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GRASS SHRIMP (*PALAEMONETES* SPP.) PLAY A PIVOTAL TROPHIC ROLE IN ENHANCING *RUPPIA MARITIMA*

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Abstract. Coupled trophic-engineer interactions are potentially important for maintaining habitat function and ecosystem services. As ephemeral submerged aquatic vegetation (SAV), *Ruppia maritima* has a short well-defined growth–senescence cycle and should benefit from any ecological interaction that enhances its physical condition and longevity. Grass shrimp (*Palaemonetes* spp.) are abundant facultative grazers of epiphytic algae and conveyors of nutrients in tidal marsh and SAV habitats. Grass shrimp addition consistently enhanced *Ruppia* biomass and shoot density in a series of three field experiments conducted in Grand Bay National Estuarine Research Reserve, Mississippi, USA. In two experiments, epiphyte grazing by grass shrimp enhanced *Ruppia* by inhibiting die-back during the mid- and latter stages of the *Ruppia* life cycle. Despite a nonsignificant epiphyte grazing effect, grass shrimp also enhanced *Ruppia* during its early growth stage in a third experiment. In that experiment, nutrient addition also significantly increased epiphyte biomass. Grass shrimp may have fostered the early growth of *Ruppia* through direct deposition of feces to the sediment in the third experiment. Grass shrimp play a pivotal trophic role in the maintenance of *Ruppia* through context-dependent interactions involving stage of the SAV life cycle, season, and nutrient limitation.

Key words: epiphytic algae; facultative grazer; grass shrimp; nutrient limitation; *Palaemonetes* spp.; *Ruppia maritima*; trophic engineer; trophic interaction; widgeongrass.

INTRODUCTION

Estuarine submerged aquatic vegetation (SAV) represents a critical habitat that is maintained through a balance between bottom-up and top-down effects. Widespread SAV losses are often attributed to overgrowth by epiphytic algae with subsequent shifts in SAV trophic webs as a result of coastal eutrophication (Duarte 1995). Sufficient epiphyte mesograzers can preclude epiphytic overgrowth; and in turn, SAV provides a structured habitat for associated macrofauna (Bologna and Heck 1999). However, findings are inconsistent regarding the relative importance of nutrient loading vs. epiphyte grazing on SAV condition (Neckles et al. 1993, Coleman and Burkholder 1994, Lin et al. 1996, Worm and Sommer 2000, Hughes et al. 2004). Some studies show that nutrient enrichment does not detrimentally affect SAV when grazing is sufficient to counteract bottom-up effects (Neckles et al. 1993, Williams and Ruckelshaus 1993). A review by Williams and Heck (2001) concluded that epiphytic overgrowth of seagrass is caused less by bottom-up nutrient loading than by the lack of an adequate grazer response. Field

enclosure experiments also demonstrate that high epiphyte biomass and depressed SAV condition correspond with low grazer density (Howard and Short 1986, Fong et al. 2000). But moderate epiphyte biomass resulting from intermediate grazing intensity may benefit SAV growth by mediating competitive interactions among algal groups (Jernakoff et al. 1996) and stimulating epiphyte production (Quiñones-Rivera and Fleeger 2005). Moreover, recent studies have found that the relative importance of top-down and bottom-up factors in controlling macroalgae can vary with stage of the algal life cycle (Worm et al. 2000, Diaz-Pulido and McCook 2003). Existing studies, however, do not consider the effects of facultative grazing on the condition of an ephemeral SAV during different stages of its life cycle.

The common ephemeral euryhaline SAV, *Ruppia maritima*, has distinct stages of growth, reproduction, and senescence (Kantrud 1991). Nutrient uptake by *Ruppia* is dominated by root-to-shoot translocation, often within nutrient limited sediments (Thursby 1984). Moreover, *Ruppia* can be nutrient limited during spring and summer (Johnson et al. 2006). Reproductive shoot emergence at the end of mid-stage growth signals the onset of senescence when aboveground biomass typically dies back within one month (Kantrud 1991). Under eutrophic conditions, the build-up of dense epiphytic algae suppresses photosynthetic efficiency and may lead to early senescence of *Ruppia* (Kantrud 1991).

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Mesograzers may help maintain *Ruppia* by promoting growth or inhibiting the die-back of epiphyte laden shoots (Kantrud 1991). Obligate epiphyte herbivores, such as amphipods, isopods, and gastropods, may lack sufficient trophic plasticity to withstand fluctuations in food supply associated with an ephemeral SAV. Thus, ephemeral SAV, like *Ruppia*, may depend on facultative grazers to maintain its condition. Although many studies focus on the role of obligate grazers in estuarine and marine SAV ecosystems (Jernakoff et al. 1996, Jernakoff and Nielsen 1998, Duffy et al. 2001), few studies consider the importance of facultative grazers like grass shrimp.

Grass shrimp (*Palaemonetes* spp.) play an important trophic role in tidal marsh and SAV habitats (Morgan 1980, Morgan and Kitting 1984, Gregg and Fleeger 1998, Quiñones-Rivera and Fleeger 2005). As omnivores, the grass shrimp diet varies with life stage and ecological setting (Welsh 1975). Grass shrimp are known facultative grazers (Kneib 1985) that consume substantial epiphytic material (Fleeger et al. 1999) and may promote SAV through the ample production of fecal pellets (Johannes and Satomi 1966). Thus, grass shrimp may play a pivotal trophic role in enhancing SAV habitat as either top-down or bottom-up agents within estuarine SAV habitats.

We examined the effects of grass-shrimp and nutrient addition on the condition (biomass and shoot density) of *Ruppia maritima* and epiphyte biomass. Our study is distinctive in that in situ field experiments were used to examine epiphyte grazing and nutrient effects on an ephemeral SAV species across a range of grazing intensity and SAV life cycle stages.

METHODS

Field experiments

Three field experiments were conducted in Middle Bay, in the Grand Bay National Estuarine Research Reserve (GB NERR; Mississippi, USA) (see Appendix A for additional site characteristics). Three *Ruppia maritima* sites along a 1-m nearshore depth contour were chosen for each field experiment (NERR map in Appendix B). Experiment 1 (E1; 30°21'12.2" N; 88°23'37.1" W) was begun on 6 June 2001, experiment 2 (E2; 30°21'36.2" N; 88°23'52.4" W) on 8 August 2001, 0.5 km north of E1, and experiment 3 (E3; 30°21'39.8" N; 88°23'52.7" W) on 9 May 2002, 1.0 km northeast of E2. Experiments were conducted during three different life-cycle stages of *Ruppia* as denoted by season and the occurrence of reproductive shoots. Absence of reproductive shoots indicated early-stage (E3), initial appearance of reproductive shoots indicated mid-stage (E1), and dense coverage of reproductive shoots indicated late-stage (E2; Kantrud 1991).

Experiment assembly and disassembly required two days (protocols found in Appendix C). Acrylic cylinders (14.6 cm inside diameter, 0.91 m high, 0.0152 m³ volume) enclosed *Ruppia* in situ in a split-plot configuration across the three sites (blocks; experiment

diagram given in Appendix D). Sites were located between 50 and 100 m from shore, depending upon the location of the 1 m depth contour. Cylinders enclosed 0.0167 m² of habitat, and ambient water flowed through eight opposing openings (7.62 cm diameter) covered with 1.8-mm Nitex mesh. Each cylinder randomly received one of the three grass shrimp treatments (no, 0 shrimp; medium, 3 shrimp; or high, 10 shrimp), and each enclosed 10 shoots of *Ruppia* (Appendix C). Plots (three cylinders and one control; 2-m² area) at two opposing corners of each site received nutrient addition (Appendix D). Experiments concluded after 28 d and each potentially yielded a total of 60 samples (i.e., 12 time-zero samples and 48 experimental samples, including 12 control samples and 36 cylinder samples comprising 3 sites × 4 plots × 3 grass shrimp treatments). Laboratory processing of grass shrimp, time-zero (pretreatment ambient), control (posttreatment ambient), and cylinder samples followed protocols detailed in Appendices E and F. For each sample, shoots were counted, surface areas for up to 10 shoots of *Ruppia* were measured, and dry and ash-free dry mass determined. Epiphyte chl *a* was quantified with high performance liquid chromatography (HPLC) and normalized to *Ruppia* surface area.

Data analysis and interpretation

A split-plot ANOVA model (Mead et al. 2003) examined responses in total *Ruppia* biomass (g), shoot density (no./m²), and epiphytic algae chl *a* (ng/cm²) (general linear model [GLM] procedure in SPSS 11.0; SPSS 2001). Variance was partitioned into main plot and split plot portions: the main plot portion comprised the random site (three levels) factor and the fixed nutrient (two levels) factor. The site × nutrient interaction term served as the main-plot error. The split-plot portion comprised the fixed shrimp factor (four levels) as well as the shrimp × nutrient interaction term. The split-plot error term took up the remaining degrees of freedom. Missing replicates were accommodated through appropriate weighting of the mean square terms within the SPSS GLM procedure.

Biomass and shoot density were analyzed either in their raw or Box-Cox transformed forms (Krebs 1989), depending upon tests of normality (one-sample Kolmogorov-Smirnov tests) and homogeneity of error variance (Levene's tests). Use of transformed data depended on whether Levene's *F* values were markedly improved by the transformation. Because they were both normal and homogeneous, log₁₀ epiphyte chl *a* values were used in the ANOVA. For cylinders lacking *Ruppia*, biomass and shoot density values were regarded as zeros, whereas epiphyte values were considered missing due to the lack of any remaining *Ruppia* surface area.

In the event of a significant shrimp effect, user-specified a priori contrasts discerned why the overall effect occurred without increasing the risk of a Type I error (Sokal and Rohlf 1981). Three orthogonal contrasts

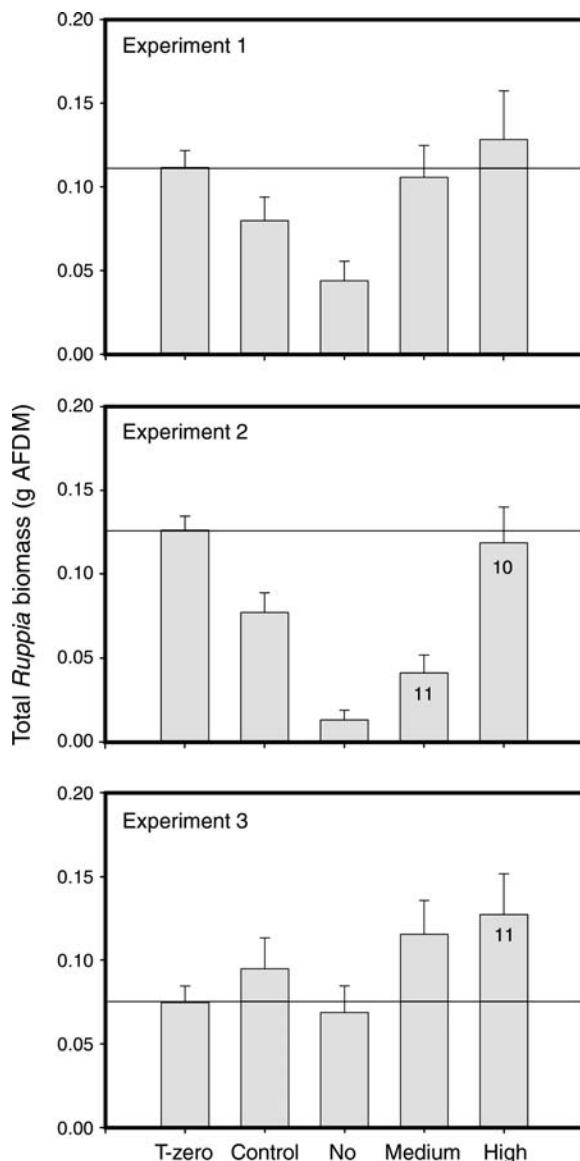


FIG. 1. Total *Ruppia* biomass (g ash-free dry mass [AFDM]; mean \pm SE) for time-zero (pretreatment) and control (ambient) conditions, and after exposure to three grass shrimp treatments for three 28-d field experiments. Pre-experimental mean biomass corresponding to time-zero values is represented as a line across treatments. $N = 12$ replicates except where indicated.

specified an enclosure effect (3, -1, -1, -1); a shrimp addition effect (0, 2, -1, -1); and a shrimp density effect (0, 0, 1, -1). The order of the contrast coefficients in parentheses parallel the treatment levels: control (ambient), no (0 shrimp), medium (3 shrimp), high (10 shrimp). Contrast t tests were conducted in SPSS 11.0 (SPSS 2001).

RESULTS

Ruppia biomass

Grass shrimp addition enhanced total *Ruppia maritima* biomass in all three experiments (E1, $P = 0.034$;

E2, $P < 0.001$; E3, $P = 0.057$; Fig. 1; Appendix G). Moreover, a priori orthogonal contrasts supported the shrimp addition effect in all of the experiments (Appendix H). The shrimp density effect was also supported for total *Ruppia* biomass in experiment 2. However, nutrient addition did not affect *Ruppia* biomass in any of the experiments (Appendices G and I).

A trend of increased *Ruppia* biomass across the three shrimp treatments occurred in all three experiments (Fig. 1). Biomass was greater from high shrimp treatments than from control samples in all three experiments. Biomass was also greater from medium shrimp treatments than from control samples in experiments 1 and 3. In contrast, *Ruppia* biomass from no shrimp treatments was consistently lower than biomass from control, medium, and high treatments in all experiments. Differences between time-zero (pretreatment) and control (posttreatment) samples illustrate that ambient *Ruppia* biomass decreased during experiments 1 and 2, when *Ruppia* was in its mid-late stages (Fig. 1). However, biomass increased during experiment 3, while in the early growth stage. The lowest biomass, relative to time-zero, was found in experiment 2, implying senescence. Moreover, experiment 2 was the only experiment where *Ruppia* biomass from the high shrimp treatment was less than biomass from time-zero samples.

Shoot density

Grass shrimp appeared to enhance *Ruppia* shoot density in all three experiments (Fig. 2). The overall Shrimp effect was significant for shoot density in the first two experiments (E1, $P = 0.032$; E2, $P < 0.001$; Appendix G). A priori orthogonal contrasts supported the shrimp addition effect in experiments 1 and 2 (Appendix H), and the shrimp density effect in experiment 2. Again, nutrient addition did not affect shoot density in any experiment.

In contrast to *Ruppia* biomass, ambient shoot densities declined between time-zero and control samples in all three experiments (Fig. 2). Shoot densities from control, medium, and high shrimp treatments were higher than densities from the no shrimp treatment in all experiments. Shoot densities from medium and high shrimp treatments were generally comparable with those from control samples. The lowest shoot densities occurred in no and medium shrimp treatments in experiment 2; and highest shoot densities occurred in the high shrimp treatment in experiments 1 and 2.

Epiphyte chl *a*

A nutrient addition effect on epiphyte chl *a* was only significant for experiment 3 ($P = 0.034$; Appendices G and I). Overall shrimp effects on epiphyte chl *a* were significant for experiment 1 ($P = 0.001$; Appendix G). Moreover, a priori orthogonal contrasts supported both shrimp addition ($P = 0.001$) and the shrimp density ($P = 0.037$) effects on epiphyte chl *a* in experiment 1 (Appendix H). Power was inherently low for tests of

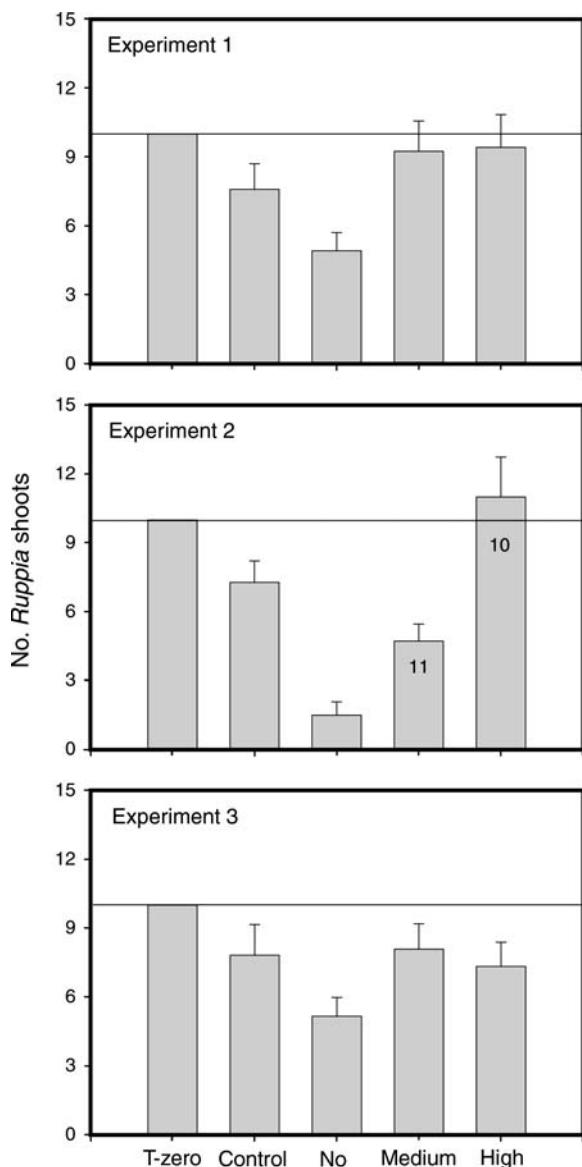


FIG. 2. Number of *Ruppia* shoots (mean ± SE) for time-zero (pretreatment) and control (ambient) conditions, and after exposure to three grass shrimp treatments for three 28-d field experiments. Pre-experimental mean number of shoots corresponding to time-zero values is represented as a line across treatments. *N* = 12 replicates except where indicated.

shrimp effects in experiment 2 owing to the complete lack of *Ruppia* from six of 12 replicates of the no shrimp treatment. The frequent lack of *Ruppia* was likely influenced by elevated senescence associated with the no shrimp treatment.

Epiphyte chl *a* increased by almost an order of magnitude with nutrient addition in experiment 3, from 2.05 ± 0.70 to $19.41 \pm 7.37 \times 10^{-4}$ ng/cm². A trend of decreased epiphyte chl *a* across shrimp treatments was apparent for both experiments 1 and 2 (Fig. 3). Also, epiphyte chl *a* from control samples was comparable to

amounts from medium shrimp treatments in all three experiments. Epiphyte chl *a* decreased almost 20-fold across shrimp treatments in experiment 1, from 44.80 ± 18.67 to $2.33 \pm 3.13 \times 10^{-4}$ ng/cm² (mean ± SE). Also the control (i.e., ambient) chl *a* value of $16.80 \pm 6.07 \times 10^{-4}$ ng/cm² was similar to the medium shrimp value of $18.20 \pm 13.07 \times 10^{-4}$ ng/cm². In experiment 2, epiphyte chl *a* decreased 7.5-fold across shrimp treatments, from 18.67 ± 12.88 to $2.33 \pm 1.17 \times 10^{-4}$ ng/cm². Again, the control chl *a* value of $12.13 \pm 5.13 \times 10^{-4}$ ng/cm² was comparable to the medium shrimp value of $14.47 \pm 5.60 \times 10^{-4}$ ng/cm² in experiment 2. In experiment 3, the control epiphyte chl *a* value of $5.60 \pm 20.07 \times 10^{-4}$ ng/cm² was again comparable to the medium shrimp value of $6.53 \pm 44.80 \times 10^{-4}$ ng/cm².

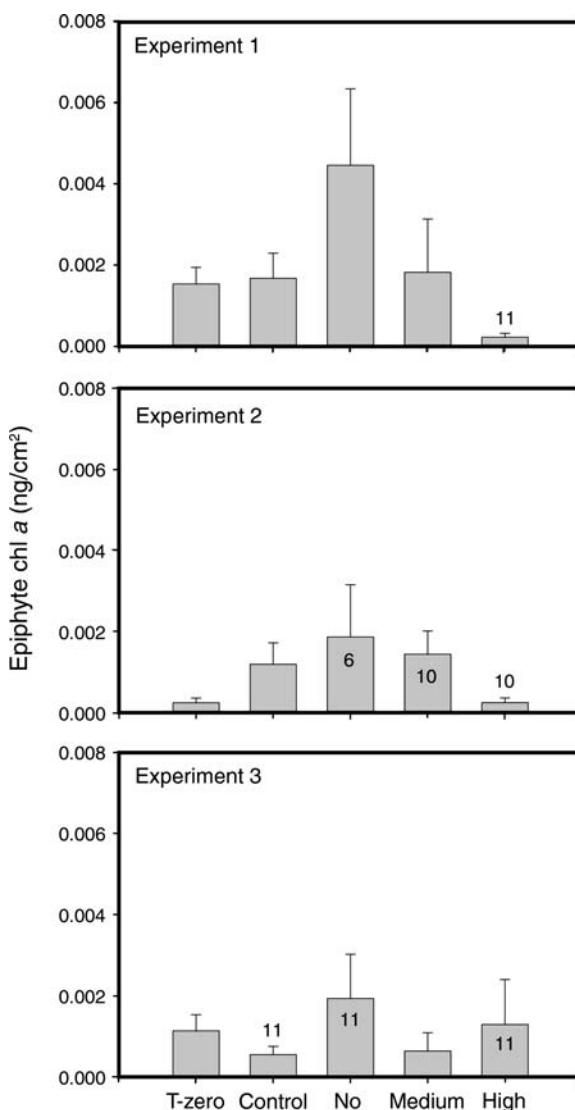


FIG. 3. Epiphyte chl *a* (ng/cm²; mean ± SE) for time-zero (pretreatment) and control (ambient) conditions, and after exposure to three grass shrimp treatments for three 28-d field experiments. *N* = 12 replicates except where indicated.

DISCUSSION

The main objective of this study was to determine whether grass shrimp enhance *Ruppia maritima* while in different stages of its life cycle. Although inherent biases associated with field experimentation were possible during the study (Appendices J and K), grass shrimp did enhance *Ruppia* in three separate experiments. There are several possible ways by which grass shrimp may positively influence *Ruppia* condition. Grass shrimp could facilitate light and HCO_3^- accessibility to *Ruppia* by reducing epiphytes, either through direct disturbance or grazing. Although the reduction of epiphytes through direct disturbance is possible, previous studies have established that grass shrimp graze epiphytic algae (Morgan 1980, Fleeger et al. 1999, Quiñones-Rivera and Fleeger 2005). Grazing was also supported in our experiments by the fact that shrimp effects on chl *a* were stronger than those on total epibiota mass (Drury 2004). Alternatively, grass shrimp might foster SAV growth by releasing and redirecting nutrients (Welsh 1975).

Our results implied that grass shrimp may play a pivotal trophic role in *Ruppia* habitat by mediating shifts in the relative importance of top-down and/or bottom-up effects. The relative importance of either effect is dependent upon the stage of the *Ruppia* life cycle, season, or whether nutrients are limiting. This conclusion is consistent with differences in the outcomes of the three experiments. In experiment 1, lower epiphyte chl *a* and increased *Ruppia* biomass and shoot density in response to shrimp density inferred that epiphyte grazing enhanced *Ruppia* condition by inhibiting dieback of mid-stage *Ruppia*. Enhancement of *Ruppia* likely continued in experiment 2 because epiphyte chl *a* decreased progressively across shrimp treatments in conjunction with significant positive effects on late-stage *Ruppia*. Power was inherently low for tests of shrimp effects on chl *a* in experiment 2 due to missing observations for the no shrimp treatment. Perhaps reflecting increased senescence, *Ruppia* biomass was especially low, and shrimp effects on *Ruppia* were particularly strong in experiment 2.

Bottom-up effects of grass shrimp conceivably enhanced *Ruppia* condition during its early growth stage in experiment 3 (see Appendix L for a discussion on possible alternative interpretations). Despite the lack of an inferred epiphyte grazing effect in experiment 3, *Ruppia* was still enhanced by grass shrimp, as indicated by the significant shrimp addition effect. Moreover, the significant nutrient addition effect on epiphyte biomass implied nutrient limitation during experiment 3. Nutrient limitation is characteristic of *Ruppia* growth (Thursby 1984) and limitation patterns vary both temporally and geographically (Johnson et al. 2006). In a meta-analysis of top-down vs. bottom-up effects in SAV systems, Hughes et al. (2004) found that seagrass is often limited by sediment nutrients rather than by light. Besides releasing nutrients through excretion (Welsh 1975) and bioturbation (Haertel-Borer et al. 2004), grass

shrimp translocate nutrients to sediments through the copious production of fecal pellets (Welsh 1975, Quiñones-Rivera and Fleeger 2005). Because *Ruppia* primarily acquires nutrients via the roots (Thursby and Harlin 1984), the proximity of fecal pellets to *Ruppia* roots may have had a more direct effect on *Ruppia* than other nutrient sources. A similar effect was observed by Taylor and Rees (1998) where nitrogen excreted by epifauna directly on host seaweeds sustains growth of the seaweeds. We estimate the sediment translocation potential of grass shrimp to be roughly $0.6 \text{ mmol N}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at the density represented by the medium shrimp treatment (Johannes and Satomi 1966; Morgan 1980). Thus, direct deposition of feces to the sediment by grass shrimp is a feasible bottom-up mechanism that may foster the early growth of *Ruppia*.

Complex top-down and bottom-up effects were also possible in our experiments. Epiphyte response across shrimp treatment levels in experiment 3 might reflect concurrent effects of both grazing and excretion (Welsh 1975). Epiphyte growth is stimulated by water column nutrients (Hughes et al. 2004), and grass shrimp excrete substantial amounts of dissolved inorganic nutrients (Haertel-Borer et al. 2004). A similar complex trophic role for grass shrimp involving opposing effects of grazing and nutrient release on epiphyte biomass was recently proposed by Quiñones-Rivera and Fleeger (2005). Moreover, epiphyte grazing and ammonia excretion by mobile epifauna sustains the growth of the seaweed *Carpophyllum plumosum* in New Zealand (Taylor and Rees 1998).

Coupled trophic-engineer interactions are potentially important for maintaining habitat function (Jones et al. 1997). Grass shrimp are coupled to *Ruppia* as facultative grazers on epiphytic algae and as potential conveyors of nutrients, but this association is not obligatory. Consequently the likelihood of the interaction is increased by the ecological plasticity of grass shrimp, a species that can utilize various food sources and vegetated aquatic habitats. Grass shrimp play a key role in the maintenance of *Ruppia* through a pivotal trophic relationship that is fostered by inherent ecological plasticity. As an engineering species (Jones et al. 1994), *Ruppia* modifies the physical environment, provides living space, concentrates resources, and fosters biological production. But *Ruppia* is also ephemeral, possessing a short well-defined growth-senescence cycle. Thus, the adjacent estuarine ecosystem should benefit from any ecological interaction that enhances the physical status and longevity of *Ruppia*.

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APPENDIX A

Description of the Grand Bay NERR study area (*Ecological Archives* E088-041-A1).

APPENDIX B

Map of the Grand Bay NERR study area (*Ecological Archives* E088-041-A2).

APPENDIX C

The protocol for assembly and disassembly of field experiments (*Ecological Archives* E088-041-A3).

APPENDIX D

Diagram of experiment layout (*Ecological Archives* E088-041-A4).

APPENDIX E

Grass shrimp collection, recovery, and processing (*Ecological Archives* E088-041-A5).

APPENDIX F

Laboratory protocol for processing samples (*Ecological Archives* E088-041-A6).

APPENDIX G

Results of split-plot ANOVA for experiments 1–3 (*Ecological Archives* E088-041-A7).

APPENDIX H

Orthogonal contrasts for response variables showing significant overall grass-shrimp effects within the split-plot ANOVA (*Ecological Archives* E088-041-A8).

APPENDIX I

Nutrient loading values for the three field experiments (*Ecological Archives* E088-041-A9).

APPENDIX J

Possible artifacts, biases, and scaling issues associated with the field experiments (*Ecological Archives* E088-041-A10).

APPENDIX K

Possible biases involving faunal interactions (*Ecological Archives* E088-041-A11).

APPENDIX L

Alternative interpretations of experiment 3 (*Ecological Archives* E088-041-A12).