PARASITES ENHANCE ECOSYSTEM FUNCTIONS AND RESISTANCE TO DROUGHT IN A COASTAL ECOSYSTEM

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ABSTRACT

Joseph Philip Morton: Parasites Enhance Multiple Ecosystem Functions and Resistance to Drought Stress in a Coastal Ecosystem (Under the direction of Charles H. Peterson).

Parasites are more diverse and numerous than the organisms they feed upon, yet we know little about how parasites affect natural ecosystems. In salt marsh ecosystems of the southeastern U.S., increasing drought stress interacts synergistically with keystone grazing by marsh periwinkles to generate marsh die-offs. Field manipulation of digenean trematode parasite prevalence within the marsh food web under both drought and non-drought conditions revealed that parasites, by suppressing keystone grazing, can sustain multiple ecosystem functions and help prevent climate-induced die-off of foundational plants. A survey along 1000km of coastline showed that trematodes parasitism is common in marsh periwinkles and that increasing infection prevalence along marsh die-off borders is correlated with decreased per capita grazing and slower rates of *Spartina* marsh ecosystem decline. Combined, these results demonstrate that parasites can simultaneously regulate both the functioning of an ecosystem and its ability to resist die-off in the face of drought.

To my grandfather, Donald C. Rudisill, who taught
me to take note of the small things.

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INTRODUCTION

A primary goal of ecology is to determine what factors influence the stability of ecosystems. The stability of ecological communities in response to disturbances is largely a function of their ability to absorb stress and remain "essentially unchanged" in terms of their taxonomic composition, process rates, trophic structure, and functions (i.e. resistance) (Grimm and Wissel, 1997). Understanding the processes that underlie ecosystem resistance is essential for more robust predictions of how communities will respond to environmental change and for development of effective conservation measures.

A sizable body of research has focused on the role of top predators in organizing communities and increasing ecosystem resistance through trophic control of prey population densities. Evidence from both terrestrial and aquatic systems suggests that ecosystems in which top predators have been retained or restored show an increased capacity to buffer against environmental stresses, including those associated with climate change (Mittelbach et al., 1995; Wilmers et al., 2006a, b; Wallach et al., 2010). Additionally, in many systems, the loss of top predators can trigger cascading effects that ultimately result in a loss of ecosystem structure and function (Estes and Palmisano, 1974; Carpenter et al., 1985; Silliman and Bertness, 2002; Myers et al., 2007; Estes et al., 2011; Rosenblatt et al., 2013; Bertness, 2014).

While predators are well-known to contribute to aspects of ecosystem stability through trophic control of their herbivorous or mesopredatory prey, parasites are also known to exert powerful controls on consumer populations (Dobson and Crawley, 1994; Kohler and Wiley, 1997; Omacini et al., 2001; Finkes et al., 2006; Wood et al., 2007). Parasites can control

herbivores directly by reducing densities or reproductive capacity or indirectly through modification of host phenotype. If a host is abundant or otherwise ecologically influential, parasites may modulate resource availability to other organisms or initiate state changes in biotic or abiotic community components (Jones et al., 1994, 1997). Because phenotypic alterations of host species may ultimately modify the habitat of all community members, parasites, like predators, may be able to affect ecosystem stability. While parasites are ubiquitous community components and parasitism represents the most common organismal feeding strategy on the planet (Dobson et al., 2008; Kuris et al., 2008), there is still very little known about how parasites modify the behavior of keystone hosts and how such modifications affect important ecosystem properties such as functional stability of ecosystem structure and function, including resistance to disturbance (but see Combes, 1996; Wood et al., 2007, and Sato et al., 2012).

In salt marsh ecosystems of the Southeastern United States, episodic, sub-lethal edaphic stress associated with drought interacts synergistically with grazing by the keystone gastropod, *Littoraria irrorata*, to produce small- to large-scale localized die-off events (Silliman et al., 2005; Angelini and Silliman, 2012). While precipitation in the Southeastern United States is predicted to increase under climate change scenarios, evaporation is expected to outpace precipitation over the next century, potentially exacerbating drought in the region (Seager et al., 2009). Die-off, triggered by regular episodic drought events, has the potential to induce major shifts in ecosystem structure, function, and services, elevating the importance of understanding marsh processes that contribute to ecosystem stability.

While the role played by predators in mitigating snail grazing through reducing their densities is well-documented (Silliman and Bertness, 2002; Silliman et al., 2004), no attention has yet been given to the role of parasites in modulating grazer interactions. *L. irrorata* serves as

the first intermediate host to three species of digenean trematodes, with the great majority of infections by the cosmopolitan species *Parorchis acanthus* (R. Heard, pers. comm.). Infection with *P. acanthus* yields marked changes to snail behavior, dramatically reducing both snail radulation of live *Spartina* tissue and circatidal climbing up *Spartina* stems (Morton, unpublished data). Moreover, infection incidence can be high enough in some marsh areas (>25%), that trematode infections could have a positive localized effect on salt marsh community structure and function.

Based on my observations in both lab and field, I hypothesized that (1) increasing infection prevalence would result in cascading ecosystem effects, decreasing the impacts of snail grazing on salt marsh plant structure and function, (2) influencing ecosystem structure and function and (3) increasing resistance to drought driven die off . To test these hypotheses, I employed a fully-factorial field experiment in which I modified soil salinity and parasite infection prevalence in a North Carolina salt marsh. Additionally, I surveyed ten east coast saltmarshes spanning a wide spatial scale to determine the generality of our findings.

METHODS

Study System

I conducted my experiment in the intermediate *Spartina alterniflora* zone of a marsh within the Hoop Pole Creek Clean Water Reserve in Atlantic Beach, North Carolina, USA (34°42'25.12" N, 76°45'1.14" W). The study site was characterized by an absence of snails, an initial subsurface soil salinity of ~35 ppt, and a relatively uniform elevation (determined by use of a laser level). The experiment was conducted over the course of the *Spartina* growing season (May- August) of 2014.

Experiment

To test the hypothesis that widespread trematode infection can diminish the capacity of snails to overgraze marsh under sub-lethal salt stress conditions, we established 0.5-m^{22} caged plots in areas of ungrazed intermediate-form *Spartina* marsh, in which we experimentally elevated marsh soil salinity by adding ocean salt and manipulated the prevalence of trematode infections in cage-enclosed snails. Plots were assigned to one of the following treatments (n=8 replicates per treatment: (i) salt addition and 30% infected; (ii) salt addition and 10% infected; (iii) salt addition and 0% infected; (iv) no salt and 30% infected; (v) no salt and 10% infected; (vi) no salt and 0% infected; (vii) caged with no snails; (viii) caged with salt added and no snails; and (ix) un-caged with ambient snail densities and infection prevalence. Treatments without snails tested for the effect of salt on marsh structure and function alone and uncaged plots acted as cage controls. The 10% infection prevalence treatment represented the average summertime infection prevalence found within the intermediate *Spartina* zone of the Hoop Pole Creek study

area, whereas the 30% treatment represented a naturally occurring high prevalence from the same site (Joseph P. Morton, unpublished data). We added 100 adult snails with shell length (mean ± SE) 18.71 ± 0.45 mm and wet weight of 1.62 ± 0.11 g per individuals to each grazer addition plot. The grazer density used was representative of naturally occurring densities along marsh die-off areas of Hoop Pole Creek determined in early summer (May 10th) by haphazardly tossing a 0.5-m^{-2} quadrat a total of 20 times along die-off borders and enumerating the snails therein.

Salt was delivered monthly to sediments in appropriate treatments for the duration of the experiment (3 months) by inserting 16 plastic centrifuge tubes (50-ml) with 16 holes (hole diameter 0.16-cm) drilled in the sides into the sediments within each plot. Each tube contained 150 g of salt. Pore water salinity was monitored and salt added monthly (May- July) to sediments within appropriate treatment plots. At total of 900-g of salt was added to each plot during the course of the experiment.

To ensure that infection prevalence assigned to each plot persisted over the course of the experiment, we marked each caged snail with a distinguishing colored dot (white for healthy, red for infected) using a water-resistant paint pen, whose mark has been demonstrated to persist for long periods on the shells of aquatic gastropods without any discernable effect on behavior or longevity (Henry & Jarne, 2007). Infected and uninfected snails within each plot were enumerated twice weekly and replaced when necessary to maintain constant snail density and assigned infection prevalence. During weekly monitoring, any predatory mud crabs found within plots were removed and their burrows plugged with marsh sediment to discourage successful re-occupation.

Changes to Salt Marsh Structure

I took measurements of several marsh characteristics in all plots initially and in each month following installation for the duration of the experiment. Because the total length of snail radulations per stem is directly proportional to the magnitude of the negative effects of snail grazing on *Spartina* production (Silliman et al., 2004), we enumerated the total length of radulations on the topmost unfurled leaf of 5 randomly selected stems within each plot. Additionally, we determined live and dead stem densities and measured the heights of ten randomly selected stems in each plot (measured to the highest extent of live, green tissue). In both instances, stems were randomly selected by tossing small plastic dowel into the plot and then taking measurements stems touching the dowel. If the number of stems in contact with the dowel was insufficient, measurements were taken from stems closest to the dowel.

At the end of the experimental period, all aboveground biomass was harvested and dried at 60°C for two weeks. Change in biomass over the growing season was calculated from height measurements using regression of stem height vs. stem biomass. Aboveground growth of *S. alterniflora* for each treatment is reported as net production (g dry mass $\cdot$ m^{-2} $\cdot$ mo^{-1}) and as live standing biomass at the end of the experiment. Belowground biomass was sampled using two 0.5-cm diameter, 30-cm deep cores taken from the center of each plot at the end of the experimental period. Because *Spartina* roots and rhizomes are typically concentrated in the top 25 cm of sediment (Howes et al. 1981), samples were representative of the total belowground biomass. Cores were sieved (2-mm mesh), sorted into live cordgrass roots and rhizomes vs. dead plant debris, and dried following the same procedure used for aboveground biomass.

Snail Climbing

Snails actively avoid predators by climbing *Spartina* stems with the incoming tide. Once they have ascended, snails produce longitudinal scars with their radula, making a suitable substrate for fungal growth. Because trematode infection affects snail locomotion and because such changes could affect grazing intensity, we assessed differences in snail movement and position relative to the substrate at both low and high tide. Within a month of the experiment's installation, we enumerated the number of infected and uninfected snails in each plot above the water line at high tide. At low tide, five infected and five uninfected snails that were closest to the center salt-addition well were selected and their height above the dry marsh substrate was measured. Snail position (on stems, on the marsh substrate, or at the base of stems) was also recorded for each individual.

Primary Production

To determine the effect of parasite infection prevalence on net primary productivity (NPP), net *Spartina* production over the duration of the experiment was estimated by measuring the difference in live aboveground plant biomass from the beginning to the end to the experiment. In May, when experimental plots were established, we measured stem height and density in all plots and converted these measurements to an initial standing biomass by using regressions based on destructive sampling of *Spartina* stems taken from just outside the plots. Initial standing biomass did not differ significantly across plots (mean estimated *Spartina* biomass: $39.8\ g \cdot 0.7^{-2}$). At the conclusion of the experiment, NPP was estimated by calculating the change in live standing biomass from the beginning to the end of the experiment.

Infiltration rate

We quantified the effect of parasite infection prevalence on marsh sediment infiltration rate (i.e. the rate at which surface water moves into and through the sediment) at the conclusion of the experiment through the use of a double-ring infiltrometer (Johnson A.I., 1963). Two hours after high tide, we placed a 2.0-L ring firmly in the center of each plot and filled it with 1.0-L of water drawn from the tidal channel adjacent to the study area. Infiltration rate was measured as the amount of time required for the water to completely drain out of the ring and into the soil ($L \cdot hr^{-1}$). This measurement was repeated in five plots for each treatment.

Nursery habitat

We quantified the effect of parasite infection prevalence on marsh nursery habitat use by juvenile snails, grass shrimp (*Palaemonetes spp.*), juvenile fiddler crabs (*Uca* spp.), and juvenile killifish (*Fundulus* and *Cyprinodon spp.)* at the end of the experimental period. At low tide, juvenile snails were enumerated by visual inspection of *Spartina* stems, and by running a thumbnail along each furled *Spartina* leaf margin. To determine the abundance of grass shrimp and juvenile killifish, we employed a dip net (net diameter = 20 cm) which was passed in an "S" shaped pattern five times through each plot at absolute high tide. Killifish and grass shrimp were considered juveniles if their length fell between 25-38 mm (Hildebrand and Schroder, 1928) and 9-15 mm (Knieb, 1987), respectively. We repeated this process each day for 3 days for a total of 15 net-passes per plot. The numbers of grass shrimp and fish caught in each plot over the 3-day period were pooled for analysis. Juvenile fiddler crabs densities were estimated by counting their burrows. Adult fiddler crab burrows can be distinguished from those made by juveniles in that they are 5–10 wider and deeper (Angelini et al 2015). Both were counted separately, but only juvenile burrows were used as a proxy for fiddler crab nursery habitat function.

Decomposition rate

One month before the end of the experiment, we quantified the effect of parasite-mediated behavioral changes on marsh decomposition rate by deploying a bundle of dead *Spartina* stems zip tied to a plastic marker flag. Standing dead *Spartina* stems were collected from an area adjacent to the experimental cages, rinsed clean, and dried to a constant weight (2 weeks at 60°C). Dried stems were cut into 10 cm pieces, which were then grouped into bunches of three and weighed to the nearest 0.001 g. Weighed bundles were then affixed to a plastic marker flag, which was placed at the center of each plot with the lower margin of each bundle positioned at 3 cm above the sediment surface. After 30 days, remaining plant matter was retrieved, carefully washed, and dried to constant weight as before. The dry remnants were weighed and mass lost was calculated for each plug. Decomposition rate was measured as the difference between initial and final stem bunch biomass per month.

Survey of die-off areas

Infection prevalence in snails on die-off borders and within healthy adjacent marsh habitat was determined from ten Mid- and South Atlantic marshes to assess the geographic generality of the results from my study in Hoop Pole Creek, NC. Marshes were surveyed in October of 2014 at Hoop Pole Creek, NC (34.705798 N, -76.750054 W), Masonboro Island, NC (34.175916 N, -77.833403 W), Ocean Isle, NC (33.897363 N, -78.439737 W), Folly Beach, SC (32.658725 N, -79.943584 W), Charleston, SC (32.779616 N, -79.965606 W), Port Royal, SC (32.394122 N, -80.770866 W), Sapelo Island, GA (31.414507 N, -81.294719 W), Jekyll Island, GA (31.059418 N, -81.453098 W), Amelia Island, FL (30.628621 N -81.478687 W), and Guana River, FL (30.011868 N, -81.342875 W). At each site, eight 0.5-m^2 quadrats were haphazardly thrown both along the die-off border and in adjacent healthy intermediate *Spartina* 5-m from the die-off

border. Within each quadrat, all visible snails were collected, transported back to the lab, measured, and dissected to determine infection status. Additionally, radulations and stem height data were collected in each quadrat as for the cages in the previous experiment.

Statistical analysis

Treatment differences in response variables measured at the end of the field experiment were assessed using two-way ANOVA followed by Tukey's honestly significant difference (HSD) test for post hoc analysis. Data analyzed using two-way ANOVA both exhibited homogeneity of variance (confirmed through Levene's test) and were normally distributed (confirmed through Shapiro-Wilk test) or were transformed using log transformations for analysis to conform to test assumptions. For data that did not meet normality assumptions (counts of *Fundulus* and *Cyprinodon* spp.), a generalized linear model (GLM) was employed for analysis. Differences in heights climbed by infected and uninfected snails within plots at low tide and differences in the proportion of infected and uninfected snails above the mean high water line at high tide were evaluated with a one-way ANOVA.

For the regional survey data, differences in parasite prevalence in die-off boarder and healthy marsh areas were determined with a nested one-way ANOVA. A general linear model was used to determine the relationship between mean radulation scar length, snail density, and parasite prevalence in die-off border survey plots.

RESULTS

Initial plot conditions, infection prevalence, and snail densities

Initial plot vegetation conditions (mean height, density of live and dead stems, and stem biomass) were not significantly different among treatments and the interaction of treatments ($P>0.35$ at least, two-way ANOVA, for each response variable). There were no significant differences in *Spartina,* NPP, stem density, or stem height means between caged controls and uncaged plots. Additionally, there were no significant differences in means of potentially confounding factors (i.e., fiddler crab abundance, elevation, porewater salinity) among treatments ($P>0.6$, two-way ANOVA, for all response variables). The final mean infection prevalence for each treatment did not differ significantly from initial conditions ($P>0.94$, two-way ANOVA, all cases) indicating that the infection rate at the study site was consistently very low. On average, less than one snail per week was removed from caged snail exclusion controls. The mean weekly deviation in snail density in snail addition treatments never exceeded 10%.

Radulations

Salt acted synergistically with grazers, significantly increasing the magnitude of top-down grazing effects (radulation scar length) in plots where it was added (Fig. 1.1). Mean radulation length decreased significantly with increasing parasite prevalence ($P<0.001$, two-way ANOVA). In salt-addition plots, parasites reduced the average length of grazing scars by 38% at a 10% infection prevalence and 69% at a 30% infection prevalence compared to plots with only uninfected snails. A similar trend was seen in un-salted plots where the average length of grazing scars decreased by 33% at a 10% infection prevalence and 75% at a 30% infection

prevalence. There was a significant interaction between salt addition and parasite prevalence (P= 0.037, two-way ANOVA).

Aboveground biomass, live stem density, and stem height

Salt addition significantly decreased mean aboveground biomass (Fig. 1.2, $P < 0.0001$, two-way ANOVA), live stem density (Fig. 1.3, $P < 0.03$, two-way ANOVA), and the change in average stem height (Fig. 1.4, $P<0.0001$, two-way ANOVA) in plots where it was added. There was no significant interaction effect of salt addition and parasite prevalence for any of these factors ($P>0.42$, at least, two-way ANOVA). Parasite-driven differences in the magnitude of grazer-induced wounds on live *Spartina* translated into marked changes in these metrics of marsh structure, quantified at the end of the experiment. Plots with healthy snails (no parasite infection) lost the greatest average amount of biomass compared to snail-free controls (69% in unsalted plots, 93% in salted plots). Mean aboveground biomass increased significantly with increased parasite prevalence (Fig. 1B, $P<0.0001$, two-way ANOVA). Increases in biomass were roughly proportional to the level of infection prevalence. A 10% increase in infection prevalence decreased the amount of biomass lost by 13% in salted plots and 11% in unsalted plots (Tukey HSD, $P<0.0001$, both cases). Likewise, a 30% increase in infection prevalence decreased the amount of biomass lost by 34% in salted plots and 23% in unsalted plots (Tukey HSD, $P<0.0001$, both cases).

Parasite prevalence and salt affected not only the amount of available marsh structure but also structural qualities. Salt addition significantly decreased the difference in mean stem height over the course of the experiment, while increased parasite prevalence was significantly associated with a net increase in mean stem height (Fig. 1.4, $P < 0.0001$, both cases, two-way

ANOVA). Likewise, live stem density decreased significantly with both the addition of salt and increasing parasite prevalence (Fig. 1.3, $P<0.0001$, both cases, two-way ANOVA).

Snail climbing behavior

Trematode infection significantly decreased average height climbed above the marsh substrate at low tide by more than 66% ($P<0.0001$, one-way ANOVA). Infected snails were 6 times more likely to be found on the marsh substrate at the base of stems than uninfected conspecifics at low tide. At high tide, a significantly smaller mean proportion of infected snails remained above the mean high water line (MHWL) (12.8%) compared to uninfected conspecifics (80.7%) (Fig. 4, $P<0.0001$, one-way ANOVA).

Primary production

Net Primary Production (NPP), calculated at the end of the experimental period, increased significantly with the increased infection treatment level and decreased significantly with the addition of salt (Fig. 3.1, $P<0.0001$, both cases, two-way ANOVA). There was no significant interaction between salt and parasite prevalence on NPP ($P>0.5$, two-way ANOVA). NPP values for salt addition plots with 0% and 10% infection prevalence treatments were negative, indicative of the net loss of biomass within those plots.

Infiltration Rate

Infiltration rate was positively correlated with the number of fiddler crab burrows enumerated in each plot ($P<0.0001$, general linear model). Salt addition induced significant decreases in mean infiltration rate across parasite treatments (Fig. 3.2, $P<0.003$, both cases, two-way ANOVA). Additionally, infiltration rate increased significantly with the level of parasite prevalence (Fig. 3.2, $P<0.0001$, two-way ANOVA). The interaction effect between salt addition and parasite prevalence was non-significant ($P>0.75$, two-way ANOVA).

Decomposition rate

Salt had no significant effect on decomposition rate in snail-free controls. In plots with snails, decomposition rate decreased significantly with increasing level of infection prevalence and significantly decreased with the addition of salt (Fig. 3.3, $P<0.0001$, both cases, two-way ANOVA). The interaction effect between salt addition and parasite prevalence was non-significant ($P>0.63$, two-way ANOVA). At both levels of salt stress, there was no significant difference in decomposition rate between the 0% and 10% infection prevalence treatments (Tukey HSD, $P>0.09$, both cases), although decomposition did decrease in the latter.

Nursery Habitat

By reducing the quality and quantity of salt marsh structure, snail grazing affected nursery habitat utilization for all mobile species quantified. The abundances of juvenile snails and grass shrimp declined significantly with the addition of salt (Fig. 4.1 and 4.2, $P<0.0001$, both cases, two-way ANOVA), while the abundances of juvenile crab burrows and juvenile killifish were not significantly affected by salt addition (Fig 4.3 and 4.4, $P>0.81$ and GLM, $P>0.40$, respectively, two-way ANOVA). The abundance of all species increased significantly with increasing levels of parasitism (Fig. 4.1 – 4.4, $P<0.024$, two-way ANOVA, for juvenile snails, grass shrimp, and juvenile fiddler crabs; $P<0.002$, GLM, for juvenile killifish)

There was no significant difference in the mean number of juvenile snails between 10% and 0% infection prevalence treatments in salt addition plots, reflective of the high level of grazer-induced damage to juvenile snail refugia in these plots (see Fig. 1.1- 1.3, Tukey HSD, $P<0.98$). A significant interaction between salt addition and parasite prevalence was found for grass shrimp abundance, such that, grass shrimp were far more abundant in plots where salt was not added. (Fig 4.2, $P<0.035$, two-way ANOVA).

Survey of marsh die-off Areas

Three of the ten sites surveyed across scales of southeastern states revealed no trematode infections. Snails at these three sites had the lowest mean shell lengths (Fig. 5). This is consistent with past observations that only adult snails (> 16mm shell length) are found to harbor trematode infections. Radulation and parasite prevalence data from the seven sites where infected snails were found were pooled and used in analysis. Parasite prevalence at each of the seven sites did not exceed 10%, likely due to the survey being conducted near the end of the growing season when infection prevalence begins to decline. Average parasite prevalence was significantly higher along die-off borders (2.5%) compared to healthy marsh areas (0.4%) ($P<0.0001$, one-way ANOVA). Lengths of radulations scars on stems sampled along die-off boarders increased significantly with snail density and decreased with increased incidence of infection (Fig. 6, $P<0.001$, general linear model, both cases).

DISCUSSION

Previous surveys have suggested that Mid-Atlantic Coast populations of *L. irrorata* do not harbor trematode parasites (Rossiter, 2013) and that infection prevalence rarely exceeds 1% in Southern Atlantic and Gulf Coast salt marshes (Holliman, 1961; Hamilton, 1978; Richard Heard, pers. comm.). The findings of my surveys (current study and unpublished data) demonstrate that summertime infection prevalence can exceed 10% in some marshes and can be as high as 30%. My experimental treatments encompassed this range in infection prevalence and, therefore, tested the maximum potential of *P. acanthus* to indirectly affect salt marsh structure and function that we could expect to observe under current natural conditions.

My investigation is one of very few studies to manipulate parasite prevalence in the field and quantify the indirect community-level consequences of parasite-induced behavioral modifications of their host species (Wood et al 2007). Additionally, my study represents the first experimental demonstration of the ability of parasites to confer ecosystem resistance to disturbance through behavioral modification of an influential host species. Because I did not account for the effects of predators, which consume infected snails at higher rates than healthy conspecifics, my study likely underestimates the effects of trematode infection in mediating snail grazing impacts.

My results suggest that sub-lethal drought stress conditions interact with grazing snails to produce die-off conditions, consistent with the findings of previous research (Silliman et al., 2005). Additionally, I provide evidence of a trait-mediated trophic cascade in which intermediate and high prevalence levels of trematode infection reduce grazing pressure, facilitate

Spartina aboveground growth, and prevented wholesale die-off of these foundational plants. The ameliorating effects of parasites on salt marsh structure increased with the incidence of infection, although not always proportionately. In both salted and unsalted treatments, a mere 10% increase in the prevalence of infection yielded an almost 30% increase in the total length of leaf scars associated with snail grazing. This is likely the result of slightly biased sampling, which did not account for trematode-induced changes to snail locomotion. Infected snails did not climb as high as uninfected conspecifics and their grazing activities were confined mainly to plant bases, dead stems, or the marsh substrate (Fig. 4). At least some of the differences observed in the intensity of snail grazing likely reflect our method of measuring radulations on the topmost unfurled leaves of individual plants where infected snails were less likely to be found feeding. These disparities were not as apparent with regard to plot aboveground biomass, where increases in plant biomass scaled roughly in proportion to parasite prevalence.

Plots with uninfected snails were characterized by a nearly complete loss of marsh structure and a loss or diminishment of multiple functions. Primary production, infiltration, decomposition, and nursery habitat functions were all enhanced by parasite facilitation of salt marsh structure, in some instances maintaining functionality near levels observed in ungrazed control plots (Figures 3.1 – 3.4). Increasing infection prevalence consistently yielded increases in the performance level of each function measured, whereas salt addition indirectly decreased the level of all measured ecosystem functions by stimulating grazers and stunting the growth of foundational plants. Because this is only the second documentation of parasites indirectly modifying ecosystem functions (see Sato et al., 2012) our results suggest some new systems in which parasites may be functionally influential. Parasites appear to indirectly stimulate infiltration, a fundamentally important component of marsh hydrology, by facilitating burrowing

juvenile fiddler crabs. This represents the first evidence of parasites indirectly modifying hydrology and prompts new questions about the roles played by parasites in important geophysical processes.

Increased infection prevalence along die-off boarders in surveyed marshes was significantly related to a decrease in the average length of radulations, consistent with the results of our field experiment. Our survey suggests that die-off borders may be infection hotspots, where increased prevalence reduces the magnitude of local *Littoraria* grazing effects and preserves marsh integrity. This pattern is likely driven by the increased usage of these areas by foraging marsh birds. Bird droppings, which potentially harbor trematode eggs, were frequently noted inside sample plots along die-off boarders in all surveyed marshes, while droppings were rarely found within healthy marsh plots. Moreover, direct observations in the field indicated that birds, including known final hosts of *P.* acanthus, such as rails and wading birds, were found in greater abundance around die-off borders than in healthy marsh areas. This is consistent with previous observations where trematode infections were much more abundant in close proximity to clapper rail nests and roosting areas (Heard, 1970; Morton, unpublished data). The existence of high infection rates at die-off borders would represent a negative potential feedback that could suppress the expansion of such borders, even in the absence of predators. It has yet to be experimentally determined, however, whether high incidence of infection along die-off borders is the result of elevated infection rates due to an abundance of bird final hosts or a diminished abundance of predators that consume infected snails at much higher rates.

My results add to a growing body of evidence that demonstrates the importance of parasites in modifying ecosystem properties. Many parasites have powerful effects on host behavior and can profoundly alter or initiate trophic cascades (Lafferty and Morris, 1996; Moore,

2002; Wood et al. 2007; Hernandes and Sukhdeo, 2008a; Libersat et al. 2009; Sato et al., 2012). While the ubiquity of parasites in natural systems is well-documented, the effects of many parasites on the behavior of their hosts, and how such changes to host phenotype affect ecosystem properties, are poorly understood. Parasites may influence aspects of resilience in many ecosystems by modifying the behavior of influential hosts, dampening consumer effects, or facilitating processes that contribute to diversity (such as predation). In order to better understand how natural systems will respond to global scale disturbances, it is important that the roles played by parasites in aspects of ecosystem resilience are better elucidated. Additionally, the potential for parasites to have positive effects on ecosystem stability, as illustrated by the current study, may provide greater impetus to conserve certain parasitic fauna and the hosts which they depend on.

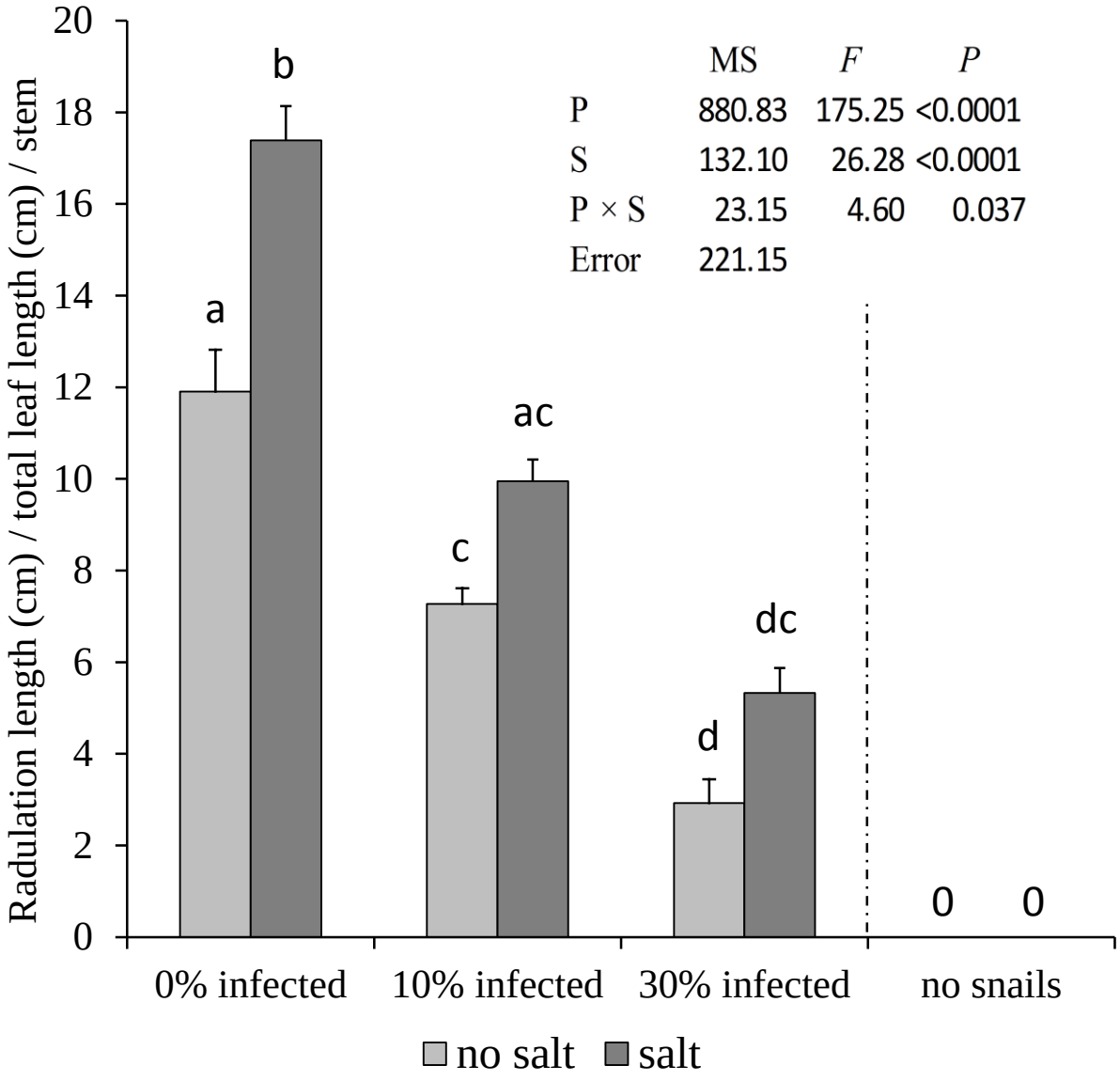

FIGURE 1.1 - The effect of parasite prevalence on *L. irrorata* radulations on *S. alterniflora*. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

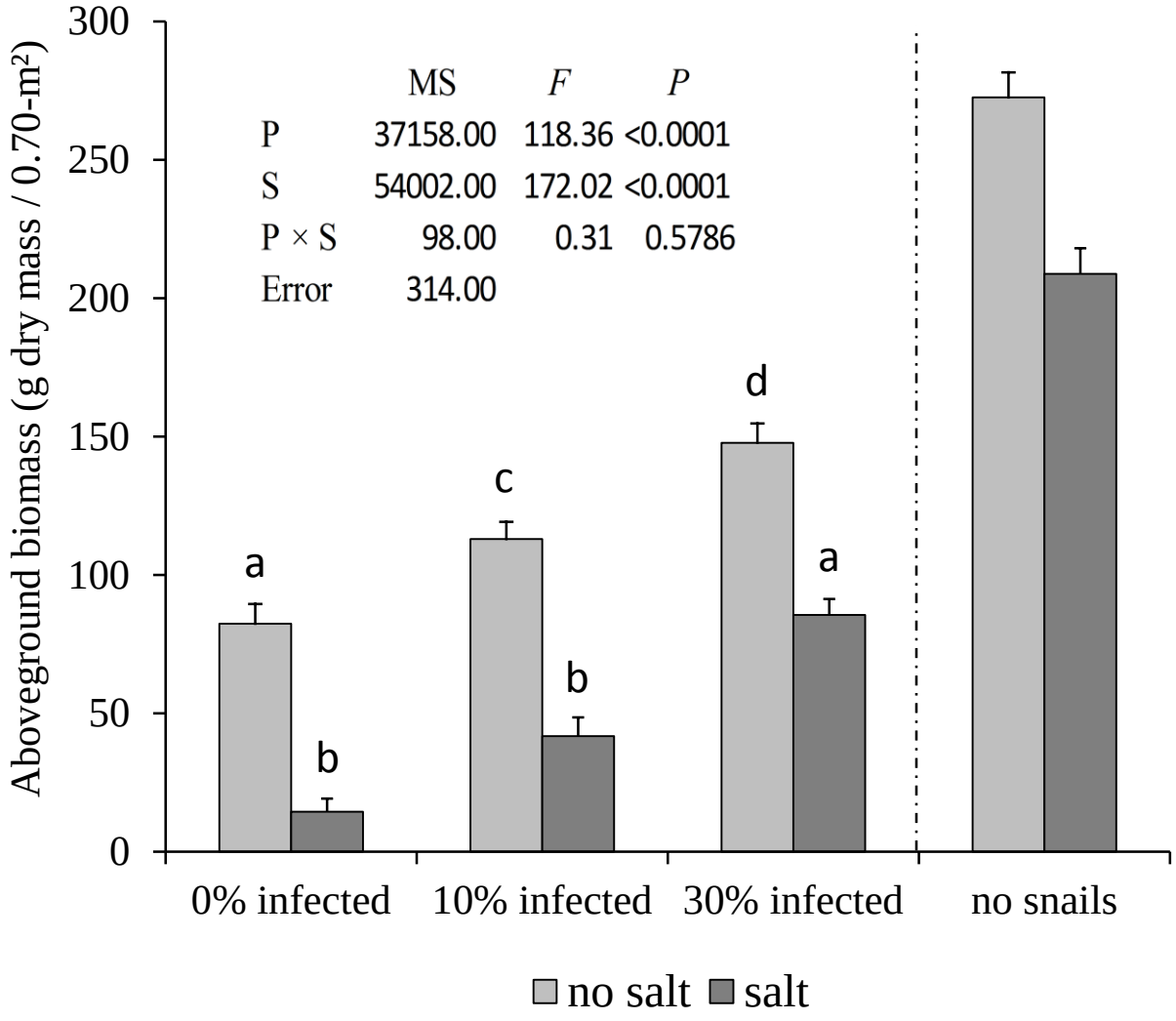

FIGURE 1.2 - The effect of parasite prevalence on *S. alterniflora* aboveground biomass. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

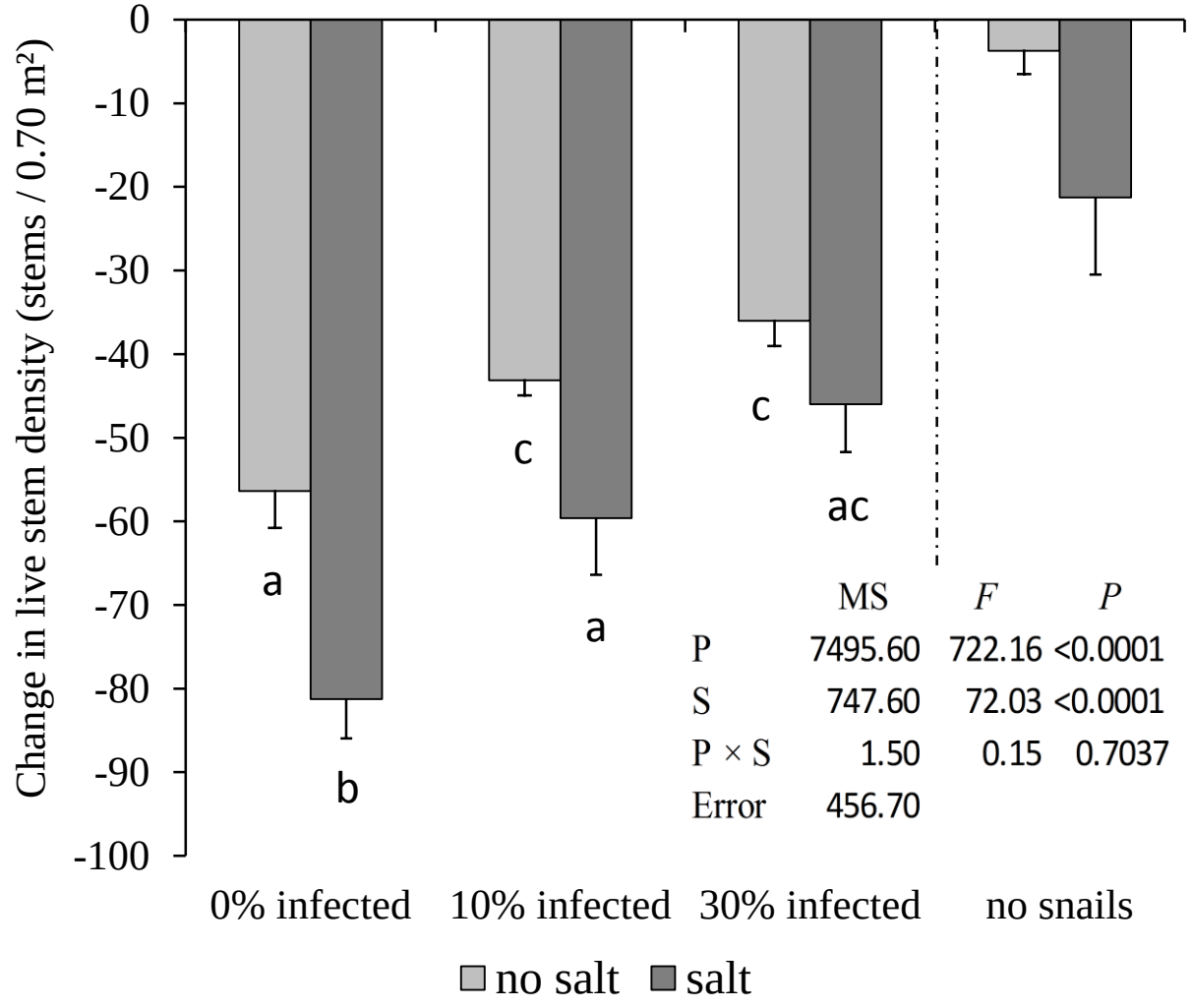

FIGURE 1.3 - The effect of parasite prevalence on *S. alterniflora* live stem density. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

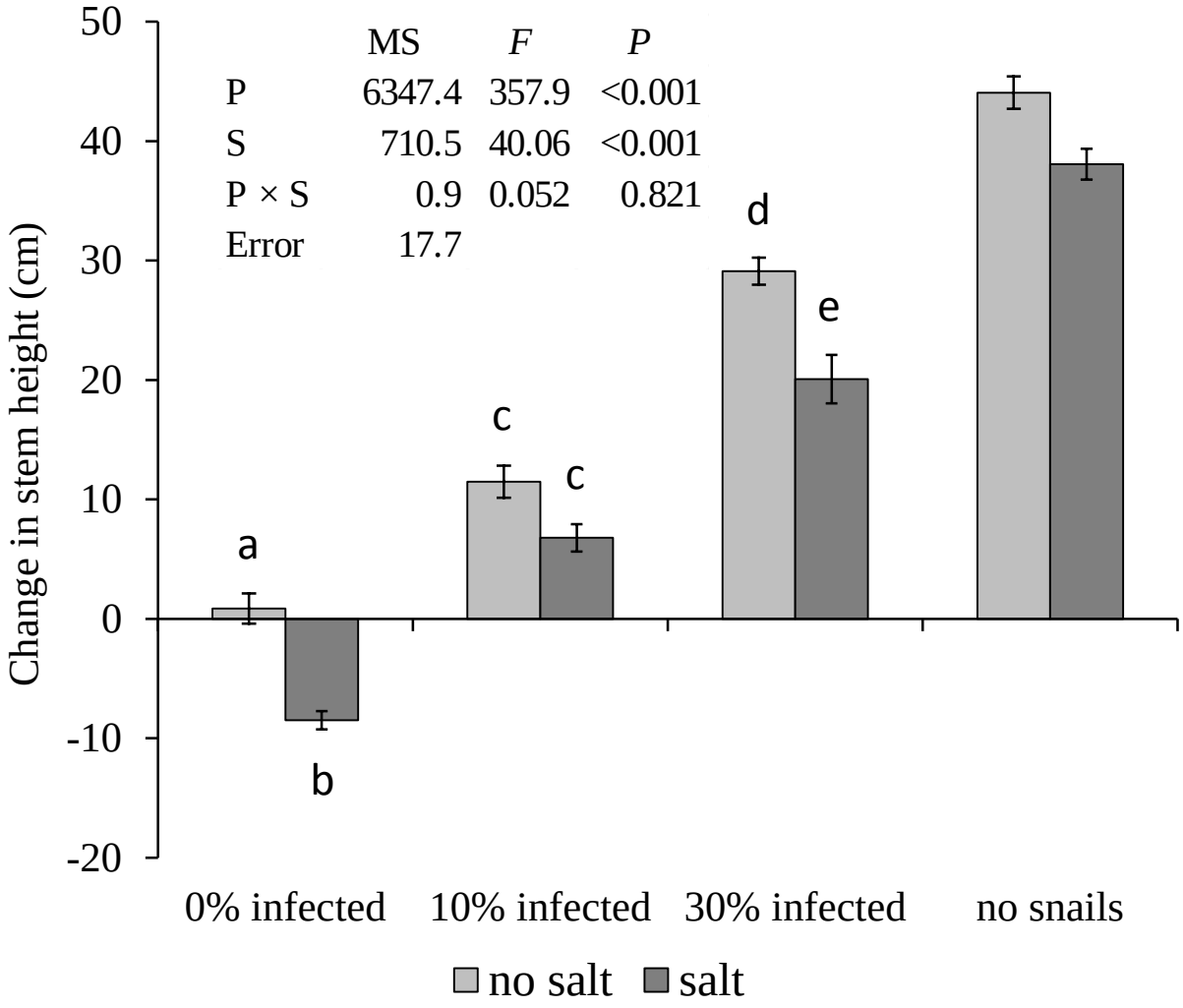

FIGURE 1.4 - The effect of parasite prevalence on *S. alterniflora* live stem height. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

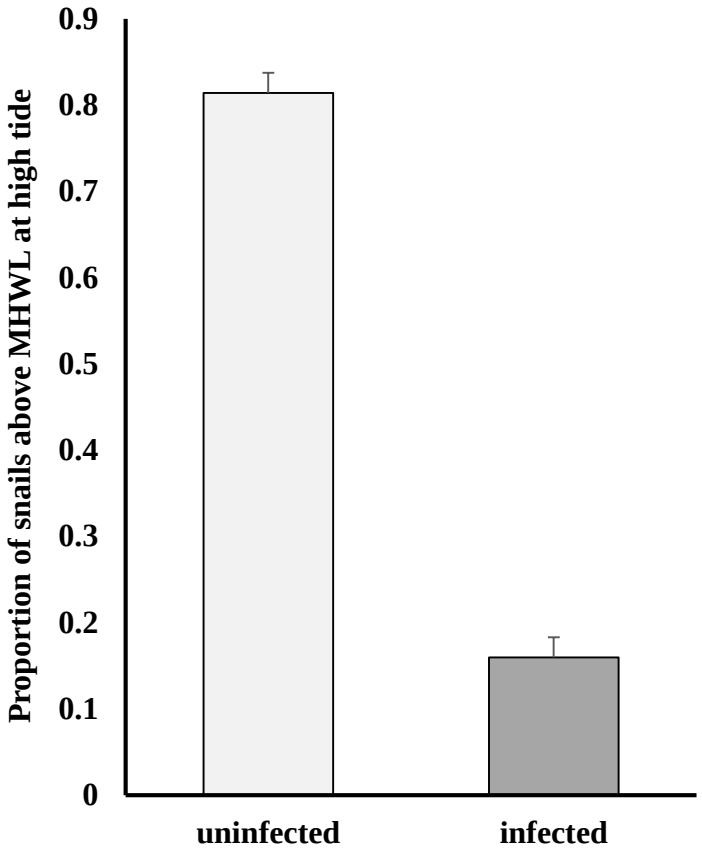

FIGURE 2 - The average proportion of infected and uninfected snails above the mean high water line (MHWL) in each plot.

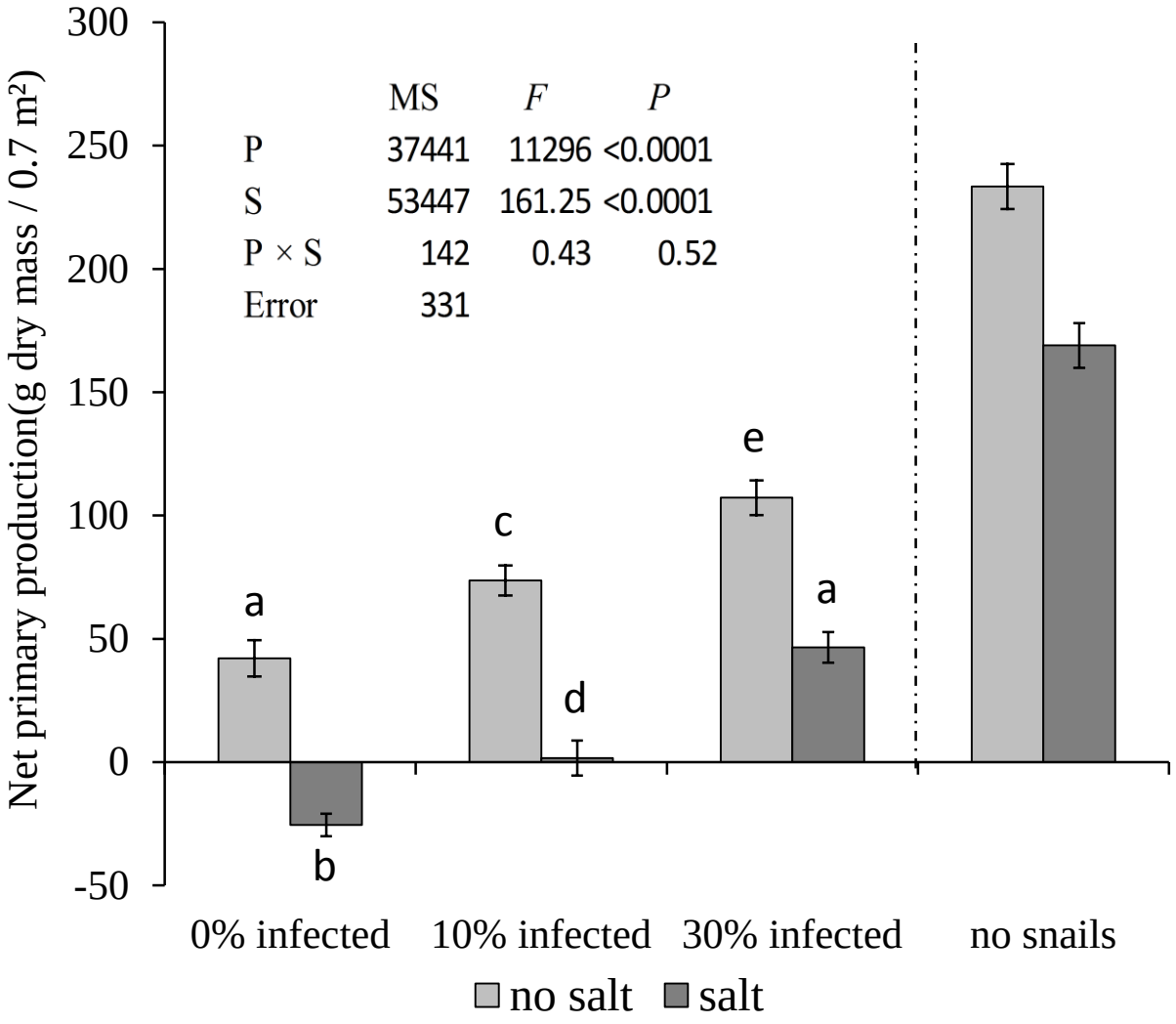

FIGURE 3.1 - The effect of parasite prevalence on *S. alterniflora* net primary production. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

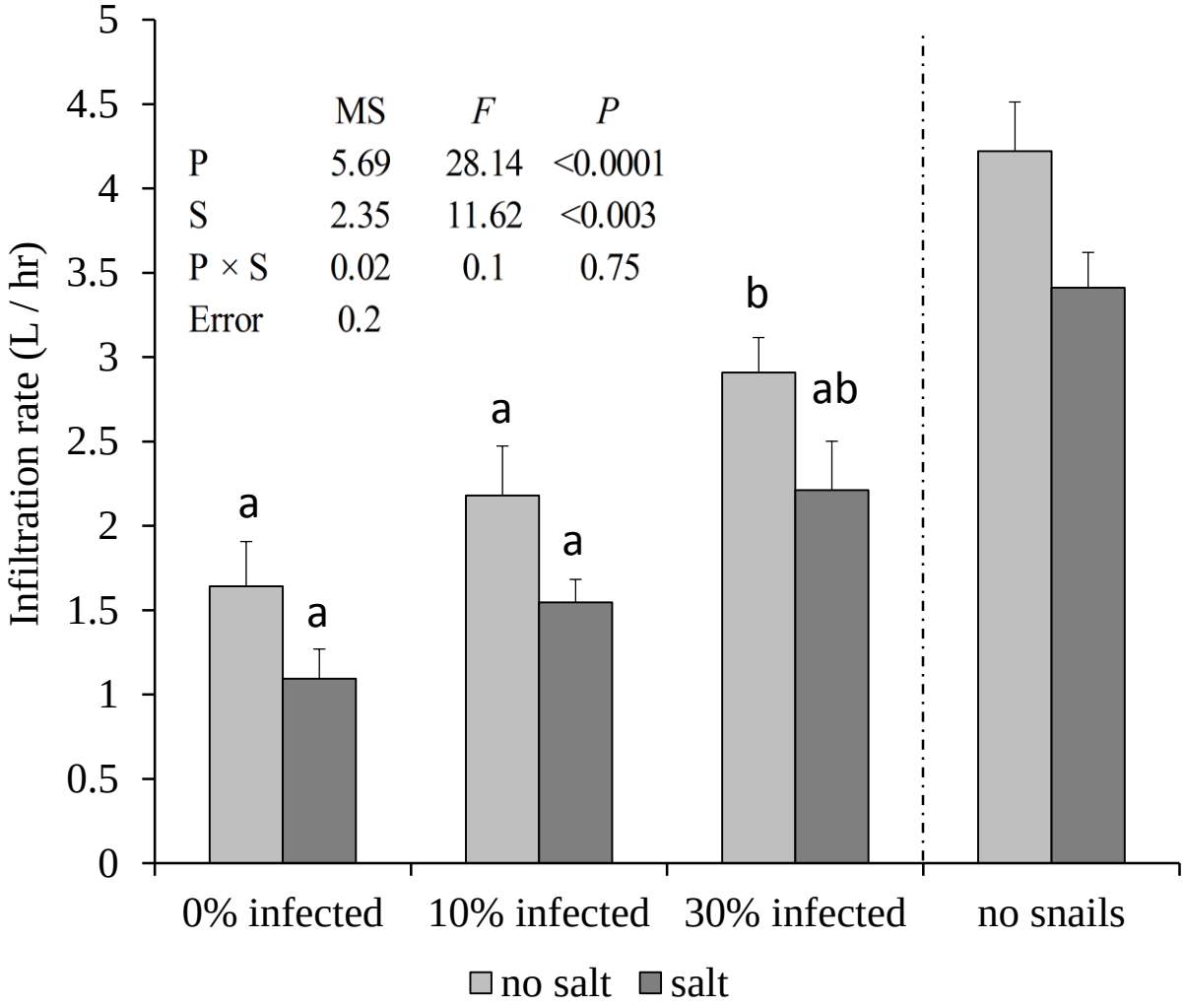

FIGURE 3.2 - The effect of parasite prevalence on infiltration rate. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=5 treatment replicates.

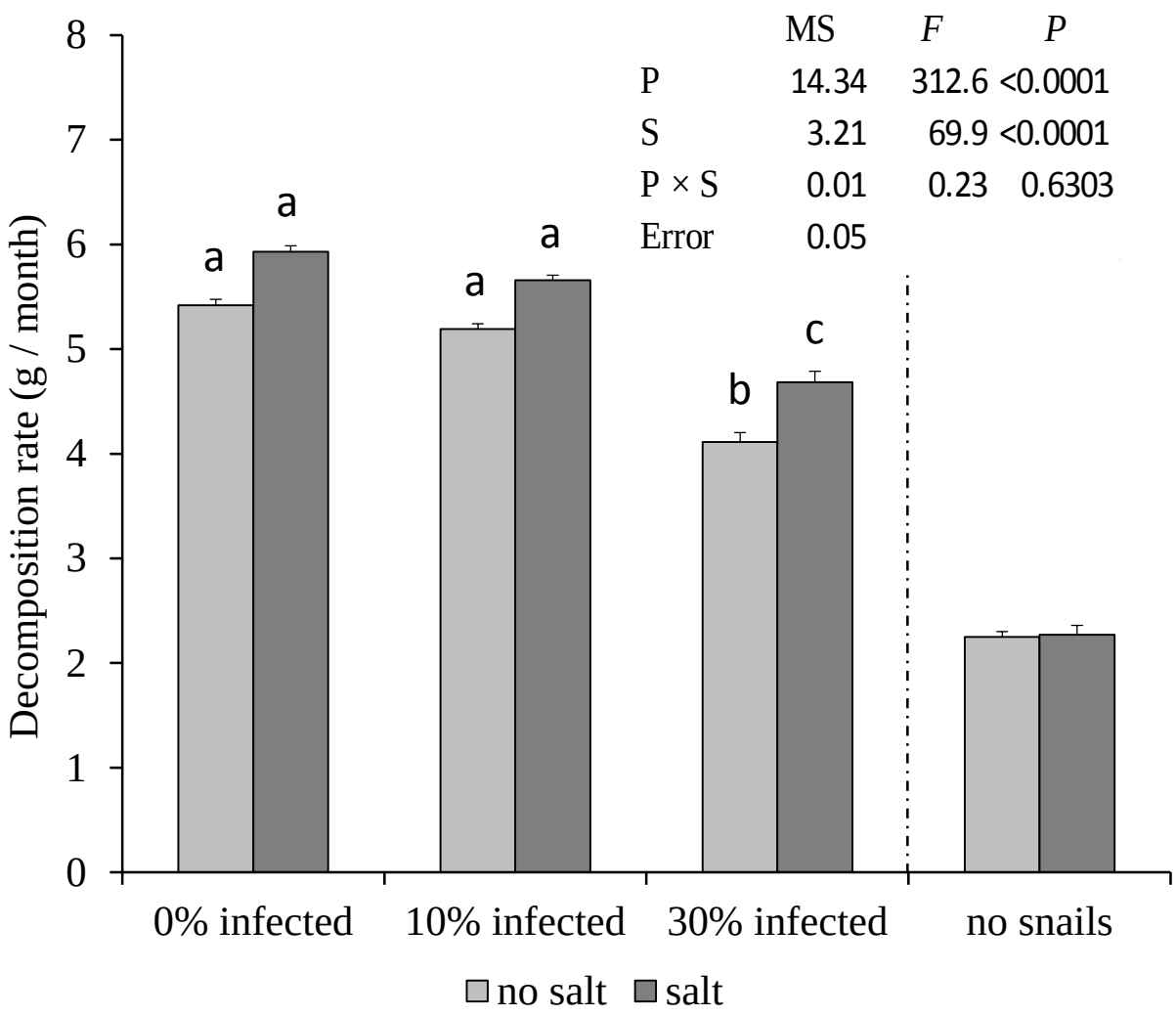

FIGURE 3.3 - The effect of parasite prevalence on decomposition rate. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

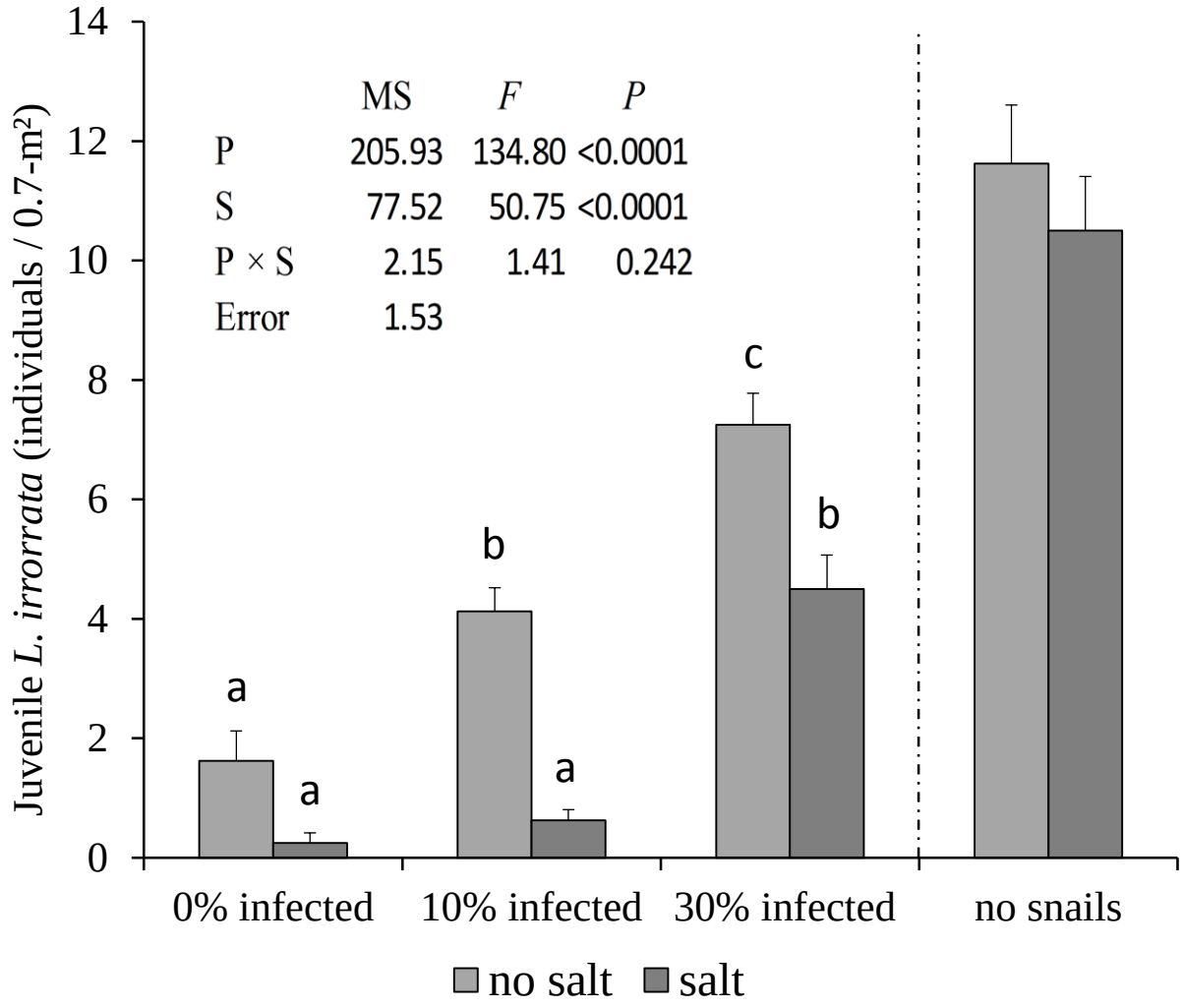

FIGURE 4.1 - The effect of parasite prevalence on the abundance of juvenile *L. irrorata*. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

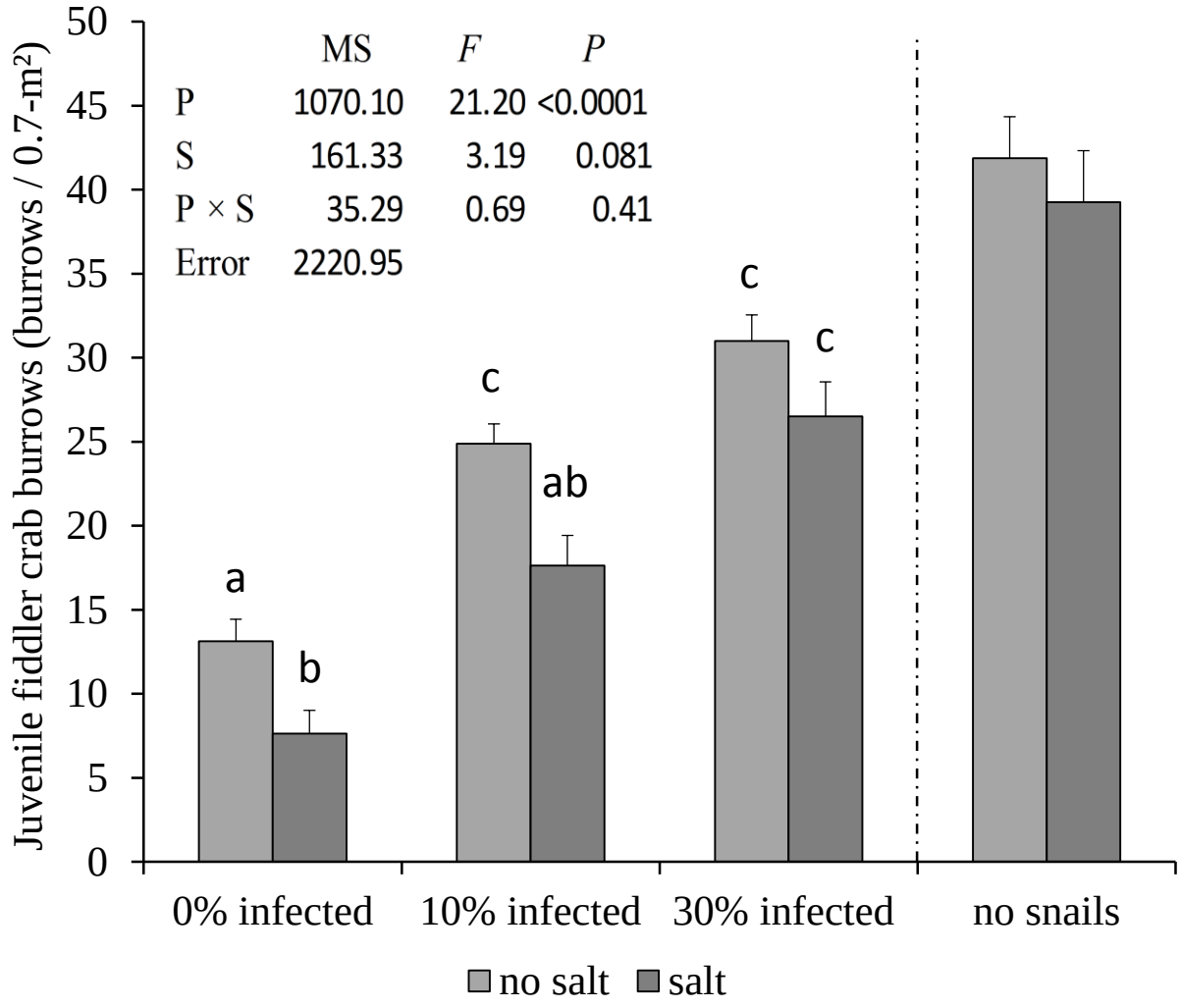

FIGURE 4.2 - The effect of parasite prevalence on the abundance of juvenile fiddler crab burrows. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

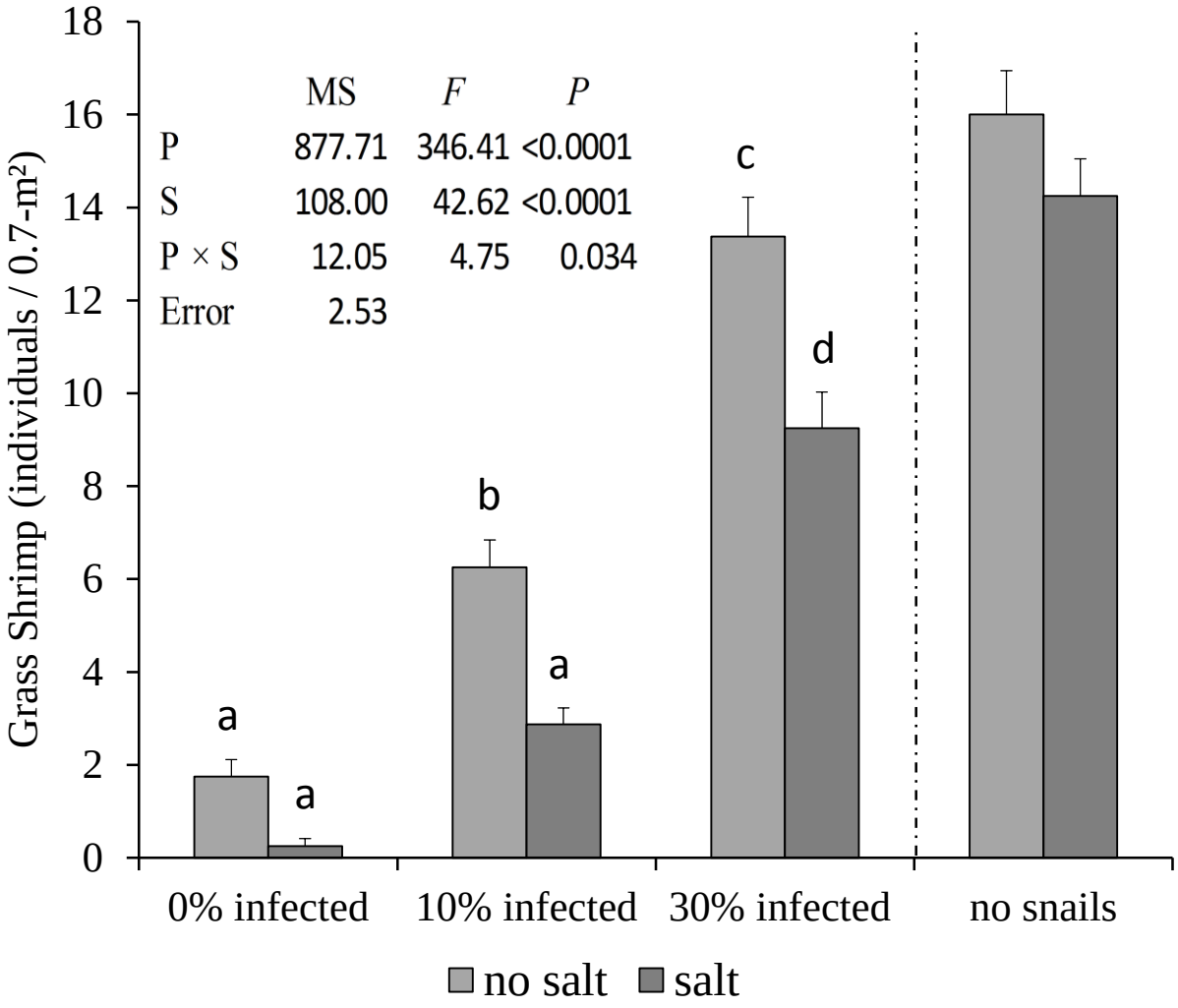

FIGURE 4.3 - The effect of parasite prevalence on the abundance of grass shrimp. Probability values are given for a two-way ANOVA testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

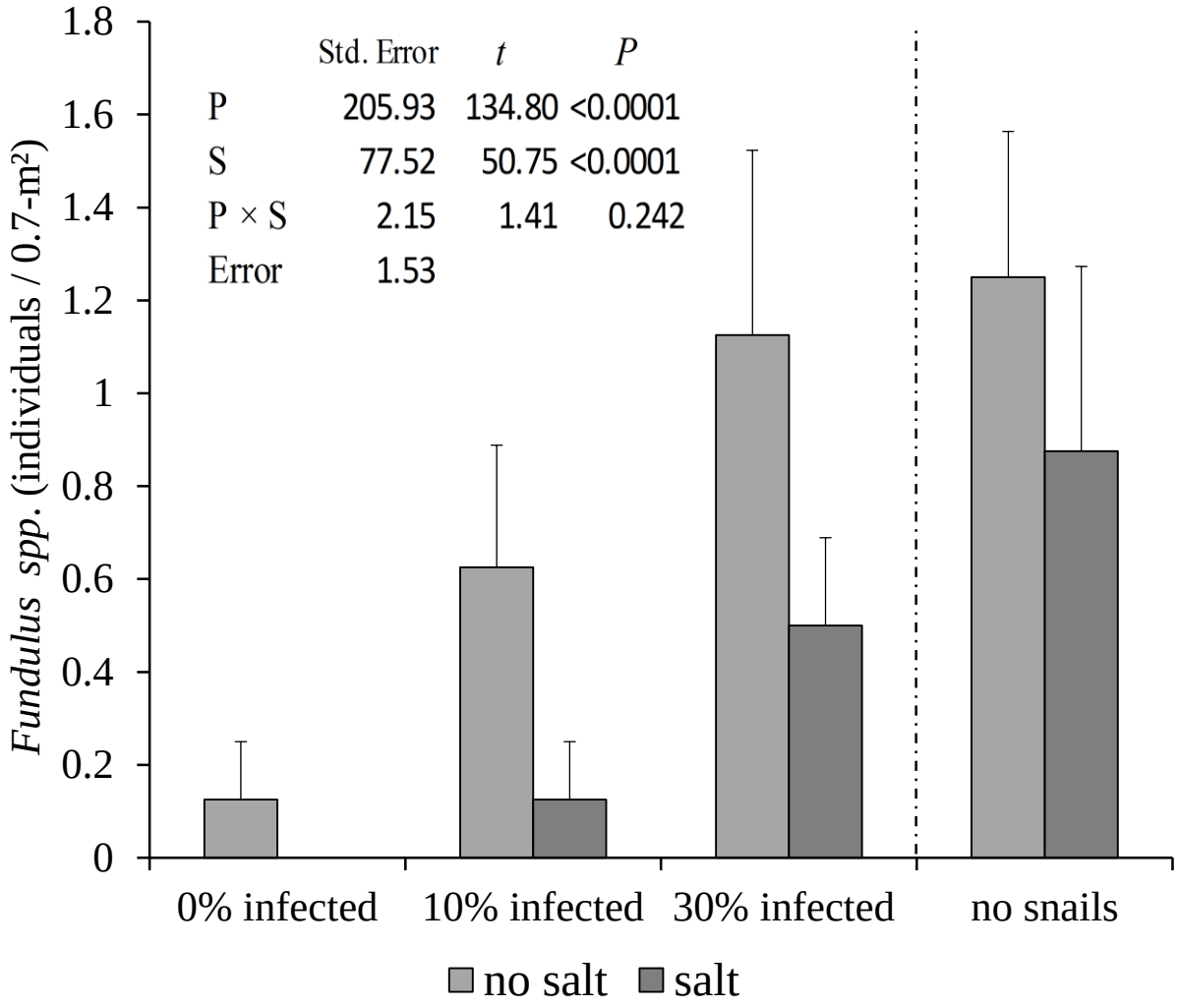

FIGURE 4.4 - The effect of parasite prevalence on the abundance of juvenile killifish.. Probability values are given for a GLM testing for main and interactive effects. P = main effect of parasite prevalence, and S = main effect of salt addition. Data are means and SE; n=8 treatment replicates.

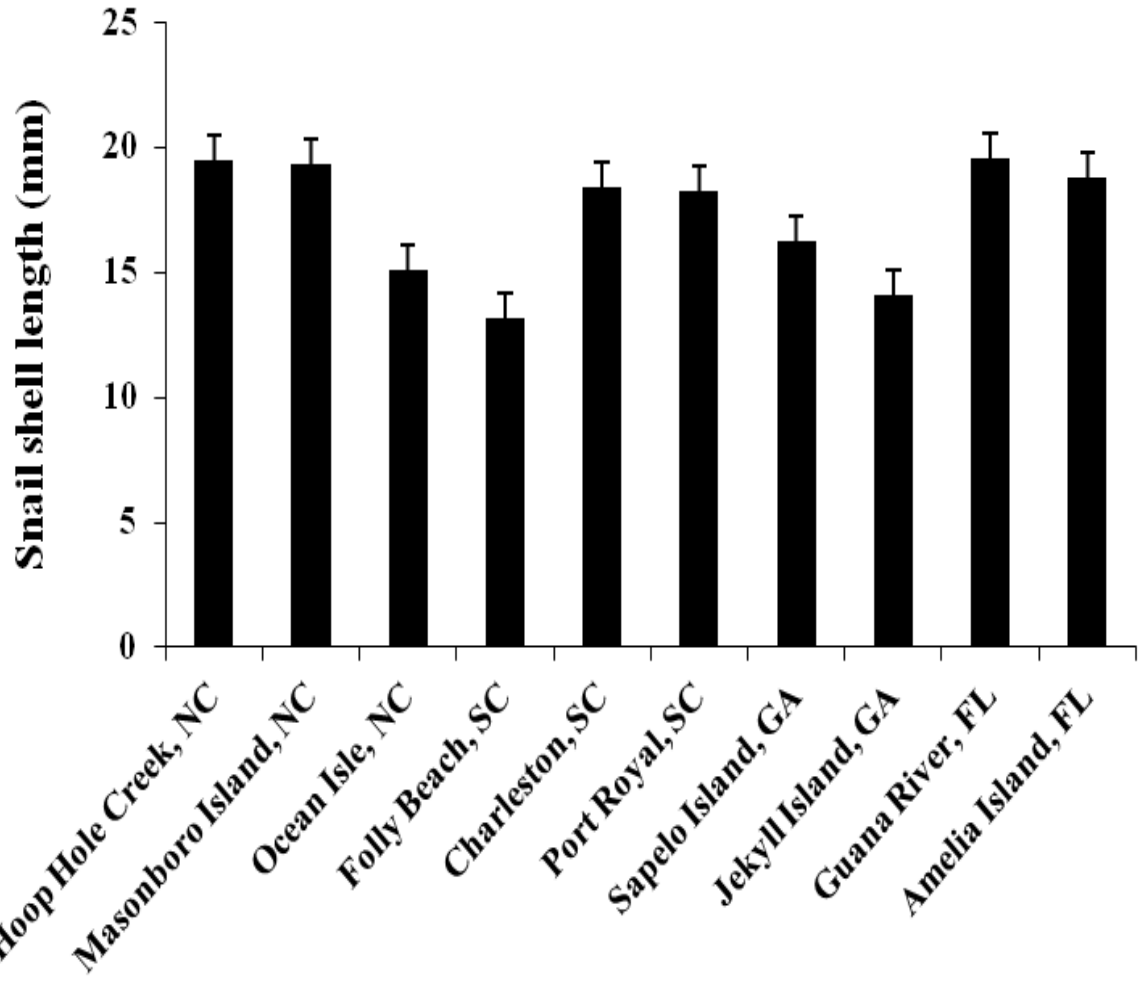

FIGURE 5 - The average shell lengths, measured from apex to arperture, of snails collected from each survey site.

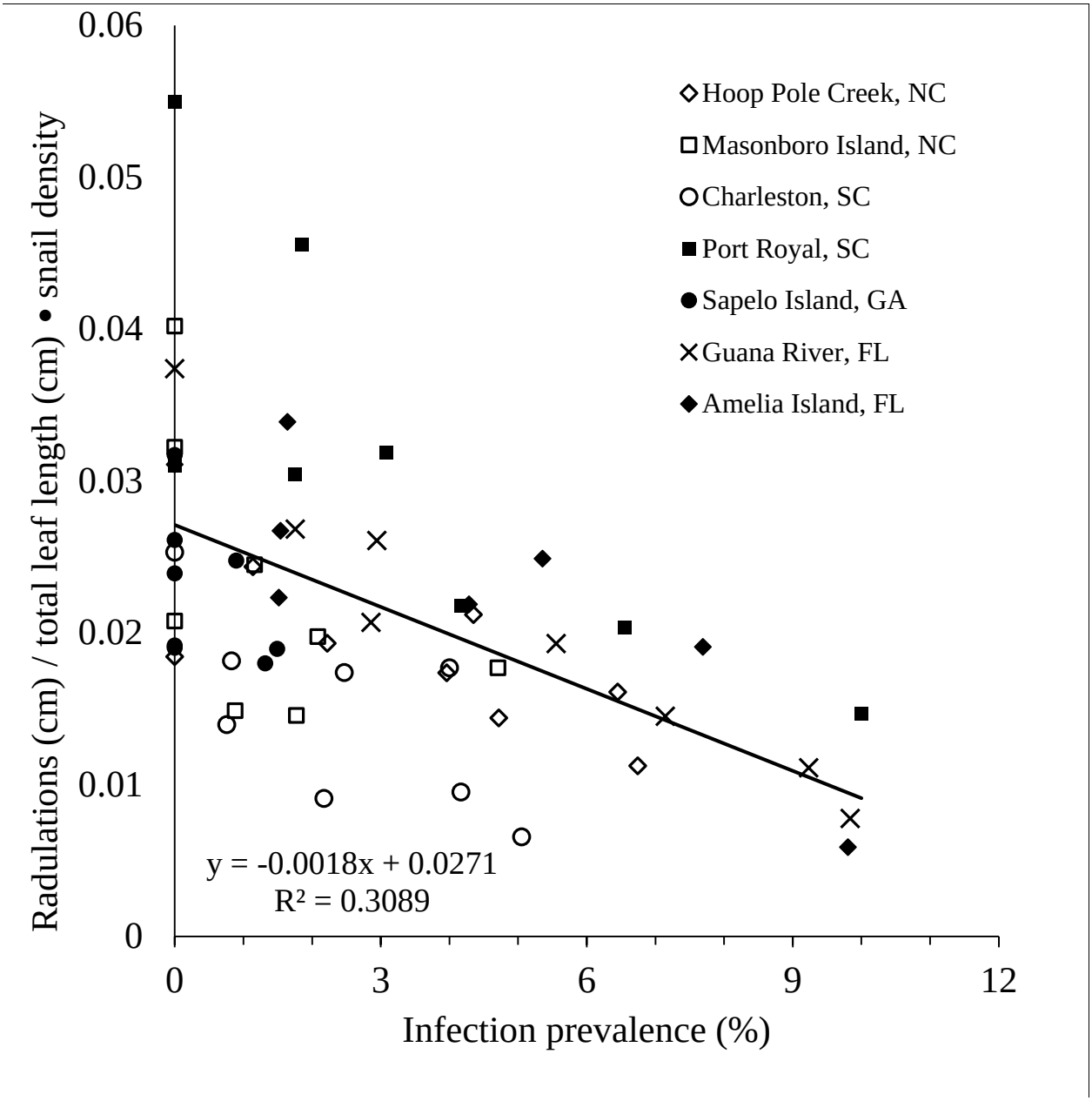

FIGURE 6 - Least Squares linear relationship between trematode infection prevalence and snail grazing intensity (mean radulations per leaf length corrected for snail density) along die-off boarders for seven marshes along the eastern US coast.

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