumption rates on various concentrations of zooplanktonic *A. salina*.

Source	DF	SS	MS	F	P
Regression	1	1,382.73	1,382.73	65.51	<0.0001
Residual	52	1,097.49	21.11		
Total	53	2,480.22	46.80		
Parameter	Coefficient	Std. Error	T		P
y0	-1.72	0.74	-2.32		0.0241
a	1.12	0.00	489.59		<0.0001

when the net rate of energy intake for that patch is equal to the average for the habitat (Charnov 1976). Because of the abundance of alternative prey available to *L. setiferus* in the field, the variety of prey items reported in *L. setiferus* gut contents (Mayer 1985), and the ability of *L. setiferus* to focus their feeding on high density prey patches (Beseres & Feller 2007b) we suspect that any low-density refuge for bivalves is caused by opportunistic switch-feeding behaviors rather than a result of reduced foraging activities.

The FR of *L. setiferus* consuming nonbivalve macrobenthic species or other species of zooplankton is unknown and likely to vary as a function of prey motility, size, defensive behaviors, spatial distribution, and other morphological or behavioral adaptations (Valiela 1995). The inclusion of multiple prey types may also result in modified predation rates (Miron et al. 2005). The fact that predators such as juvenile *L. setiferus* display variable consumption rates in response to predation on different prey types is a demonstration of their dietary plasticity as omnivores. The relative contribution of zooplankton prey to the *L. setiferus* diet *in situ* remains to be quantified, but this study indicates that *L. setiferus* are much more effective as benthic predators, suggesting a less significant trophic role of zooplankton prey. Nevertheless, the ability of *L. setiferus* to capture and consume prey from the water column indicates that zooplankton may be a viable alternative prey source for

L. setiferus when benthic prey occur in isolated patches (Beseres & Feller 2007b) or are unavailable or inaccessible.

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