

IMACTS OF THE INVASIVE GRASS SALTWATER PASPALUM (*PASPALUM  
VAGINATUM*) ON AQUATIC COMMUNITIES OF COASTAL WETLANDS ON  
THE GALÁPAGOS ISLANDS, ECUADOR.

A Thesis

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## ABSTRACT

Invasive plants species pose a threat to ecosystem function, and island ecosystems are particularly vulnerable to their impact. The grass saltwater paspalum (*Paspalum vaginatum*) has successfully invaded Galápagos Islands, potentially threatening coastal lagoons and their globally significant avifaunal biodiversity. I conducted two studies to assess potential changes in invertebrate populations associated with increased *P. vaginatum* abundance.

The first study evaluated the relationship between abundances of fiddler crab (*Uca galapagensis*) burrows and habitat conditions (including above ground *P. vaginatum* densities) measured along transects that spanned lagoon shore-line habitat. Results show that at intermediate *P. vaginatum* densities, fiddler crab burrow abundance increased proximal to the shoreline and at high water tables and demonstrates the importance of moisture in fiddler crab habitat selection. However, burrow densities were reduced at high and low *P. vaginatum* densities regardless of habitat. This result suggests that *P. vaginatum* invasion may benefit the crab at early stages of invasion, but once *P. vaginatum* reaches high densities fiddler crabs may be excluded from lagoon shoreline habitats.

In the second study I assessed whether *P. vaginatum* is impacting aquatic invertebrates by comparing invertebrate communities across 4 lagoon habitats: *P. vaginatum*, the interface between *P. vaginatum* and open water (edge), open water, and emergent mangroves. The invertebrate community in *P. vaginatum* showed increased species richness and was characterized by more terrestrial species such as polychaetes, tabanid larvae, and syrphid larvae. Invertebrate communities in open water were dominated by highly abundant aquatic species such as corixids (*Trichocorixa reticulata*) and ostracods. Although invertebrates in *P. vaginatum* had

greater mass/individual than those in water, edge and mangrove, average overall invertebrate biomass was similar in all habitats and across seasons. This suggests that the invasion of *P. vaginatum* does not affect annual average invertebrate production *per se*, but rather the relative contribution of each species to the overall biomass.

To evaluate whether the shift in invertebrate communities may impact lagoon avifauna, I conducted bird observations, estimated maximum habitat potentially affected by *P. vaginatum*, and assimilated bird feeding ecology data into an impact assessment table. Results suggest that most waterbirds (flamingos, ducks, herons, migratory shorebirds) generally do not associate with *P. vaginatum* while food availability for terrestrial birds (yellow warblers, smooth billed ani, mocking birds) may increase. Furthermore, the *P. vaginatum* invasion degrades foraging habitat and food resources for waterbirds and with further increase may potentially occupy 90.6 % of the lagoon surface area. This potential habitat degradation poses a particular threat to the viability of the Galápagos flamingo (*Phoenicopterus ruber glyphorhynchus*) population, an endemic subspecies, since a further population reduction may increase extinction risk.

My results show that the invasion of *P. vaginatum* is associated with a shift from an aquatic to a more terrestrial invertebrate community. The continued invasion of *P. vaginatum* degrades water bird and fiddler crab habitat. Control of *P. vaginatum* may be necessary to maintain the Galápagos lagoon's status as an Internationally Important Wetland.

## BIOGRAPHICAL SKETCH

Tania Siemens was born in Eugene, Oregon in 1974. Tania loved her family and the cycle-friendly Eugene lifestyle, so rather than fleeing the Willamette Valley like many of her classmates, she stayed to attend the University of Oregon. In 1997 she received her Bachelors Degree (*Summa Cum Laude*) in Biology. Tania loved school and worked hard in college, earning an Honors Degree by conducting an independent research project on population genetics. However, in retrospect, she often wishes she had spent more time mountain biking than studying. In the 4 years between College and Graduate School, Tania worked for the Forest Service in the summer and played in Mexico and South America in the winters. A 7 month bicycle tour in South America ended on the Galápagos Islands, where she interned for 8 months in the Plants Department of the Charles Darwin Research Station. It was on the Galápagos where she encountered some important inspirations: she met her husband Jorge and developed her interest in the ecology and management of invasive plants. In 2000, Tania applied to Graduate School and was accepted at Cornell University to study the ecological impacts of the invasive grass Saltwater Paspalum (*Paspalum vaginatum*) on the Galápagos. While at Cornell, Tania also conducted research on the invasive plant Japanese knotweed (*Fallopia japonica*) and took advantage of opportunities to improve her teaching skills. In 2003, Tania won a Cornell Science Inquiry Partnership teaching fellowship where she worked with middle and high school teachers and students to help make their science curriculum more inquiry-based. Upon graduation from Cornell, Tania hopes to find work that blends education and science to manage invasive plants in natural areas.

To my husband and our son.

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## CHAPTER 1

# IMPACT OF THE INVASIVE GRASS SALTWATER PASPALUM (*PASPALUM VAGINATUM*) ON GALÁPAGOS FIDDLER CRABS (*UCA GALAPAGENSIS*)

## ABSTRACT

Invasive plant species pose a threat to ecosystem function, and island ecosystems are particularly vulnerable to invasions. The grass saltwater paspalum (*Paspalum vaginatum*) has successfully invaded Galápagos Islands threatening coastal lagoons and their avifaunal biodiversity, which are of global significance. By dominating lagoon shorelines and forming mats of floating vegetation, *P. vaginatum* may degrade lagoon biodiversity through food-web and habitat alterations in both shoreline and open water habitats. I evaluated the relationship between abundances of fiddler crab (*Uca galapagensis*) burrows and habitat conditions (including *P. vaginatum* above ground densities) measured along transects spanning lagoon shoreline habitat. In the presence of *P. vaginatum*, burrow abundance increased proximal to the shoreline and where the water table was high, probably because *P. vaginatum* roots increased burrow stability in the soft mud. However, burrow abundance was reduced at high and low *P. vaginatum* densities regardless of habitat. This result suggests that *P. vaginatum* invasion may benefit the crab at early stages of invasion, but once *P. vaginatum* reaches high densities fiddler crabs may be excluded from lagoon shoreline habitats. The potential long-term negative effect suggests that control of *P. vaginatum* may be necessary to preserve *U. galapagensis* lagoon habitat

## INTRODUCTION

The rapid proliferation of invasive plants in natural ecosystems is a principal threat to biodiversity world wide. Invasive plants can alter nutrient cycling, fire regime, hydrology, and food webs (D'Antonio and Vitousek 1992; Cronk 1995; Blossey 1999; Mack et al. 2000). Such dramatic alterations can lead to decreased ecosystem productivity and stability, and reduced biodiversity (Vitousek et al. 1996; Wilcove 1998; National Research Council 2002). However, our knowledge of invasive plant impacts comes from only a handful of well documented examples and anecdotal evidence (Blossey 1999; Parker 1999). Clear documentation of impact would be especially useful for the conservation of islands, whose delicate and isolated ecosystems are particularly vulnerable to plant invasions (Loope 1988; Schofield 1989; Fritts and Rodda 1998). Indeed, the needs to study impacts and control invasive plant spread on the Galápagos Islands have been identified as primary strategies for conserving the Island's famous, yet fragile, biodiversity (Mauchamp 1997; Tye 2001).

Like other Galápagos ecosystems, the Southern Isabela Wetlands (SIW) support biodiversity of local and global significance. This network of at least 20 coastal lagoons is home to endemic bird, plant, and invertebrate species (Ramsar 2002; Gelín and Gravez 2002). And, like other Galápagos ecosystems, these wetlands are vulnerable to plant invasions (Mauchamp 1997; Tye 2001). The lagoon's brackish conditions prevent the spread of most plant invaders, but not of the saline tolerant grass seashore paspalum (*Paspalum vaginatum* Sw., Poaceae). By invading along SIW shores and forming dense mats of floating vegetation, *P. vaginatum* has the potential to alter both terrestrial and aquatic habitats of these tropical lagoons.

Uncertain origin has led to the designation of *P. vaginatum* as "doubtfully native" on Isabela Island (Tye, pers. comm 2003), a status that complicates

management decisions. The Galápagos Islands are valued for their biodiversity; therefore, exotic invaders are often controlled without a refined understanding of their impact (Tye 2003). Such action to prevent habitat degradation is justified by the precautionary principle (Underwood 1997); however, if *P. vaginatum* is native, a negative impact cannot simply be assumed, underscoring the need to document its impact on the lagoon ecosystem.

The lagoon ecosystem is valued for its ability to support resident and migratory bird populations (Ramsar 2002; Vargas 1989), which congregate in these coastal wetlands largely to forage on abundant invertebrate food resources (Sosa 1985; Vargas 1989; Castro and Phillips 1996; Zwarts 1996; Gelín and Gravez 2002). Fiddler crabs constitute important prey for migratory shorebirds such as whimbrels (*Numenius phaeopus*) (Zwarts and Blomert 1990; Ribeiro et al. 2004) and the endemic lava heron (*Butorides sundevalli*) (Castro and Phillips 1996). A reduction in crab abundances as a result of *P. vaginatum* may affect the quality of SIW as stopover or permanent foraging sites for many bird species.

I evaluated impacts of *P. vaginatum* invasion on fiddler crab (*Uca galapagensis*) populations. I tested the hypothesis that *P. vaginatum* would have a negative impact on *U. galapagensis* populations by relating burrow numbers to the abundance of *P. vaginatum* along lagoon shorelines where their distributions overlapped.

## MATERIALS AND METHODS

### *Study Site*

The Southern Isabela Wetlands (00°57'S 90°58'W) includes inland and marine wetlands and covers 359 ha. This research focused on the inland portion, which

consists of at least 20 shallow, brackish lagoons with an average depth of 2 m and a total area of 211 ha (Chávez 2002). Salinity in these lagoons depends on the water level and their proximity to the sea, but ranges from 6 to 79 ppt with an average of 10 ppt (Gelín and Gravez 2002). Water levels vary seasonally and are controlled primarily by rainfall percolating easily through the newly formed (< 500,000 years) volcanic soils. Most of the lagoons are located near (within 1 km) or within the municipal boundaries of the small (approximately 3,000 residents) fishing community Puerto Villamil.

As critical habitat for 25 % of the endemic Galápagos flamingo (*Phoenicopterus ruber glyphorhynchus*), more than 1 % of Galápagos white-cheeked pintail (*Anas bahamensis galapaguensis*), and lava heron (*Butorides sundevalli*) populations (Chávez 2002), the SIW has been designated a wetland of international importance by the Convention on Wetlands intergovernmental treaty (Ramsar 2002). Furthermore, 27 migratory bird species, including whimbrel (*Numenius phaeopus*), lesser yellowleg (*Tringa flavipes*), red-necked phalarope (*Phalaropus lobatus*), and ruddy turnstone (*Arenaria interpres*), make annual visits to SIW (Castro and Phillips 1996). The vegetation along the lagoon shoreline is dominated by red (*Rhizophora mangle*) black, (*Avicennia germinans*) white (*Laguncularia racemosa*) and button mangrove (*Conocarpus erectus*).

I selected the lagoons Baltazar and Puerta del Jelí (Figure 1.1) for this study. The ecology of these lagoons is typical of the entire SIW, with representative biotic and abiotic components. Baltazar has intermediate salinity levels (13 ppt) is of median size (1 ha) and has average depth of 2 m (Appendix II). Puerta del Jelí is located closer to the sea than Baltazar (100 and 400 m from the sea, respectively), has higher salinity levels (37 ppt), but similar size (0.7 ha). In both lagoons button mangrove (*C. erectus*) dominates the shoreline, except for some areas of bare mud and large patches of the invasive grass *P. vaginatum*. Most importantly, both lagoon's

shoreline contain segments where both *P. vaginatum* and *U. galapagensis* distributions have variable (from absent to dense) and overlapping distributions, thus allowing me to assess potential correlations between changes in *P. vaginatum* and *U. galapagensis* abundances. The shoreline segment I studied at Baltazar was substantially larger (occupying 60 m<sup>2</sup>) than the 14 m<sup>2</sup> Puerta del Jelí site.

### *Study Species.*

*Uca galapagensis* (Decapoda: Ocypodidae) is a small (maximum 22 cm carapace width), semi-terrestrial burrowing crab distinguished by the disproportionately large size of one of the chelipeds in males. The species' range extends from the Sea of Cortez in Mexico to the Atacama desert of Northern Chile (Crane 1975); however, *U. galapagensis* has also been considered endemic to the Galápagos (Hickman and Zimmerman 2000). In general, their distribution is restricted to the high inter tidal zone (Morgan and Christy 1995), but in the SIW, their distribution extends inland from areas of daily tidal influence (Gelín and Gravez 2002; pers. obs. 2002). Fiddler crabs feed by sifting bacteria and meiofauna out of sand and mud. Burrows can reach 30 cm deep and provide refuge from predators, shelter during high tide, and serve as mating dens (Crane 1975).

The stoloniferous and rhizomatous semi-aquatic perennial grass *Paspalum vaginatum* Sw. is considered invasive in many tropical and subtropical coastal and estuarine regions of the world (Randall 1996; Graeme and Kendal 2001; Shaw and Allen 2003). Its invasiveness in coastal habitats is not surprising given its saline tolerance (up to 30ppt), ability to withstand frequent inundations, and ability to establish on sand, mud, heavy clays, and bogs (Duncan and Carrow 2000; Graeme and Kendal 2001). Despite its cosmopolitan distribution within the sub-tropics, with notable dominance of some New Zealand and Australian estuaries, little information

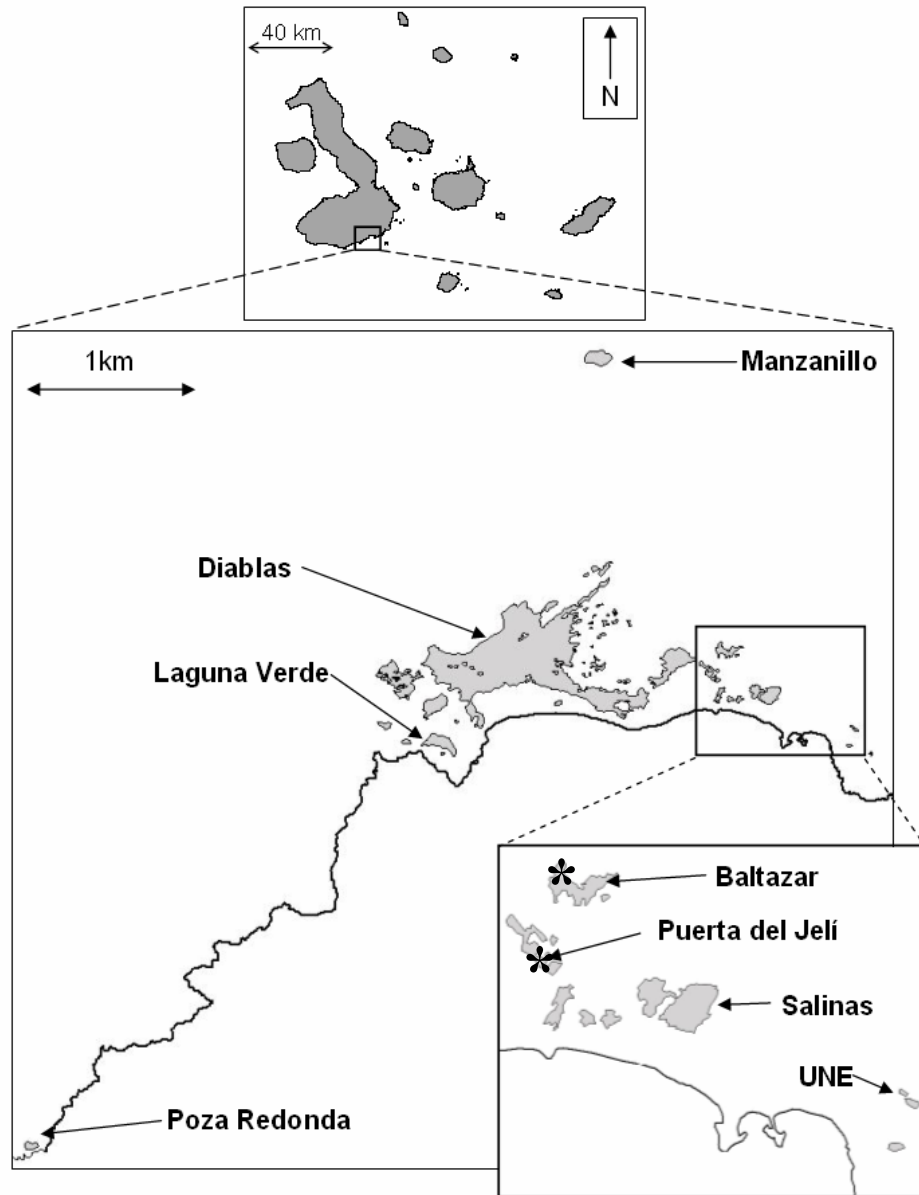


Figure 1.1 Map of Southern Isabela Wetlands showing their location on Isabela Island in the Galápagos Islands (upper map). Study sites are located along the shore of lagoons Baltazar and Puerta del Jeli and are indicated with an asterisk (\*). Grey areas on upper map are islands and grey areas on lower 2 maps are lagoons.

about the specific ecological effects of *P. vaginatum* exists (Graeme and Kendal 2001). Furthermore, the origin of *P. vaginatum* is in dispute, with Europe (Edgar and Conner 2000), Central and South America (Duble 1996), and South Africa (Duncan and Carrow 2000) all mentioned as native ranges of *P. vaginatum*.

Putatively native populations of *P. vaginatum* remained unnoticed on Isabela until the 1990's, when a rapid range expansion into the lagoons (potentially favored by changes in disturbance regimes and salinity) was noticed by the Galápagos National Park Service (GNPS). The actual distribution of *P. vaginatum* in the SIW is unknown; it is generally denser in areas near the village and it is possible to observe large satellite populations of *P. vaginatum* up to at least 7 km from the town (Near Laguna Barahona, personal observation, 2001). Although its growth rate is variable, it can spread up to 56 cm/month (see Appendix I), suggesting potential for further, rapid expansion of *P. vaginatum* into less disturbed lagoons.

### *Experimental Design*

A tourist boardwalk facilitated access to the sites and minimized disturbance from trampling. At Baltazar, I established three parallel 40 m transects 1 m apart. At Puerta del Jeli I established two parallel transects (19 and 9 m long) 5 m apart (Figure 1.2 A & B). At both sites, transects were parallel to the boardwalk and generally parallel to the shoreline of the lagoon. Transects spanned a range of shoreline habitats, incorporating a gradient of *U. galapagensis* and *P. vaginatum* abundance, including areas where the populations did not overlap or were absent (Figure 1.2 A & B).

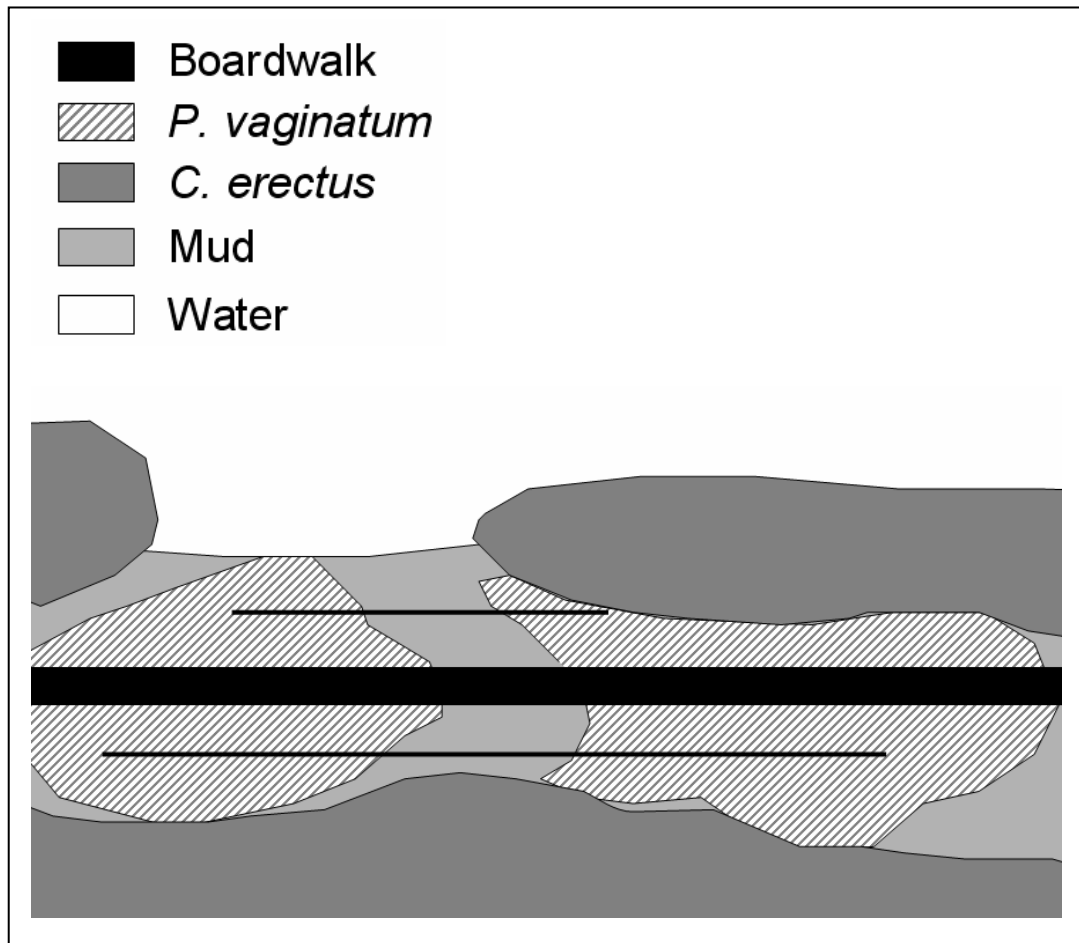


Figure 1.2 A Diagram showing placement of transects at Puerta del Jeli. Transects are 8 and 19 m long, placed 5 m from the boardwalk and are depicted as thin solid black lines.

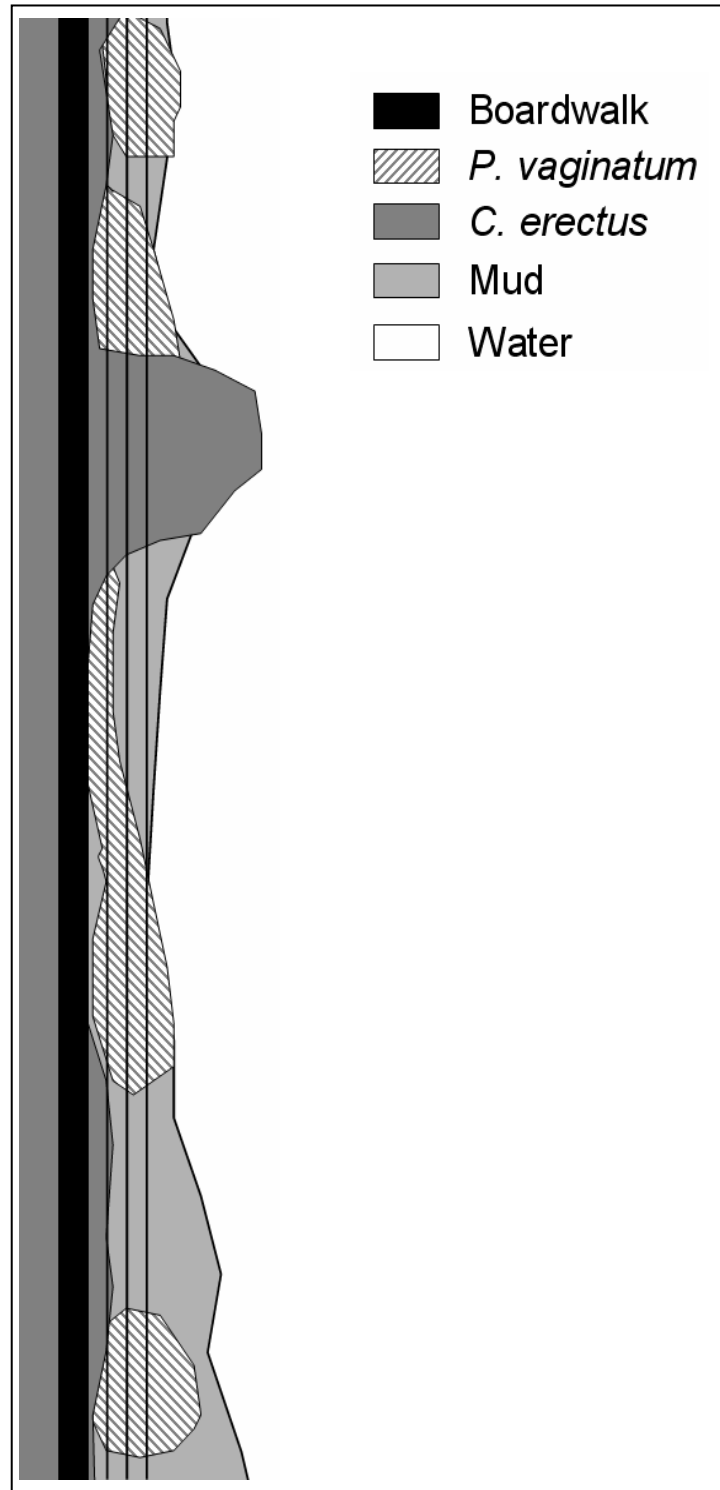


Figure 1.2 B. Diagram showing placement of transects at Baltazar. Transects are 40 m long, placed 1 m apart and depicted as thin solid black lines.

I counted the number of *U. galapagensis* burrows in a 25 x 50 cm quadrat (0.125 m<sup>2</sup>) placed every 25 cm along each transect. I placed quadrats such that the long (50 cm) edge was centered on and perpendicular to the transect line. Although counting the number of burrows tends to over estimate actual fiddler crab abundance, it is the most reliable alternative to excavation (Skov and Hartnoll 2001). I visually estimated the cover (%) of *P. vaginatum*, mud or soil, and mangrove canopy at each sampling location. The small size of the quadrat allowed me to estimate % cover on a continuous scale, rounded to the nearest 5%. Mangrove canopy was measured as the proportion of three dimensional space occupied by mangrove from zero to three meters above the quadrat. I also measured water table depth and distance to the lagoon shore line, which has been suggested to influence burrow abundance in other systems (Mouton and Felder 1996). I measured water table depth by creating a 3cm diameter and 50 cm deep well and measuring the depth below the surface to which the water returned within 3 minutes. I made the well by inserting a wooden rod at a randomly selected location within the quadrat. I measured distance to the lagoon shore line using a 3m long 1cm diameter PVC pipe marked in 1 cm intervals. Data collection occurred from the 5<sup>th</sup> to the 10<sup>th</sup> of August, 2002.

### *Statistical analysis*

I used SAS version 9.1 (SAS Institute Inc., Cary, NC, USA) for all analyses. Burrow number per quadrat did not follow a normal distribution; therefore, I used a multinomial logistic regression to explore the influence of habitat characteristics on burrow abundance. Logistic regression allows the investigator to examine the individual effects of continuous predictor variables on categorical response variables (Allison 2001). I categorized burrow number/quadrat into three abundance levels: I = no burrows, N=234; II = 1-4 burrows, N=161; III = >5 burrows, N=80. I used PROC

GENMOD to calculate the odds that the level of burrow abundance will increase in response to changes in my 5 continuous habitat factors (% *P. vaginatum*, % Soil, % Mangrove canopy, distance to lagoon shore line, and water table depth). I included site as a fixed factor in the model. In order to account for possible spatial autocorrelation, I blocked the data and included it as a repeated fixed factor. I used quadrat location along transects as blocking criteria: adjacent quadrats across transects that were within 2 m intervals were considered one block, totaling 23 blocks. Two meter intervals was an appropriate interval since habitat patches (mud, mangrove, and *P. vaginatum*) are at least 2 m across with abrupt transitions between them; 2m therefore captured the habitat variation at the scale of this investigation. Portions of transects spanning areas clearly not *U. galapagensis* habitat (defined as greater than 55 % water) had no burrows and were excluded from the analysis.

In order to address whether burrows are more abundant at intermediate levels of *P. vaginatum* and water table depth, I included their respective quadratic terms in the model (termed *P. vaginatum*<sup>2</sup> and water table depth<sup>2</sup>). Because I was primarily interested in the relationship between *P. vaginatum* and burrow abundance, I limited my analysis to interactions between *P. vaginatum* terms and the other aforementioned habitat predictors. I arrived at the most parsimonious model by removing from the full model those terms that were both not significant predictors of burrow level and not significant contributors to model fit. I evaluated goodness of fit of the final model by conducting a  $\chi^2$  test on the change in  $-2\log$  likelihood of the final model as compared to the model evaluated with just the intercept (Allison 2001). The significance of the parameter estimates were determined by the Wald's  $\chi^2$  test (Allison 2001).

## RESULTS

### *Model validation*

The likelihood ratio  $\chi^2$  test suggests the final model is a very good fit to the data. The  $-2 \log$  likelihood of the model with just the intercepts is 964.72 while the  $-2 \log$  likelihood for the full model is 693.32 ( $\chi^2=304.53$ ,  $df=10$ ,  $p<0.0001$ ). Also, all standard errors were below 2 indicating there were no major aberrations in the data (Allison 2001). Parameter estimates and their associated p values are not influenced by multicollinearity since the variance inflation factors, as determined by the VIF option in PROC REG, are well below the accepted threshold of 10 (Allison 2001).

### *Overall habitat composition*

I found a total of 1244 burrows in a total of 475 quadrats (374 quadrats in Baltazar and 101 quadrats at Puerta del Jeli). The number of burrows/quadrat (burrows/0.125 m<sup>2</sup>) ranged from 0 – 35, with an average of  $2.62 \pm 0.24$  (mean  $\pm$  SE). The shoreline habitat was dominated by bare soil. Soil was present in 64 % of the quadrats and represented 42 % of the total habitat surveyed. Ground cover of *P. vaginatum* was widespread but patchy as it was present in 56 % of the quadrats, but represented only 23 % of the total habitat surveyed. Mangrove canopy was present in 31 % of the quadrats. These quadrats were primarily clustered along the shore at Baltazar. The soil was moist, with water table depth ranging from 0 – 25 cm, with an average of  $6.24 \pm 0.18$  cm/quadrat (mean  $\pm$  SE). Quadrat distance from the lagoon shore ranged from .01 to 8 m and was on average  $3.6 \pm .007$  m (mean  $\pm$  SE) from the shore.

### *Differences across sites*

The sites differed both in their habitat characteristics and the number of *U. galapagensis* burrows present (Table 1.1). The smaller site, Puerta del Jelí, was characterized by a higher proportion of soil and *P. vaginatum* (28% and 75% more, respectively) than Baltazar. However, Baltazar had 2.5 times more mangrove canopy and 2.8 times lower water table than Puerta del Jelí. Quadrats at Puerta del Jelí had a 5 fold increase in burrow density compared to Baltazar. Indeed, the logistic regression model results showed that the odds of encountering burrows in Baltazar was 88% less ( $\chi^2 = 42.87$ ,  $P < 0.0001$ ) than at Puerta del Jelí.

### *U. galapagensis' burrow habitat association*

Logistic regression model results show that burrow number was significantly affected by distance to lagoon shore ( $\chi^2 = 11.19$ ,  $P = 0.0009$ ), and this relationship is altered by the presence of *P. vaginatum* (*P. vaginatum* X distance to shore:  $\chi^2 = 17.01$ ,  $P < 0.0001$ ) (Figure 1.3). Without *P. vaginatum*, burrows appear more abundant at intermediate distances from the lagoon shore (Figure 1.3). However, in the presence of *P. vaginatum*, burrow distribution is shifted closer to the water with fewer burrows occurring in quadrats at greater distances from the shore (Figure 1.3).

Significantly more burrows (66.2% of total) occurred at intermediate water table depths (5-15 cm). (Water table depth,  $\chi^2 = 64.67$ ,  $P < 0.000$ ; quadratic  $\chi^2 = 36.24$ ,  $P < 0.0001$ ). The relationship between burrow number and water table depth is also affected by *P. vaginatum* (significant quadratic interaction between water-table depth and *P. vaginatum*,  $\chi^2 = 17.01$ ,  $P < 0.0001$ ), with more burrows occurring when *P. vaginatum* presence coincided with a high water table (Figure 1.4)

Table 1.1 Comparison of habitat characteristics and burrow density across site

Site	Soil*	<i>P. vaginatum</i> *	Mangrove canopy*	water table (cm)	Burrows/0.125m <sup>2</sup>
Puerta del Jeli	34±5	35±6	10±2	6±1	7.9±1.5
Baltazar	25±2	19±3	35±2	17±3	1.3±0.1

\* Units are % cover. Data are means ±1 SE

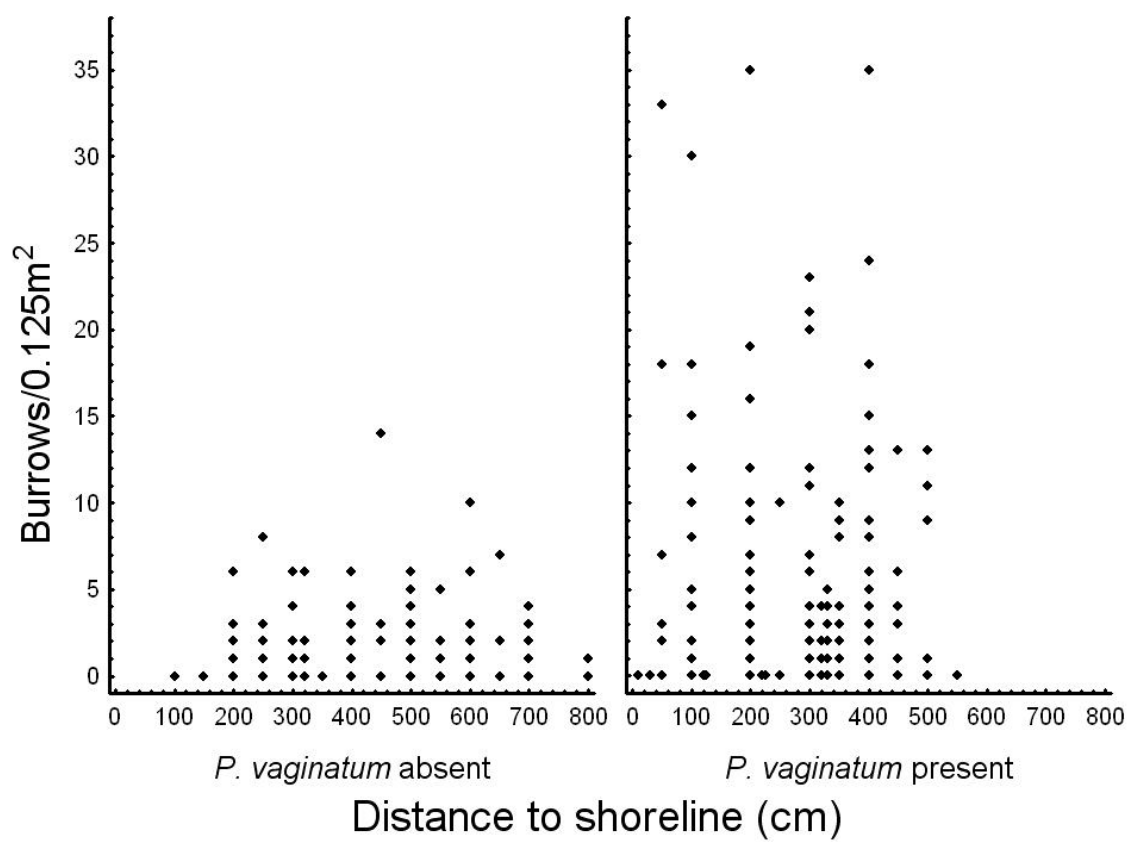


Figure 1.3 Number of *U. galapagensis* burrows/0.125m<sup>2</sup> as a function of distance to lagoon shore and presence or absence of *P. vaginatum*.

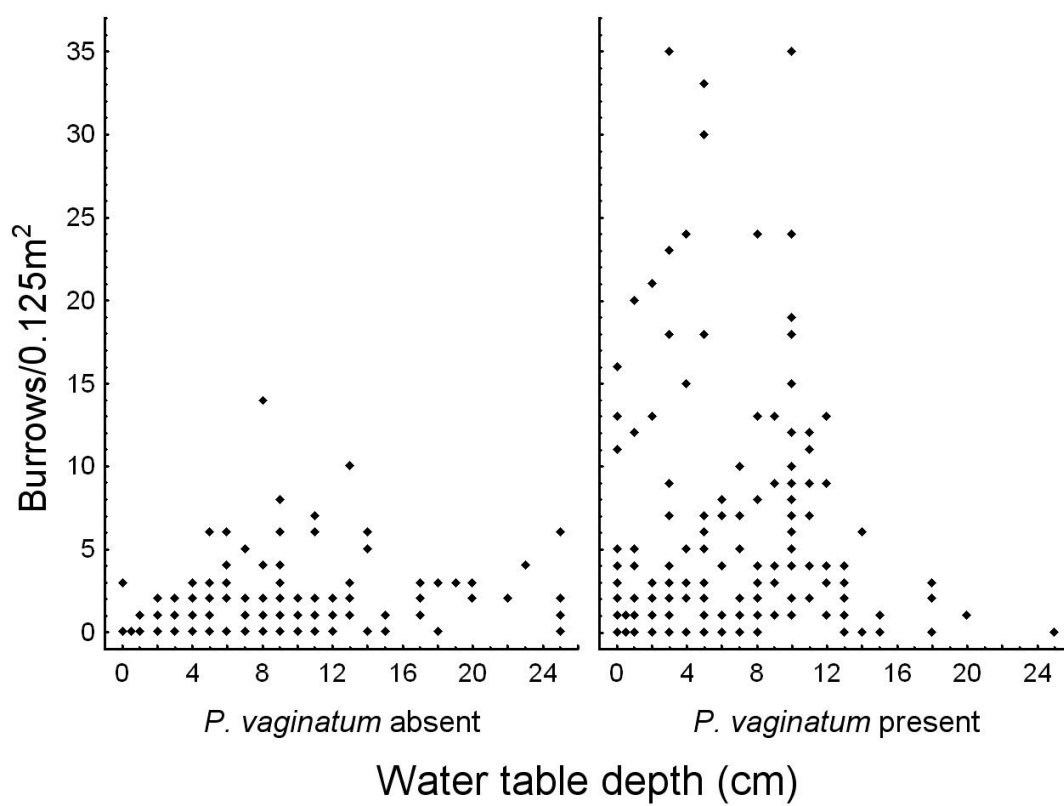


Figure 1.4 Number of *U. galapagensis* burrows/0.125m<sup>2</sup> as a function of water table depth in the presence or absence of *P. vaginatum*.

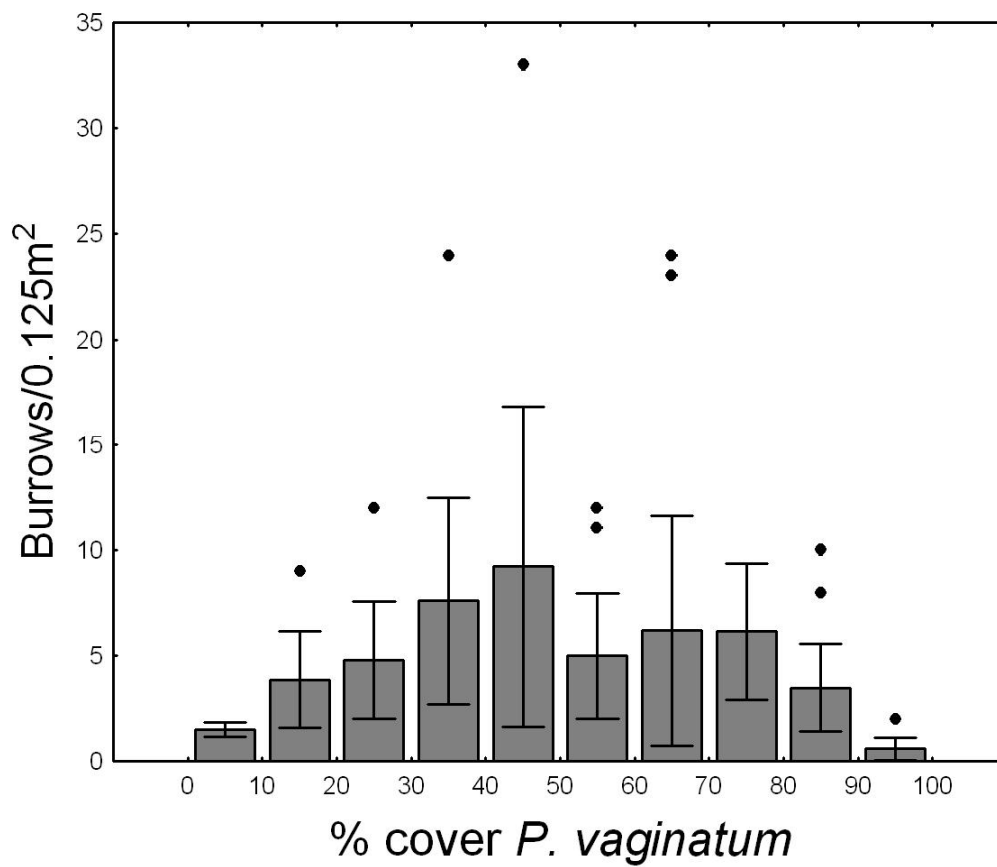


Figure 1.5 Number of *U. galapagensis* burrows/0.125m<sup>2</sup> at different *P. vaginatum* densities (% cover). Filled circles are outliers as calculated with a coefficient of 1.5.

Patterns in the data show a clear quadratic relationship between *P. vaginatum* levels and burrow numbers, with few burrows occurring at either very high or very low *P. vaginatum* cover levels (Figure 1.5). In the 30 quadrats that had >90 % *P. vaginatum*, only 6 contained burrows and for a total of only 18 burrows. However, the quadratic of *P. vaginatum* ( $P. vaginatum^2$ ) significantly predicts burrow levels not as a main effect but as interactions with water table depth ( $P. vaginatum^2 \times \text{water table depth}^2$ ,  $\chi^2 = 21.19$ ,  $P < 0.0001$ ) and distance to shore line ( $P. vaginatum^2 \times \text{distance to shore}$ ,  $\chi^2 = 17.01$ ,  $P < 0.0001$ ).

## DISCUSSION

My results suggest that *P. vaginatum* does impact *U. galapagensis* populations and that the nature of this impact is complex. Water table depth and distance to the lagoon were the most important habitat factors affecting the abundance of *U. galapagensis*, even when accounting for site differences. However, *P. vaginatum* mediated the relative value of these habitats. The presence of *P. vaginatum* was associated with an increase in burrow number where the water table was high or at proximal distances from lagoon edge, and a decrease in burrows in areas distal to the shore (Figure 1.3 & Figure 1.4).

The importance of water, both in terms of distance to shore and water table depth, was expected. Fiddler crabs are semi-aquatic organisms that depend on the proximity to water for reproduction, foraging, and respiration; however, they are fully aquatic only as nauplii and will drown if submerged in water as adults (Crane 1975). Indeed, in a study by Moulton and Felder (1996), burrow number decreased with increased distance to the shore due to lack of soil-moisture availability. They also found that burrow depth increased with increasing elevation from the sea (Moulton and Felder 1996), possibly because fiddler crabs normally need standing water in their

burrows to prevent desiccation of their brachial chambers (Crane 1975). On the other hand, fiddler crabs will abandon burrows that fill with water since they need to breathe air (Crane 1975). Therefore, it is likely that in my study, the distribution of fiddler crabs reflects a search for optimal moisture levels, with fewer fiddler crabs located where accessing water is difficult (low water tables) or where their burrows become inundated with water (near the shore).

Concurrent with water availability, access to suitable forage sites also influences fiddler crab burrow distributions (Genoni 1985; Klassen and Ens 1993). Fiddler crabs burrow in the vicinity of their forage grounds to insure rapid escape from predators (Klassen and Ens 1993). Reinsel and Rittschof (1995) found that substrate texture along with soil saturation levels determine the quality of forage conditions and that optimal foraging conditions accurately predicts *Uca pugilator* burrow location within habitat (Reinsel and Rittschof 1995). Therefore, a greater number of *U. galapagensis* burrows at intermediate distances to the lagoon shore may also reflect the presence of optimal foraging conditions.

While foraging and water resources are clearly important, *U. galapagensis* distribution is also influenced by *P. vaginatum*, with increased burrows at intermediate *P. vaginatum* abundance (Figure 1.5). The ability of *P. vaginatum* to alter *U. galapagensis* burrow distributions agrees with extensive literature documenting the importance of vegetation to fiddler crab distributions. In general, fiddler crabs are attracted to intermediate levels of vegetation because it can provide heat amelioration (Nomann and Pennings 1998), serve as a refuge from predators (Lee and Kneib 1994; Nobbs 2003), provide a food source (decomposing vegetation can accumulate bacteria) (Haines 1976; Mouton and Felder 1995), or increase burrow stability (Ringold 1979; Bertness and Miller 1984; Bertness 1985; Mouton and Felder 1996). Heat amelioration (shade) provided by *P. vaginatum* is unlikely a driving factor since, at my site, mangrove vegetation (also providing shade) actually excluded crabs.

While it is possible that *P. vaginatum* does provide food resources or refuge from predators, the fact that *P. vaginatum* increased burrow numbers in soft sediment areas (near the shore and at high water tables) where burrows are less stable, suggests that increased burrow stability is likely the primary cause of this pattern.

Increased burrow stability does not imply increased burrow occupancy, and, because I did not excavate burrows to confirm occupancy, increased burrows in *P. vaginatum* may be a result of slower burrow decay rate after abandonment. However, the presence of *P. vaginatum* was also associated with a reduction of burrow number at distal locations from the shore and low water tables (Figure 1.3 and 1.4) where rapid burrows decay is not expected due to dryer soil conditions. Therefore, *P. vaginatum* may be actively affecting *U. galapagensis* habitat choice rather than simply changing burrow decay rates.

Earlier studies documenting relationships between in fiddler crabs and vegetation also hypothesized that this pattern is a result of vegetation's influence on burrowing conditions (Ringold 1979; Bertness and Miller 1984). This hypothesis was proven experimentally in temperate marsh ecosystems by Bertness (1985), who showed that, not only does intermediate vegetation (and root density) stabilize burrows, but also heavy *Spartina alterniflora* root mat accumulation results in a hard substratum limiting crab burrowing. Patterns in my data are consistent with the explanation proposed by Bertness (1985), suggesting that heavy *P. vaginatum* root mat accumulation interfering with burrowing ability may explain low burrow counts associated with high *P. vaginatum* % cover.

I did not sample over multiple time intervals to allow direct association of changes in plant density to changes in biotic community, which would be ideal (Blossey 1999). However, although actual *P. vaginatum* abundance may vary seasonally with possible die back associated with prolonged flooding or exposure to high (> 50 ppt) salinity (Graeme and Kendal 2001), its abundance generally increases

over time scales relevant to succession (Paradis 1989; Graeme and Kendal 2001). Therefore, varied levels of *P. vaginatum* may be likened to temporal stages of its invasion (a density-for-time substitution), with responses of burrow abundance to high *P. vaginatum* levels reflecting the long term consequence of *P. vaginatum* invasion to *U. galapagensis* populations. While during initial invasion *P. vaginatum* attracts and possibly benefits *U. galapagensis* (through burrow stability in its ideal moisture level and forage ground), fewer burrows at high densities of *P. vaginatum* suggests that the long-term consequences of the *P. vaginatum* invasion is the exclusion of *U. galapagensis* from its habitat.

This study was limited to two study sites where *U. galapagensis* and *P. vaginatum* habitats coincide. Such overlap represents a small portion of *U. galapagensis* distribution. *P. vaginatum* is limited to lagoon margins with salinities < 50 ppt whereas *U. galapagensis* is abundant not only along lagoons shores but also in sandy tide pools and mangrove margins periodically flooded by the tide. However, the negative impact seen by *P. vaginatum* on *U. galapagensis* populations even within confines of the SIW may be of significant consequence to the fiddler crabs who access these areas for improved foraging (Crane 1975).

This study demonstrates that the invasion of *P. vaginatum* does affect *U. galapagensis* distributions and this interaction may result in the loss of *U. galapagensis* populations in the long-term. Loss of the *U. galapagensis* along lagoon margins may have negative effects on higher trophic level avifauna such as the whimbrel and endemic lava heron who access the lagoons (Chapter 2) and are known to prey on fiddler crabs (Zwarts and Blomert 1990; Castro and Phillips 1996; Ribeiro et al. 2004). Therefore, despite its doubtfully native status, continued expansion of *P. vaginatum* represents a potential threat to bird biodiversity values inherent to the lagoons (Ramsar 2002) and its control may therefore be warranted.

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## CHAPTER 2

# IMPACT OF THE INVASIVE GRASS *PASPALUM VAGINATUM* ON AQUATIC INVERTEBRATE AND WATERBIRD COMMUNITIES IN GALÁPAGOS COASTAL WETLANDS, ECUADOR

## ABSTRACT

Coastal lagoons on the Galápagos Islands, Ecuador are recognized by the Ramsar treaty as Wetlands of International Importance with avifaunal biodiversity of local and global significance. Invasive plants such as the grass saltwater paspalum (*Paspalum vaginatum*), which has successfully invaded the Galápagos lagoons, are potential threats to ecosystem function, and island ecosystems appear particularly vulnerable. By dominating lagoon shorelines and forming mats of floating vegetation, *P. vaginatum* may threaten lagoon biodiversity through food-web disruption and habitat alteration. To address whether *P. vaginatum* may be impacting aquatic invertebrate communities and thereby reducing waterbird prey availability, I compared aquatic invertebrate communities across 4 lagoon habitats: *P. vaginatum*, the interface between *P. vaginatum* and open water (edge), open water, and emergent mangroves in July 2002 and January 2003. I observed a shift in invertebrates from an open water aquatic to a more terrestrial community. The invertebrate community in *P. vaginatum* showed increased species richness and was characterized by more terrestrial species such as polychaetes, tabanid larvae, and syrphid larvae. Invertebrate communities in open water were dominated by highly abundant aquatic species such as Corixids (*Trichocorixa reticulata*) and Ostracods. Overall invertebrate biomass was similar across all habitats and seasons, suggesting that *P. vaginatum* invasion does not affect

annual average invertebrate production per se, but rather, the relative contribution of each species to the overall biomass.

To evaluate whether the shift in invertebrate community may impact lagoon avifauna, I conducted bird observations, estimated maximum habitat potentially affected by *P. vaginatum*, and assimilated data into an impact assessment table. Results suggest that most waterbirds generally do not associate with *P. vaginatum*. The *P. vaginatum* invasion degrades foraging habitat and food resources for waterbirds and may potentially eventually occupy 90.6% of the lagoon surface area. This potential habitat degradation poses a particular threat to the viability of the Galápagos flamingo (*Phoenicopterus ruber glyphorhynchus*), and endemic subspecies, since a further population reduction may increase extinction risk. Control of *P. vaginatum* may be necessary to prevent loss of waterbird habitat and maintain the Galápagos lagoon's status as an Internationally Important Wetland.

## INTRODUCTION

The Southern Isabela Wetlands (SIW) of the Galápagos Islands, Ecuador, include the only extensive island lagoon ecosystem in the Tropical Eastern Pacific (Gelín and Gravez 2002; Ramsar 2002). More than 20 mangrove-lined lagoons support biological diversity of local and global significance particularly valued for their viable populations of both resident and migratory waterbirds (Chávez 2002). Indeed, the SIW's ability to support 25% of the population of the endemic Galápagos greater flamingo (*Phoenicopterus ruber glyphorhynchus*) and at least 1% of the endemic Galápagos white cheeked pintail (*Anas bahamensis galapagensis*) population was a central factor in its designation as a Ramsar Wetland of International Importance (Chávez 2002; Vargas 1995). (Adopted in the Iranian city of Ramsar in

1971, this Intergovernmental treaty on conservation and wise use of natural resources designates wetlands as internationally important to waterbirds only if they regularly support at least 1% of the individuals in a population of one species or subspecies of waterbird (Ramsar 2002)). Although the SIW is protected as part of the Galápagos National Park, anthropogenic disturbances such as mangrove clearing (Gelin and Gravez 2005), alteration of the hydrologic regime (Vargas 1995), and the spread of invasive plant species (Schofield 1989; Mauchamp 1997; Tye 2001), pose a formidable threat to the integrity of this ecosystem, potentially jeopardizing its status as an Internationally Important Wetland.

Invasive plants can compromise ecosystem integrity and function by altering processes such as nutrient cycling, fire regime, hydrology, and food web dynamics (D'Antonio and Vitousek 1992; Cronk 1995; Blossey 1999; Mack et al. 2000). Food web impacts can manifest themselves through changes in species abundances, impacting other biotic community members through trophic interactions (Tschamtker and Hawkins 2002) often leading to reduced biodiversity (Wilcove 1998; Blossey 1999; National Research Council 2002). Island ecosystems are particularly susceptible to the impacts of invasive plants (Loope 1988; Schofield 1989; Fritts and Rodda 1998) and plant invasions are considered a primary threat to Galápagos biodiversity (Mauchamp 1997; Tye 2001). Therefore, the invasion of the grass seashore paspalum (*Paspalum vaginatum* Sw., Family: *Poaceae*) into the SIW raised concerns about its potential effect on lagoon ecosystems. By invading along lagoon margins, often forming large mats of vegetation that can completely cover small lagoons, *P. vaginatum* has the potential to affect aquatic invertebrate and waterbird populations (Sosa 1985; Vargas 1989; Castro and Phillips 1996; Zwarts 1996; Gelín and Gravez 2002). However, management decisions regarding *P. vaginatum* are complicated due to a lack of quantitative data on its ecological impact (Graeme and Kendal 2001).

Low density emergent vegetation may benefit aquatic invertebrates by providing habitat structure and a food source (Cantrell 1985; Olson et al. 1995). However, dense vegetation can cause plant decomposition and sediment accumulation resulting in anoxic conditions that can exclude invertebrates desirable to birds (Cardonale et al. 1997; Netto and Lana 1997; Hedge and Kriwoken 2000). Invertebrates inside dense vegetation, although abundant, may be physically inaccessible to birds whose beaks are specialized for filter feeding in open water (such as pintail ducks and flamingos) (Baldassarre et al. 2000). In addition, seasonal variations in water levels may change the nature of plant-invertebrate interactions (Smith and Collopy 1995; Joy and Pullin 1997; Stinson et al. 1997; Flinn et al. 2005). Flooded conditions may cause invertebrates to preferentially associate with vegetation (Murkin and Kadlec 1986; Murkin et al. 1992; Batzer et al. 1993) potentially attracting waterbirds to vegetated areas. Thus, *P. vaginatum* invasion clearly has the potential to affect waterbird habitat by altering patterns of food availability.

I evaluated how the abundance, biomass, and species richness of aquatic macroinvertebrates differed in four lagoon habitats: open water, emergent mangrove vegetation, a previously open water area now invaded by *P. vaginatum*, and the transition between the *P. vaginatum* and the open water (edge). Aquatic invertebrates can serve as useful indicators of ecological change due to their abundance, diversity, ease of collection, and rapid response to environmental perturbation (Rosenberg et al. 1986; Reynoldson 1992), thus providing a measurable property by which invasive species impact may be gauged (Pik et al. 2002). Furthermore, invertebrates are an important food resource for waterbirds (Schneider 1983; Vargas 1995; Zwarts 1996), and the quality of waterbird habitat is often a function of the abundance and distribution of invertebrates (Euliss and Grodhaus 1987; De Szalay and Resh 1997). I hypothesized that the invertebrate community in *P. vaginatum* would be different from invertebrate communities in the other habitats. My observations of bird-habitat

associations were focused primarily on understanding flamingo and white cheeked pintail duck interactions with *P. vaginatum* since their dependence on lagoon habitat underpins the SIW's International Importance designation. I hypothesized that most birds would avoid dense *P. vaginatum* habitat due to lack of food and inaccessibility. I repeated the invertebrate, but not the bird, study in the rainy season to evaluate whether changes in water levels between the dry and rainy affected the invertebrate community. I created a table that assesses the potential impact of *P. vaginatum* on bird feeding ecology using data generated from my study and knowledge of bird feeding ecology from the literature. I also calculated the maximum potential spread of *P. vaginatum* into the lagoons. This assessment of *P. vaginatum*'s potential spread and impact on bird feeding ecology will help illuminate whether *P. vaginatum* poses a threat to SIW's status as a Ramsar Wetland of International Importance.

## MATERIALS AND METHODS

### *Invertebrate study site description*

The Southern Isabela Wetlands (SIW) (00°57'S 90°58'W) occupy an area of 211 ha (Figure 1.1) and are located near the fishing community Pto. Villamil (approx. 3,000 inhabitants). The wetlands consist of at least 20 permanent lagoons which vary greatly in size (from 0.1 to 79 ha) and salinity (average 10 ppt; range 6-79 ppt).

Salinity depends on the water level and their proximity to the sea and all lagoons have a thick sediment layer that occupies much of the shallow (average 2 m) water column. Water levels are controlled primarily by rainfall rather than tidal fluctuations. Rain events inland also affect water levels as water percolates easily through the newly formed (< 500,000 years) volcanic soils. Higher water levels generally correspond to

the December through May rainy season (Vargas 1995). The importance of ground-water (versus tidal influence) has increased with the gradual closure of the lagoons from the sea due to road construction in 1983 and general filling of lagoons as the village expands (Vargas 1995).

The plant community is dominated by four mangrove species: red (*Rhizophora mangle*), black (*Avicennia germinans*), white (*Laguncularia racemosa*) and button mangrove (*Conocarpus erectus*) (Vargas 1995; Gelín and Gravez 2002). Mangroves provide important ecological functions as their roots and branches often extend into the lagoons creating refuge and nursery sites for fish and nesting sites for birds (Castro and Phillips 1996; Nagelkerken et al. 2002).

I chose the lagoon Baltazar (Figure 1.1) to study the invertebrate communities of the lagoons as its ecology is typical of the entire SIW complex. Baltazar has intermediate salinity levels (13 ppt) is of median size (1 ha) (Appendix II) and has an average depth of 2 m (Appendix II). Aquatic invertebrate species richness and abundance in Baltazar is comparable to other lagoons in the SIW (Gelín and Gravez 2002; Appendix II), and harbors species representative of both saline and fresh SIW habitats (Appendix II). Button mangrove (*Conocarpus erectus*) dominates the shoreline, except for some large patches of the invasive grass *P. vaginatum*, which has completely covered one shallow bay. Baltazar has breeding populations of the white cheeked pintails and flamingos frequently forage in this lagoon (pers. obs 2002).

#### *Invertebrate study species*

*Paspalum vaginatum* Sw. is a stoloniferous and rhizomatous semi-aquatic perennial grass broadly distributed throughout tropical and sub-tropical latitudes (Graeme and Kendal 2001). The native range is in dispute and different authorities consider it native to North and South America (Duble 1996), Europe (Edgar and

Conner 2000) or South Africa and south-east America (Duncan and Carrow 2000). On the Galápagos archipelago, *P. vaginatum* is listed as a native species (Wiggins and Porter 1971), but has recently been designated as “doubtfully native” to Isabela island (Alan Tye, pers. com. 2003). Verbal testimony (pers. com. Don Gustavo Jaramillo; Vargas 1995) combined with herbarium records (Alan Tye, pers. com. 2003) suggest *P. vaginatum* was deliberately introduced to Isabela in the early 1900s as cattle fodder, but did not expand its range into the lagoons until the late 1970s (detailed in appendix III).

*Paspalum vaginatum* is considered invasive in many tropical and subtropical coastal regions of the world (Randall 1996; Graeme and Kendal 2001; Shaw and Allen 2003). Its invasiveness in coastal wetlands is likely due to its salinity tolerance (up to 30ppt), rapid growth (up to 2.7cm/day, Appendix I), ability to tolerate frequent inundations, and ability to establish on sand, mud, heavy clays, and in bogs (Duncan and Carrow 2000; Graeme and Kendal 2001). Mangrove destruction (creating open areas) coupled with changes in the hydrologic regime (decreasing salinities to below 30‰) favored rapid *P. vaginatum* establishment and spread in the Ivory Coast (Paradis 1989). Similar anthropogenic habitat alterations may help explain *P. vaginatum* population explosion in SIW close to the village; however, it is also possible to observe large *P. vaginatum* populations growing in less disturbed areas. The leading edge of the invasion is advancing up to 56cm/month in fresh lagoons (Appendix I) into the Galápagos National Park, growing along shorelines and forming large mats that cover small bays or entire small lagoons. The precise *P. vaginatum* distribution has not been mapped, but can be categorized as very abundant. During my 2002 visit, it occupied approximately 40% of SIW shoreline within 1 mile of the village Puerto Villamil.

### *Invertebrate study design*

My invertebrate study asked whether invasion of *P. vaginatum* would affect aquatic invertebrate communities. I selected an area in Baltazar lagoon with an invasion front stretching from mangroves to open water. I first confirmed that this site lacked detectable environmental gradients (such as depth) that could affect aquatic invertebrate distributions. I then divided the area into 4 distinct zones (1) open water, (2) *P. vaginatum*, (3) the transition area between water and *P. vaginatum* (“edge”) and (4) mangroves (*C. erectus*).

I established a 14 x 7 m sampling grid that encompassed all lagoon habitat zones and incorporated the leading edge of the *P. vaginatum* invasion both along the shoreline into the mangrove and out toward the center of the lagoon (Figure 2.1). The grid consisted of 7 parallel transects 2 m apart with 10 sampling points 50cm apart on each transect (Figure 2.1). The close proximity of the sampling points allowed me to detect changes in invertebrate communities despite potential spatial heterogeneity in invertebrate populations.

At each sampling point, I measured water temperature and dissolved oxygen with a YSI 550 DO and Temperature probe (YSI Corporation, OH), salinity with a hydrometer (SeaTest, Marine Depot, Anaheim, CA), pH with paper indicator strips, and total lagoon depth with a 3 m PVC pipe marked in 1cm increments. I visually estimated *P. vaginatum* percent cover within the 15 cm diameter area encompassed by the core sampler (see below for a description of the corer) and measured its height above the water. I multiplied % cover and height to determine *P. vaginatum* volume at each sampling point. Similarly, I determined the volume of the mangrove vegetation above each sampling point by multiplying mangrove % vertical cover by its

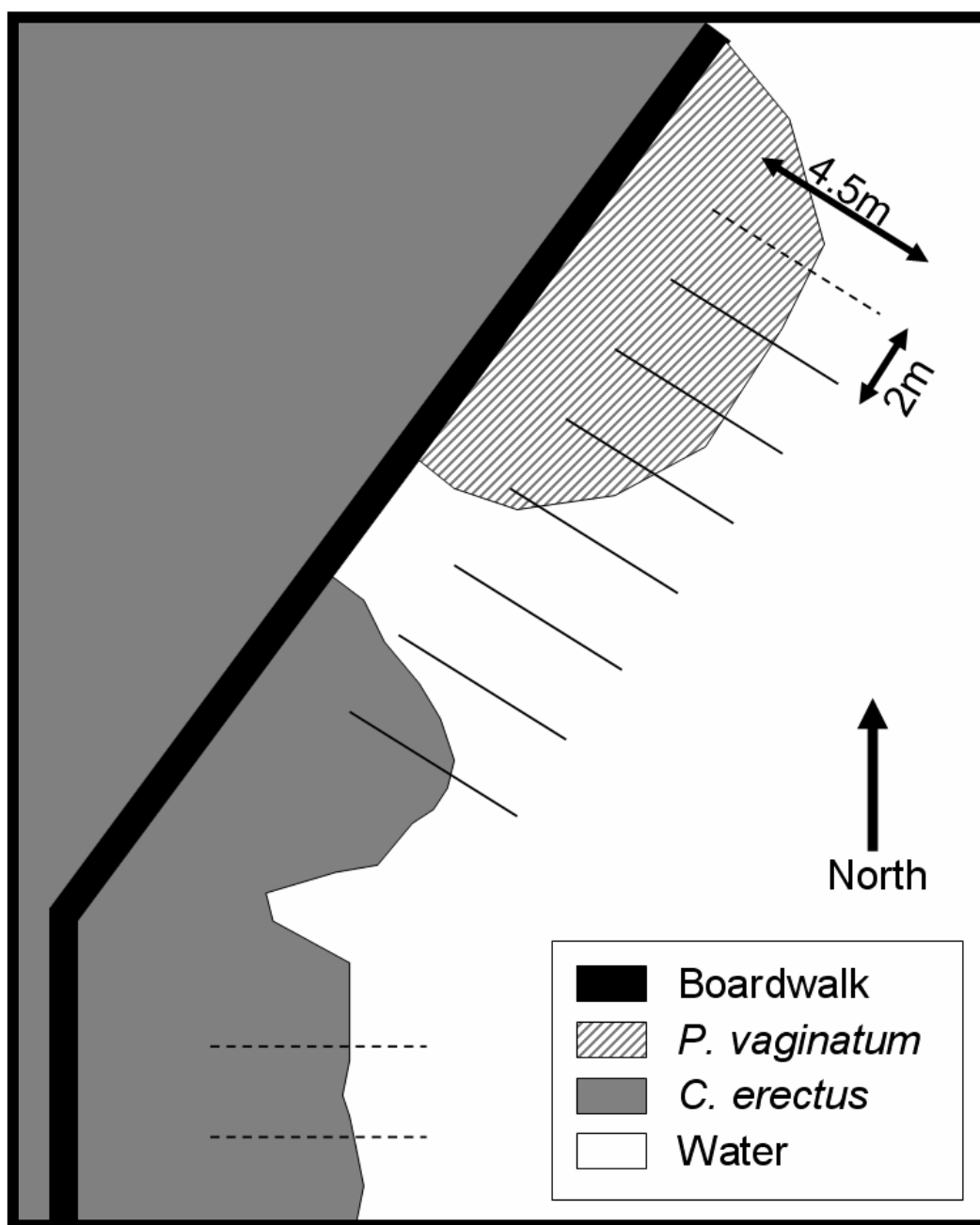


Figure 2.1. – Invertebrate Sampling Grid Design. Lines represent transects; dashed lines are transects added in January 2003. There are 10 sample points (50 cm apart) along each transect.

height. I visually estimated mangrove % vertical cover as the % of area occupied by mangrove vegetation above the water (in 10 categories 0-10 %, 11-20 % etc.). I determined mangrove and *P. vaginatum* height with the 3 m PVC pipe marked in 1 cm increments. I sampled aquatic invertebrates by taking cores of the substrate at each sampling location. I used a 50 cm long, 15 cm diameter PVC tube to take the cores. Initial trials confirmed that the corer forms a seal in the mucky sediment thus preventing any influx of water as the contents were removed. I removed core contents by scooping the water and mud out with a small cup and pulling vegetation out by hand. To facilitate core extraction in the *P. vaginatum* and to insure I only removed vegetation originating from inside the core, I cut rhizomes along the inside edge of the corer using hand clippers and a machete. I accessed open water sample points with a canoe to avoid disturbing the sediment at the sample locations. I accessed the mangrove habitat by walking along a wooden plank supported by the above-water mangrove branches. After sample removal, I measured its volume to the nearest 50 ml using a graduated cylinder and transported the samples to the Charles Darwin Foundation Laboratory for immediate sorting. Minimizing invertebrate mortality through refrigeration was not feasible due to limited laboratory facilities; therefore, a maximum of 10 samples were taken each day to reduce processing times and hence insect mortality.

I sampled both in July 2002 and January 2003 to incorporate potential temporal variations in invertebrate communities. Also, in order to attain a more even representation from each habitat type, I added three transects in January 2003, one transect in *P. vaginatum* and two in *C. erectus* (Figure 2.1). Destructive sampling in the *P. vaginatum* necessitated shifting transects by 20cm (parallel to the shoreline) in January. I sampled between the times 10:00 and 14:00 each day to avoid errors due to potential diurnal variations in the distribution of invertebrates. For both sample dates, I needed at least 12 days to complete sampling the entire grid.

I hand sorted samples using soft forceps or a pipette to remove larger (>5 mm) specimens. I included the small (<5 mm) and very abundant ostracods in this study by sub-sampling volumetrically. I sub-sampled by filtering (mesh size  $\leq 0.1$  mm) and preserving contents of 1/10 of each sample. I preserved all specimens and subsamples in 70 % Ethyl Alcohol on the Galápagos and transported them to Cornell University for identification and quantification. Species were separated into morphospecies before identifying to the lowest taxonomic level possible using a dissection microscope. I identified Ostracoda and Polychaeta to Order, Syrphidae and Chironomidae to Family, *Tabanis* (Tabanidae) and *Paraplea* (Pleidae) to genus, and *Enochrus waterhousei* (Hydrophilidae) and *Trichocorixa reticulata* (Corixidae) to species.

I determined invertebrate biomass by drying samples (sorted according to morphospecies and sample origin) at 50 °C until constant weight and measure their mass on a scale accurate to 0.0001 g (Model BP211D, Sartorius Corporation, NY). I predicted ostracod biomass/sample from the following regression relationship:

$$\text{Log}_{10} \text{ ostracod biomass} = -4.39 + 0.892 (\text{Log}_{10} \text{ ostracod abundance})$$

I found this relationship by weighing duplicates of 41, 48, 79, 110, 202, 300, 500, 810, and 1000 ostracods, and one collection each of 1490, 1778, and 2280 ostracods. The 95% confident interval of the predicted biomass is  $\pm 0.003$  g.

### *Invertebrate study - statistical analysis*

I performed a two-way ANOVA to evaluate seasonal and habitat (fixed factors) differences in invertebrate species richness, density (no/L), and average biomass (g/L). Differences in abiotic variables across sampling dates were compared using t-tests or Kruskal Wallance non-parametric tests. I performed a discriminant function analysis to determine which variables significantly discriminate between habitats. For this analysis, I classified samples according to whether they belonged to *P. vaginatum* habitat (80 – 100 % *P. vaginatum* cover), the edge (the area of transition between *P. vaginatum* and water, 20 – 80 % *P. vaginatum* cover), water (no *P. vaginatum* and no mangrove), or mangrove habitat. In order to relate invertebrate community composition to habitat, I used a canonical correspondence analysis. Canonical correspondence analysis (CCA) is a multivariate technique useful for relating community composition to known habitat variation in the environment (ter Braak 1986). For this analysis, I used relative invertebrate biomass of morphospecies sufficiently abundant (> 10 individuals) or large (> than 5 mm) to influence relative biomass and discern between habitats. Invertebrate groups analyzed were Ostracoda, Corixidae, Hydrophilidae larvae, Hydrophilidae adult, Mesoveliidae, Pleidae, Chironomidae, Syphridae, Polychatae, and Tabanidae. Analyses were conducted in Statistica version 6.0 (© 2002, StatSoft, Tulsa, OK).

### *Bird observation study sites*

I conducted bird observations at 17 sites within 5 SIW lagoons (Las Diablas, Puerto de Jeli, Baltazar, and Salinas) (Figure 2.2). I selected each site in order to maximize the amount of lagoon habitat observable while minimizing redundancy. I

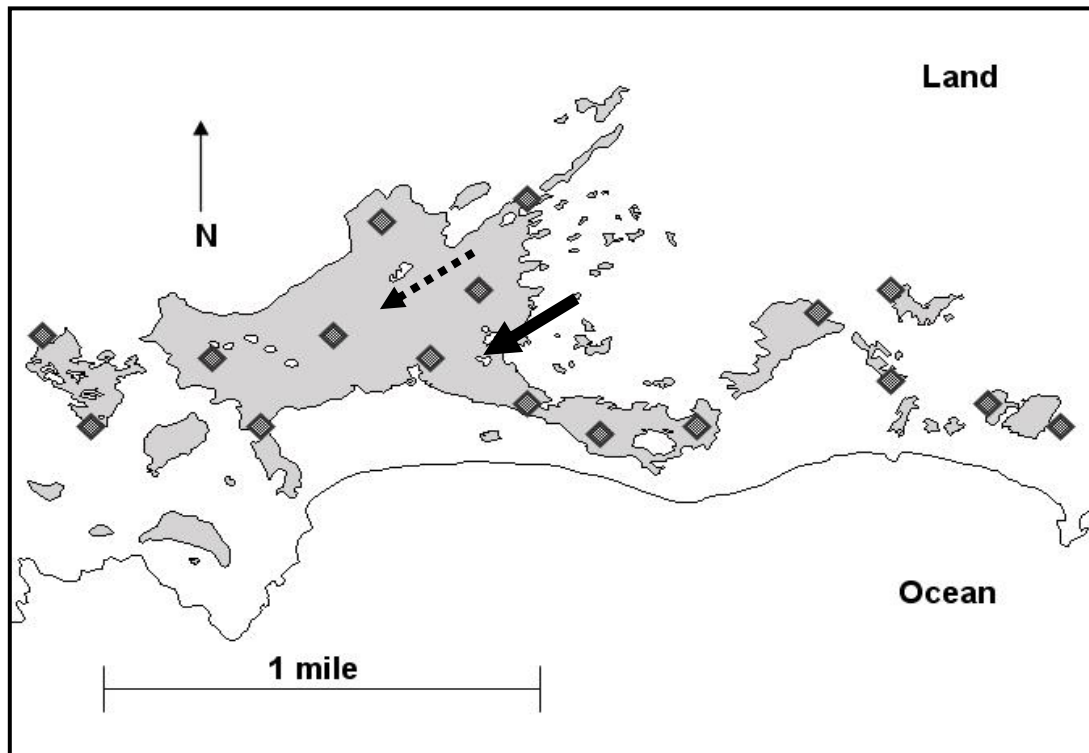


Figure 2.2 Map of Southern Isabela wetlands (lagoons are shaded areas) showing bird observation sites (diamonds). Thick arrow indicates flamingo colony. Dashed arrow indicates cattle egret colony.

limited my observations to habitats already invaded or likely to be invaded by *P. vaginatum* (open water, mangrove, *P. vaginatum*, and mud).

#### *Bird observation study species*

The Galápagos flamingo (*Phoenicopterus ruber glyphorhynchus*) is considered an endemic subspecies with a population of approximately 500 individuals (juveniles and adults) (Vargas 1989). Flamingos feed by passing their heads through water and filtering aquatic invertebrates with their specialized beaks (Sosa 1985; Baldassarre et al. 2000). On the Galapagos their diet likely consists primarily of corixids, ostracods, and copepods. Estimates of breeding pairs is useful for assessing extinction risk (Jones and Diamond 1976), but this data is not available for the Galápagos flamingo population as distinguishing breeding from non-breeding birds is impossible using physical characteristics alone. Based on a study done by Meninger et. al (1995), Wetlands International suggests multiplying waterbird population sizes by 1/3 to estimate number of breeding pairs (Meininger et al. 1995; Wetlands International 2002). This estimation method suggests the Galapagos population may have as few as 166 breeding pairs. Although at least 25% of the flamingos reside in the SIW; inter-island migration suggests that a larger proportion of the population may depend on the SIW as food resources become seasonally abundant (Vargas 1989).

The white checked pintail duck (*Anas bahaensis galapagensis*) is also an endemic subspecies and occurs in all inland water bodies on the Galápagos Islands. Although their population was estimated in 1988 to be 1099 individuations, they are known to experience dramatic losses when their preferred foraging ground (small shallow lagoons) dry up. This substantial fluctuation in population sizes demonstrates sensitivity to environmental stochasticity (Vargas 1989). Pintail ducks nest very close to lagoon shorelines and lay as many as 10 eggs. While there is no information

regarding the specific diet of the Galápagos white cheeked pintail, it is possible that, as dabbling ducks, they eat shoreline vegetation such as *P. vaginatum*. However, Sosa (1985) notes that they appear to be filter feeding at the deepest part of lagoons and away from the shore-line. Therefore, it is very likely that they consume the corixids, ostracods, and copepods present in these deeper waters since they are generalist surface feeders (De Gonzo and Mosqueira 1996).

#### *Bird observation study design*

I observed birds at each site on three separate occasions (July 7<sup>th</sup>, July 14<sup>th</sup>, and August 2<sup>nd</sup>, 2002) and at different times (morning, noon, and evening) in order to reduce bias associated with daily variations in bird behavior. I observed for 5 minutes at each site and made a concerted effort to remain completely silent and still to minimize my interference with bird location and behavior. I used 42mm objective binoculars for identification when necessary, noting species and location of all birds visible from each vantage point. I classified a bird as associated with shoreline habitat (not open water) if it was located within 5 m of the shore or if it was actually on the shore. I conducted snap-shot observations; that is, I did not record any changes in an individual bird's behavior after the initial encounter.

#### *Bird observation statistical analysis*

I normalized the frequency of bird observations in each habitat by dividing each bird frequency/habitat by the proportion of actual habitat available: *P. vaginatum*, 10 %; Mangrove, 25 %; mud, 5 %; and water, 60 %. I measured the proportions of shoreline habitat available using Geographic Information Systems maps displayed in ArcView. I used a chi-squared goodness of fit test to test the null hypothesis that an

equal proportion of birds occurred in each habitat according to habitat availability. I evaluated white cheeked pintail ducks, flamingos, and gallinules (*Gallinula chloropus*) habitat association separately as they were very abundant. I assigned the remaining birds according to either “migratory” or “heron/egret” category for the data analysis. Cattle egrets (*Bubulcus ibis*), great white egrets (*Ardea alba*), lava herons (*Butorides sundevalli*), striated herons (*Butorides striatus*), and blue herons (*Ardea herodias*) were assigned to the “heron/egret” category. Black-necked stilts (*Himantopus mexicanus*), whimbrels (*Numenius phaeopus*), and semipalmated plovers (*Charadrius semipalmatus*) were assigned to the “migratory” category.

#### *Assessment of P. vaginatum impact*

I created an impact assessment table to systematically evaluate the potential impact of *P. vaginatum* on bird feeding habitat, feeding mechanism, and food resources. This impact assessment table assimilates invertebrate and bird observation data from this study and information from the following literature: (Soothill and Soothill 1982; Schneider 1983; Zwarts and Blomert 1990; Mercier and McNeil 1994; Castro and Phillips 1996; Williams 1996; Zwarts 1996; Stinson et al. 1997; Ntiamoa-Baidu et al. 1998; Baldassarre et al. 2000; U.S. Fish and Wildlife Service 2002; Ribeiro et al. 2004; U.S. Fish and Wildlife Service 2004; Sánchez-Zapata et al. 2005). Impact (positive +, negative -, or neutral 0) assumes highly dense *P. vaginatum* and is evaluated separately for each feeding attribute (habitat, mechanism, and resources). Food resources only include items known to occur in lagoons and is categorized in general terms (as found in the literature) as well as for the specific invertebrates found in this study. Evaluation of impact on food resources is in reference only to open water (not muddy shoreline) habitat since there is no information on the relative abundance, species richness, or biomass of invertebrates in SIW muddy shore habitat.

Although the focus of this assessment is to evaluate potential impacts of *P. vaginatum* on the more sensitive flamingo and white checked pintail duck populations, other birds present in the observation study as well as those known to access the lagoon habitat and possibly interact with *P. vaginatum* are included in the table. To simplify interpretation, only the more abundant birds were analyzed individually (flamingo, white checked pintail duck, and the gallinule), while less abundant birds were grouped into categories known to have similar attributes (terrestrial, migratory, and herons and egrets). Terrestrial birds include yellow warblers (*Dedroicia petechia*), smooth billed ani (*Crotophaga ani*), warbler finch (*Certhidea olivacea*), and mockingbird (*Nesomimus parvulus*). The herons and egrets are: yellow-crowned night heron (*Nycticorax violaceus*) cattle egret (*Bubulcus ibis*), great blue heron (*Ardea herodias*), great white heron (*Ardea alba*), endemic lava heron (*Butorides sundevalli*), and the striated heron (*Butorides striatus*). Migratory birds include: black-necked stilt (*Himantopus mexicanus*), semipalmated plover (*Charadrius semipalmatus*), lesser yellowleg (*Tringa flavipes*), red-necked phalarope (*Phalaropus lobatus*), Wilson's Phalarope (*Phalaropus tricolor*), red phalarope (*Phalaropus fulicarius*), and whimbrel (*Numenius phaeopus*).

#### *Assessment of P. vaginatum potential spread*

In order to better understand the potential future threat posed by *P. vaginatum*, I calculated its maximum potential spread based on my own data describing *P. vaginatum* behavior in the SIW. Spread of *P. vaginatum* is limited primarily by water depth and salinity; I observed *P. vaginatum* growing in depths up to 111 cm, and at salinity levels of 50 ppt. Therefore, I calculated maximum potential % habitat covered by *P. vaginatum* by assuming that *P. vaginatum* has the potential to invade lagoons with a max depth  $\leq 1$  m and average salinity levels  $\leq 50$  ppt. Only lagoons Tercer and

Cuarta Playa lacked salinity and bathometric data in which case I assumed similar parameters as nearby Quinta Playa lagoon. I used lagoon data reported by Vargas (1989), Gelin and Gravez (2002), and those which I collected.

## RESULTS

### *Invertebrate study habitat characteristics*

Season appeared to have minimal impact on the variation in abiotic conditions across habitat. A significant increase in water depth (15 %;  $t = -3.87$ ,  $p < 0.0001$ ) and water temperature (9 %;  $t = -5.54$ ,  $p < 0.0001$ ) occurred in all habitats (Table 2.1). On both sampling dates, *P. vaginatum* habitat was characterized by lower (44.7 %) water temperatures compared to other habitats and anoxic conditions (Table 2.1). Also, the *P. vaginatum* habitat had 1/58<sup>th</sup> the above ground vegetation volume as the mangrove habitat (Table 2.1) and, although not measured quantitatively, a notably larger fraction of the sample was sediment. Water and mangrove were characterized by high dissolved oxygen (mg/L), especially in January where dissolved oxygen increased 36 % in the water to supersaturated levels (Table 2.1). The grass-water edge habitat characteristics were intermediate in all abiotic values as compared to the open water and grass habitats (Table 2.1). Salinity ( $12.8 \pm 0.12$  ppt [over all mean  $\pm$  SE]) and pH ( $8.7 \pm 0.04$  [over all mean  $\pm$  SE]) were not statistically different across season (pH:  $t = 1.86$ ;  $p = 0.064$ . Salinity:  $t = 0.924$ ;  $p = 0.35$ ) or habitat (pH:  $F_{3,166} = .146$ ,  $p = .93$ , Salinity:  $F_{3,166} = .376$ ,  $p = .77$ ).

Because abiotic variables were similar between seasons, I did not distinguish between seasons in my discriminant and canonical analyses. All abiotic habitat

Table 2.1. Abiotic habitat characteristics of different habitats in July 2002 and January 2003. Data are means [ $\pm$ SE].



Table 2.2 Results of Discriminant and Canonical analysis of abiotic habitat characteristics.



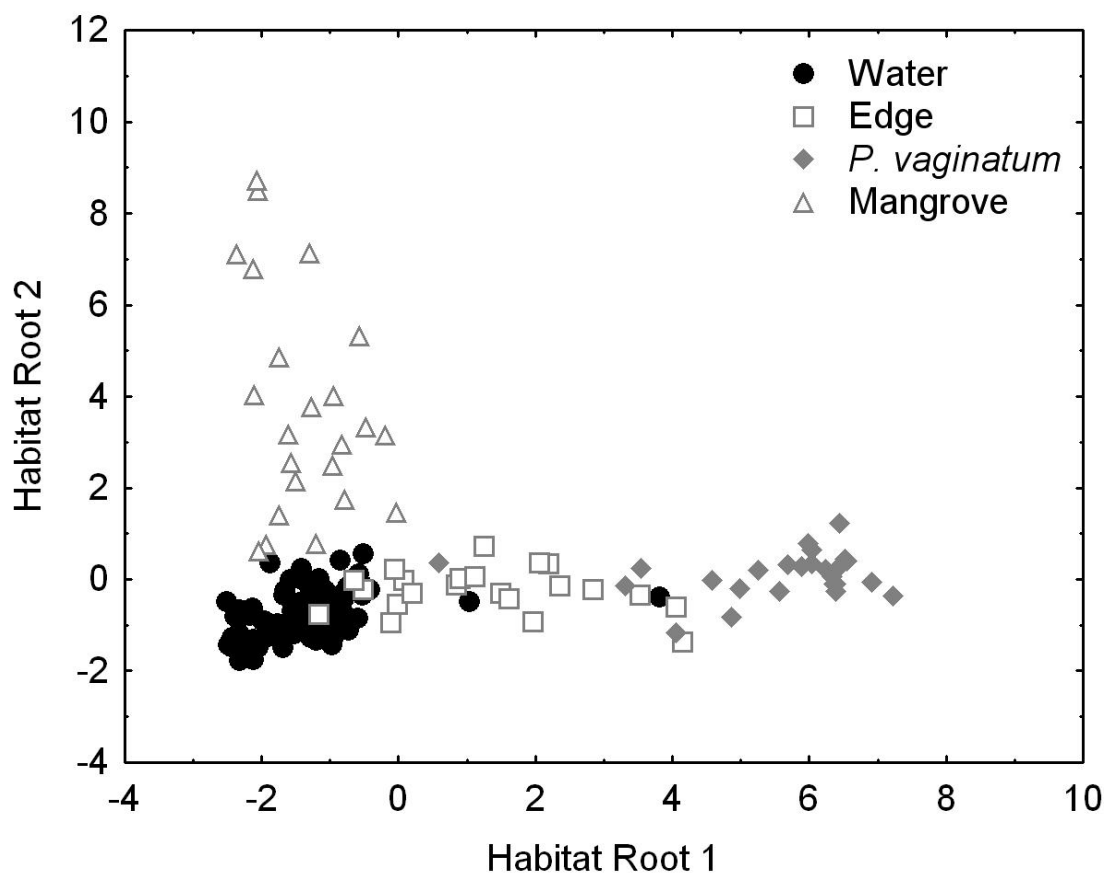


Figure 2.3. Abiotic habitat characteristic canonical root 1 scores plotted against root 2 scores. Habitat root 1 scores clearly discriminate between Water, Edge, and *P. vaginatum* habitats. Habitat root 2 scores discriminates between Mangrove and Water habitats.

variables significantly discriminated between habitats (Table 2.2). The canonical analysis yielded three significant roots, the first two of which clearly separated my four habitat-types based on dissolved oxygen levels and amounts of open water and vegetation (Table 2.2). The first root explained 69 % of the variation in habitat variables ( $X^2 = 548$ ,  $P < 0.001$ ; Table 2.2) and clearly distinguished between grass, grass edge, and open water and mangrove habitats (Figure 2.3). This transition from grass to water is explained primarily by percent water cover and dissolved oxygen (Table 2.2) (factor structure correlation coefficient of 0.85 and 0.42, respectively). The second root explains 28 % of the variation in abiotic habitat variables ( $X^2 = 232$ ,  $P < 0.001$ ; Table 2.2) and separated mangrove habitat from the other three habitats (Figure 2.3). Vegetation volume, which was significantly greater within the mangrove habitat, was the factor contributing most to variation along this axis (factor structure correlation coefficient of 0.87). The third root explained only 3 % of the variation ( $X^2 = 32$ ,  $P < 0.001$ ; Table 2.2) and distinguished slightly between more vegetated and more open-water habitats.

#### *Invertebrate study community characteristics*

I identified 31 distinct morphotypes representing 11 orders, at least 19 families and 19 genera (Table 2.3). These are conservative estimates since I could not further resolve Ostracoda and Chironomidae. Ostracoda represented 97% of the 126,671 individuals encountered. *Trichocorixa reticulata* (Family Corixidae) represented 2 % and the remaining 1 % of invertebrates were dominated by water scavenger beetles, *Enochrus waterhousei* (Family: Hydrophilidae), and chironomid larvae (Table 2.3). Ostracoda and *T. reticulata* accounted for 71.1% and 12.8% of total invertebrate biomass and one individual weighed on average 0.02 mg and 0.16 mg, respectively.

Table 2.3. Summary of invertebrate morphotypes abundances organized by season and habitat.

Taxonomic determination		Season (N)		Habitat (N)					
Taxon			July 2002 (70)	Jan 2003 (100)	<i>P. vaginatum</i> (25)	Edge (22)	Water (100)	Mangrove (23)	Total (170)
Ostracoda*		w	57067	66475	4087	19614	83180	16661	123542
Hemiptera		w							
Corixidae ( <i>Trichocorixa reticulata</i> )		w	945	1769	45	285	2187	179	2696
Mesoveliidae ( <i>mesovelia hambletoni</i> or <i>amenoena</i> )		w	6	15	7	3	8	3	21
Pleidae ( <i>Paraplea puella</i> (?))		w	30	9	19	17	1	2	39
UK1		w		2	2				2
UK2		w	1	1	2				2
Coleoptera		w							
Hydrophilidae		w							
Enochrus waterhousei		w	70	24	63	30	1	1	95
Enochrus waterhousei (larvae)		?	3	76	68	11			79
Dytiscidae ( <i>Thermonectes</i> (?) <i>basilaris galapagoensis</i> (?))		w		1	1				1
Hydraenidae ( <i>Ochthebius</i> sp. **)		w	5	4	4	3	2		9
Staphylinidae (?)		w		1	1				1

Table 2.3. (Continued)

Taxonomic determination		Season (N)		Habitat (N)				
Taxon		July 2002 (70)	Jan 2003 (100)	<i>P. vaginatum</i> (25)	Edge (22)	Water (100)	Mangrove (23)	Total (170)
<b>Dipteran larvae</b>								
<b>Chironomidae*</b>								
<b>Syrphidae (<i>Eristalis</i> sp. (?))</b>								
<b>Tabanidae (<i>Tabinus</i> sp.)</b>								
UK1	s	7	2	8		1		9
UK2	s/w	3	3	4		1	1	6
	s/w	1	6	1	1		5	7
<b>Culicidae</b>								
<i>Culex quinque-fasciatus</i> (?)	w		1	1				1
UK1	w		1				1	1
UK2	w		1				1	1
<b>Odonata (larvae)</b>								
<i>Coenagrionidae (Ishnura hasata)</i>	w	3		1	2			3
<i>Libellulidae</i>	w	1		1				1

Table 2.3 (Continued)

Taxonomic determination		Season (N)		Habitat (N)				
Taxon		July 2002 (70)	Jan 2003 (100)	<i>P. vaginatum</i> (25)	Edge (22)	Water (100)	Mangrove (23)	Total (170)
<i>Araneae</i>								
	UK1	w	3	2			1	3
	UK2	w	1	1				1
	UK3	w	1		1			1
	UK4	w	1			1		1
	UK5	w	1		1			1
<i>Hymenoptera</i>								
	UK1	w	3	1	1		1	3
	UK2	w	3			2	1	3
	UK3	w	2	1	1	1		3
<b><i>Polychaeta (Neridae ??)</i></b>								
		s	1	25	1			26
<i>Isopoda</i>		s	2	2				2
<i>Foraminifera (?)</i>		s	7			4	3	7
<b>Total</b>		<b>58154</b>	<b>68587</b>	<b>4365</b>	<b>20008</b>	<b>85436</b>	<b>16916</b>	<b>126725</b>
<b>Average</b>		<b>831</b>	<b>980</b>	<b>62</b>	<b>286</b>	<b>1221</b>	<b>242</b>	<b>1810</b>

\* : not identified to morphospecies (number of species within category unknown)

UK: indicates distinct morphotypes within a category

**Bolded ID** : morphotype used in statistical analysis

Larval specimens are indicated as such, all others are either adult or nymphs.

(N): number of samples

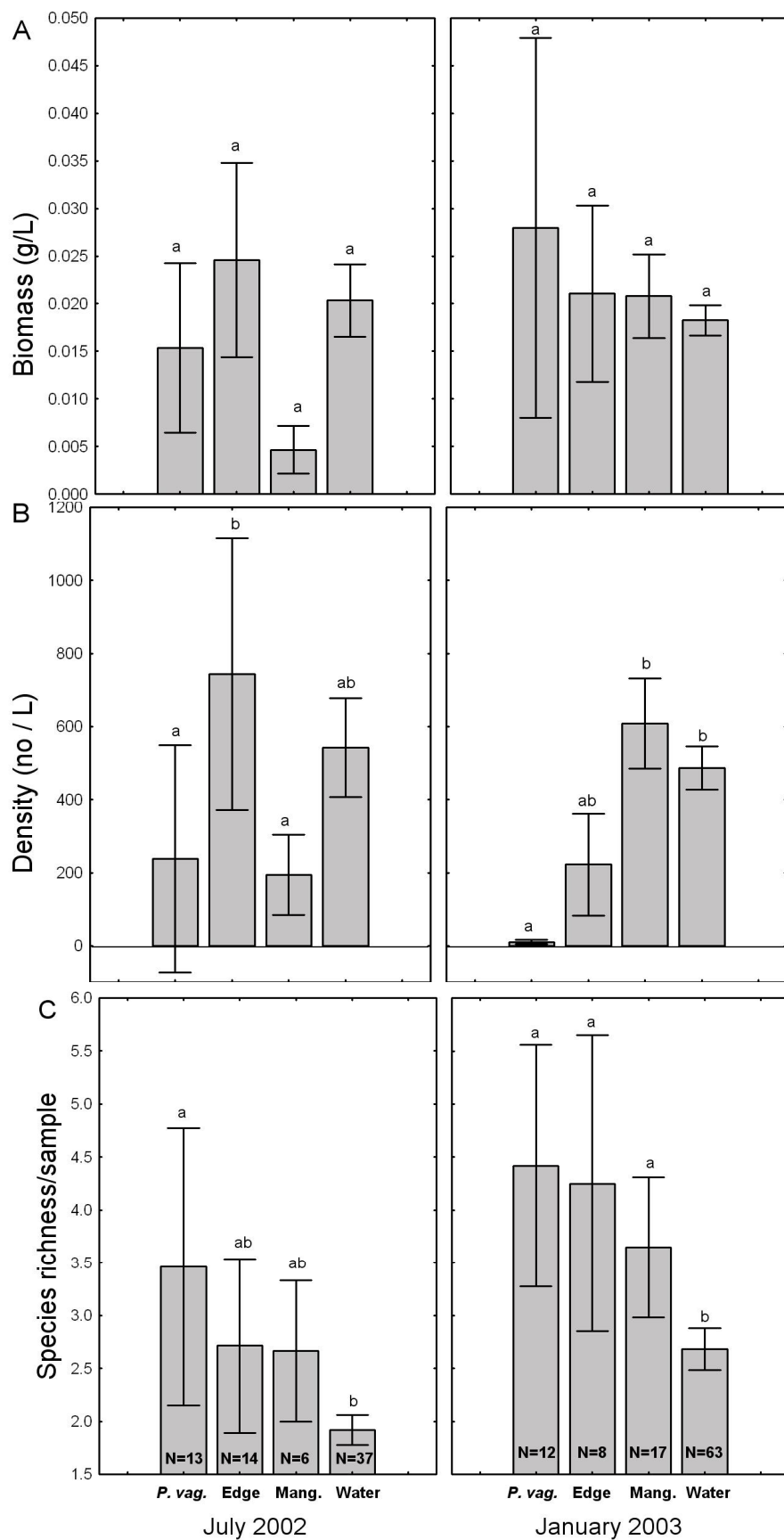
(?): unsure about ID at this level

\*\* : Endemic

s : found in sediment fraction of the sample

w : found in water fraction of the sample

Figure 2.4: Invertebrate biomass (A), density, (B), and species richness (C) grouped by habitat and by season. Data are means ( $\pm 2SE$ ). Different lower case letters above columns depict significant differences using Tukeys Adjusted differences across habitats within season.



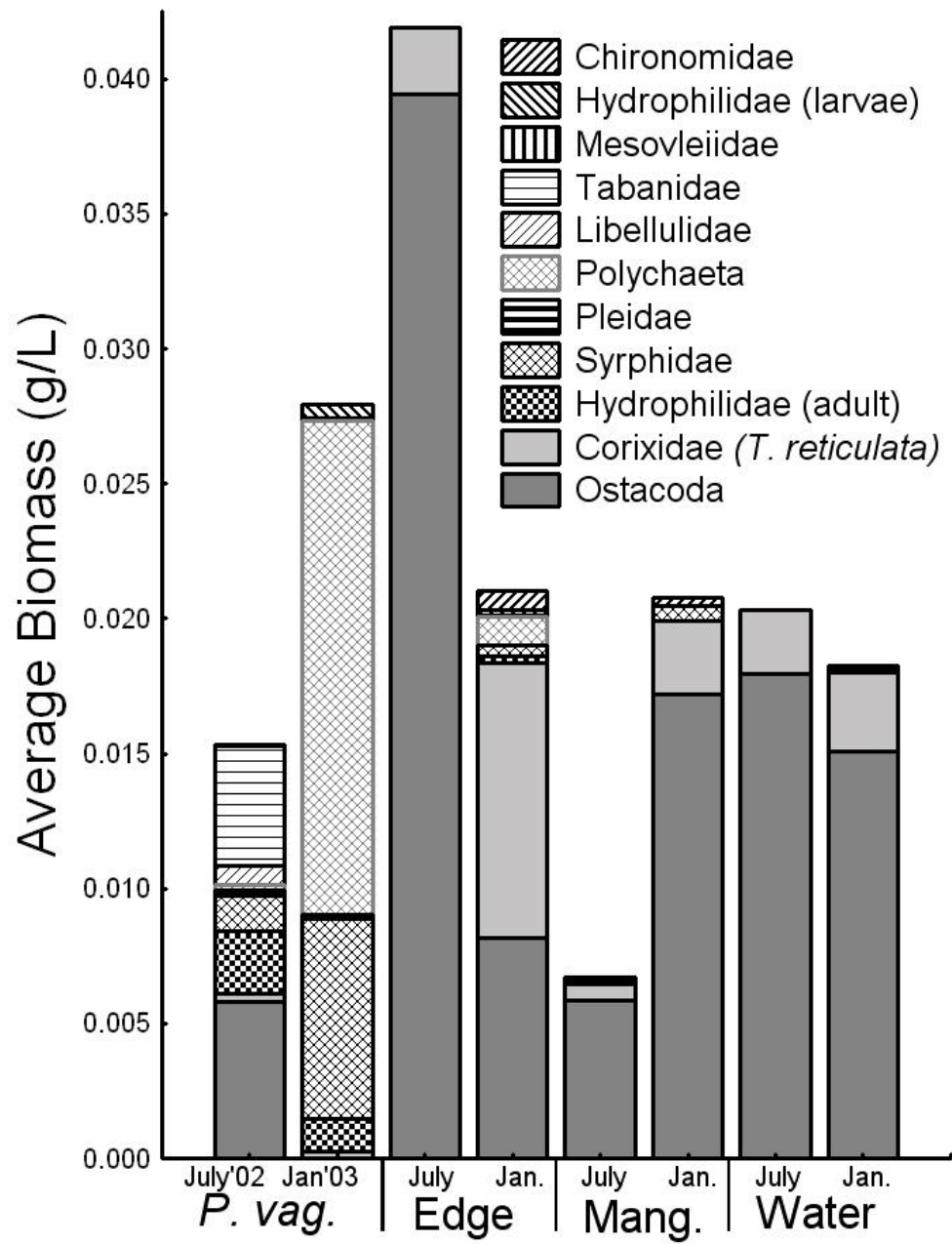


Figure 2.5. Composition of average invertebrate biomass (g/L) in each habitat by season.

The remaining biomass consisted primarily of Polychaetes (6.9%, average weight: 8.89 mg) and Syrphid larvae (3.6% average weight: 5.17 mg).

I found no seasonal differences in total invertebrate biomass (summed across habitats) ( $F_{1,162} = 0.06$ ,  $P=0.8069$ ), nor was there a significant Habitat X Season interaction ( $F_{3,162} = 0.56$ ,  $P=0.6427$ ). Tukeys–adjusted pair-wise comparisons revealed no significant differences in biomass between habitats within each year (Figure 2.4 A). However, the relative contribution of species comprising the total biomass changed substantially across season (Figure 2.5). In January 2003, there was a large increase in average polychaete (55 fold) and chironomidae (54 fold) biomass, whereas tabanid larval average biomass dropped by  $1/12^{\text{th}}$ , hydrophilid adults by  $1/5^{\text{th}}$ , and pleidae by  $1/5^{\text{th}}$  as compared to July 2002 (Table 2.3).

Although overall invertebrate density (no/L) did not change substantially from July 2002 to January 2003 ( $F_{1,162} = 1.75$ ,  $P=.188$ ), significant variation in density across habitats ( $F_{3,161} = 8.46$ ,  $P<0.0001$ , Figure 2.4 B) depended on season (Habitat X Season:  $F_{3,162} = 5.78$   $P=0.0009$ ). The *P. vaginatum* habitat had substantially lower density than water habitat in both seasons; in January 2003, it had the lowest invertebrate density of all habitats (Figure 2.4 B).

Morphospecies diversity (species richness) was significantly higher in January 2003 (31) compared to July 2002 (16) ( $F_{1,162}=18.88$ ,  $P <.0001$ , Table 2.3) and this increase was uniform across habitat types (Habitat X Season =  $F_{3,162}=0.55$ ,  $P=0.647$ , Figure 2.4 C). Species richness did vary across habitat ( $F_{3,162} = 14.77$ ,  $P<0.0001$ ) with edge showing more morphospecies than water in January 2003 and *P. vaginatum* showing more morphospecies than water in both seasons (Figure 2.4 C).

In the discriminant analysis, only Ostracoda and *T. rediculata* abundance was significantly different between habitat type ( $F_{3,157} = 9.91$ ,  $P<0.0001$ ;  $F_{3,57} = 8.36$   $P<0.0001$ , respectively). Canonical analysis of relative biomasses of different invertebrate groups yielded only one significant root that explained 96% of the

Table 2.4 Canonical analysis of relative invertebrate biomass

Canonical Analysis	Root 1	Root 2	Root 3
Eigenvalues	2.630	0.082	0.023
Cumulative proportion of variance explained	0.961	0.992	1.000
Mean root scores			
<i>Ostracoda</i>	-0.837	-0.076	0.564
<i>Trichocorixa</i>	-0.580	-0.549	-0.370
<i>Mesoveliidae</i>	-0.188	-0.263	-0.074
<i>Chironimidae</i>	-0.157	-0.575	0.847
<b><i>Hydrophilidae Larvae</i></b>	<b>0.062</b>	<b>-0.148</b>	<b>-0.268</b>
<b><i>Pleidae</i></b>	<b>0.118</b>	<b>-0.051</b>	<b>0.274</b>
<b>Hydrophilidae adult</b>	<b>0.238</b>	<b>-0.445</b>	<b>0.333</b>
<b>Polychaete</b>	<b>0.262</b>	<b>-0.008</b>	<b>0.128</b>
<b>Syrphidae</b>	<b>0.264</b>	<b>-0.004</b>	<b>0.649</b>
<b>Tabanidae</b>	<b>0.327</b>	<b>0.115</b>	<b>0.134</b>
<i>Italics: Open Water and Mangrove species</i>			
<b><i>Italics and Bold: Edge species</i></b>			
<b>Bold: Grass species</b>			

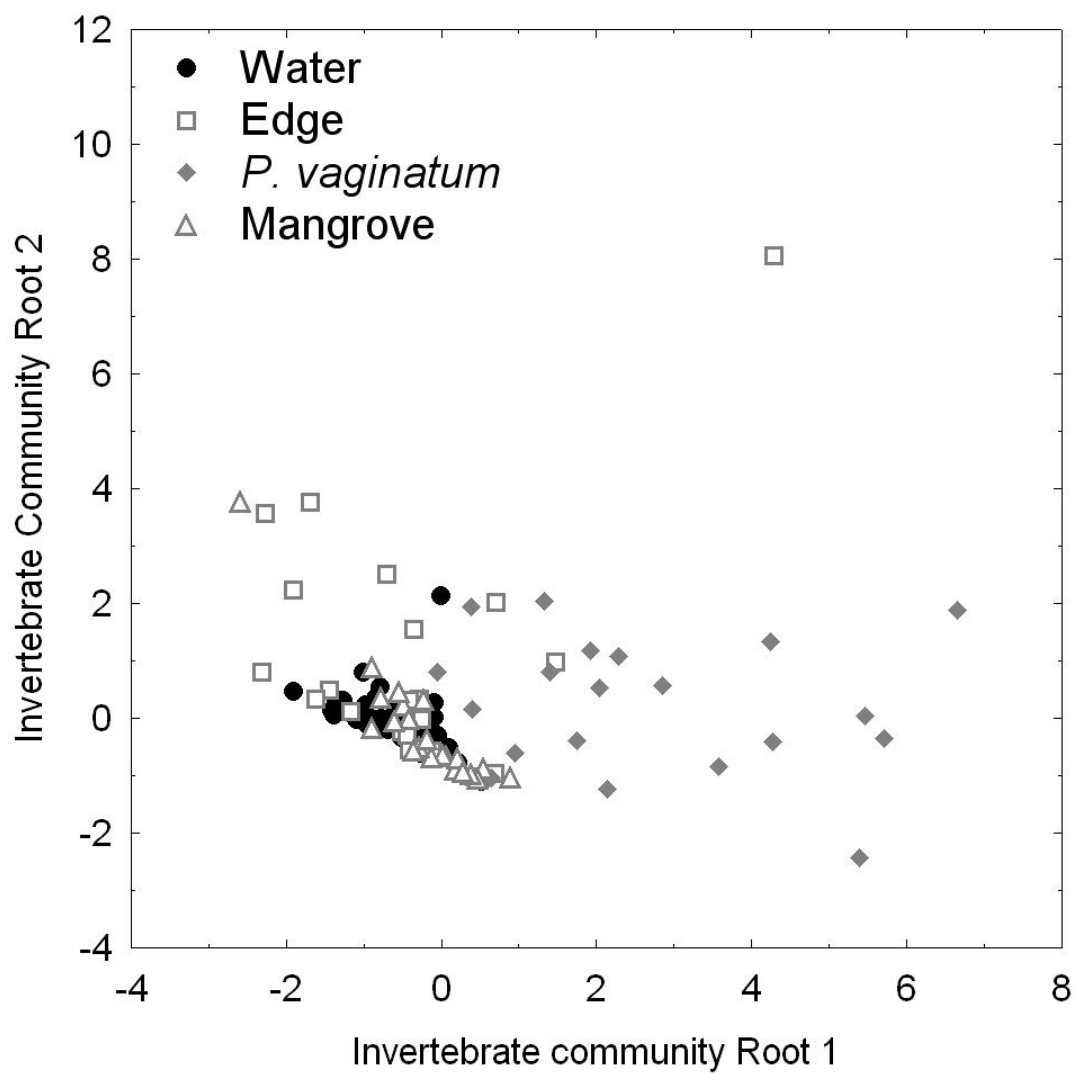


Figure 2.6 Invertebrate community root 1 canonical scores versus root 2 scores. Root 1 score clearly distinguishes invertebrates in *P. vaginatum* from invertebrates in other habitats.

Table 2.5 Means of invertebrate relative biomass canonical variables in each habitat type

Habitat Category	Root 1	Root 2	Root 3
P. vaginatum	3.82	0.09	-0.02
Edge	-0.09	-0.72	0.06
Mangrove	-0.64	0.22	0.35
Water	-0.79	0.09	-0.09

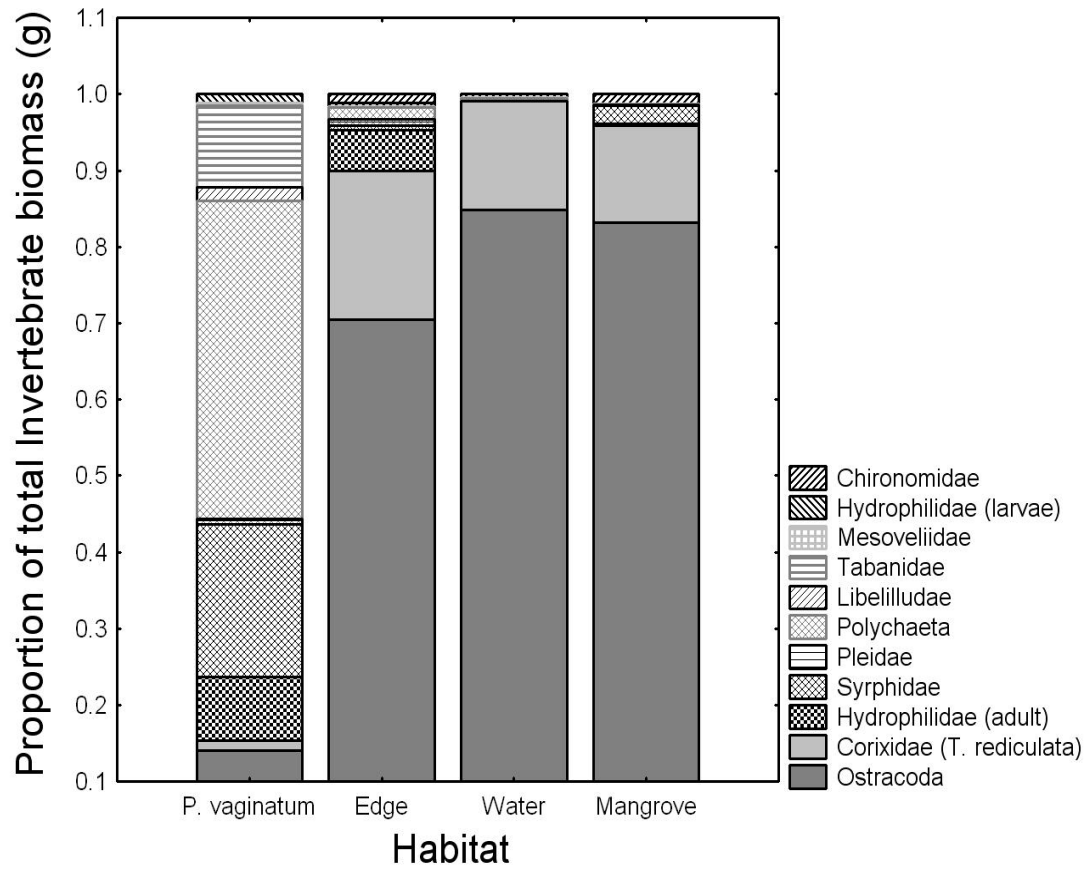


Figure 2.7 Invertebrate biomass composition (% of total) found in each habitat type across all sampling dates.

variation in invertebrate community composition among habitat types ( $X^2 = 225$ ,  $P < 0.001$ ; Table 2.4). The means of relative invertebrate biomass canonical root 1 scores distinguished the invertebrate community in *P. vaginatum* from open water, edge and mangrove habitats (Figure 2.6, Table 2.5). The invertebrate community of the *P. vaginatum* habitat was distinct from other habitats and characterized by lower relative biomass of ostracods, corixids, chironomids and mesoveliids and higher relative biomass of hydrophilid adults, polychaetes, syrphids, and tabanids (Figure 2.7, Table 2.4). Invertebrate communities in the open water and mangrove habitats were not different from each other, and consisted primarily of ostracods and corixids (Figure 2.6, Table 2.4). The edge invertebrate community composition was highly variable and overlapping both the grass and water/mangrove communities (Figure 2.6, Table 2.4). Root 1 scores from both the habitat and invertebrate community canonical analyses were highly correlated ( $r^2 = 0.73$ ,  $p < 0.001$ ; Fig. 2.8), showing a clear relationship between habitat and invertebrate community composition.

#### *Bird observation study*

I observed a total of 457 birds over the three observation days (Table 2.6). I rejected the null hypothesis that birds were distributed equally across all habitats for all bird categories (gallinules  $\chi^2 = 12.4$ ,  $p < 0.01$ ; herons and egrets  $\chi^2 = 15.87$ ,  $p < 0.01$ ; flamingos  $\chi^2 = 91.55$ ,  $p < 0.001$ ; migratory birds  $\chi^2 = 8.06$ ,  $p < 0.05$ ; white cheeked pintails  $\chi^2 = 95.76$ ,  $p < 0.001$ ). I can therefore conclude that all birds associate preferentially with at least one of the habitat categories. Gallinules occurred primarily along mud shoreline (52%) and many occurred in *P. vaginatum* (36%) (Figure 2.9). The only other birds showing a substantial proportion of individuals associated with *P.*

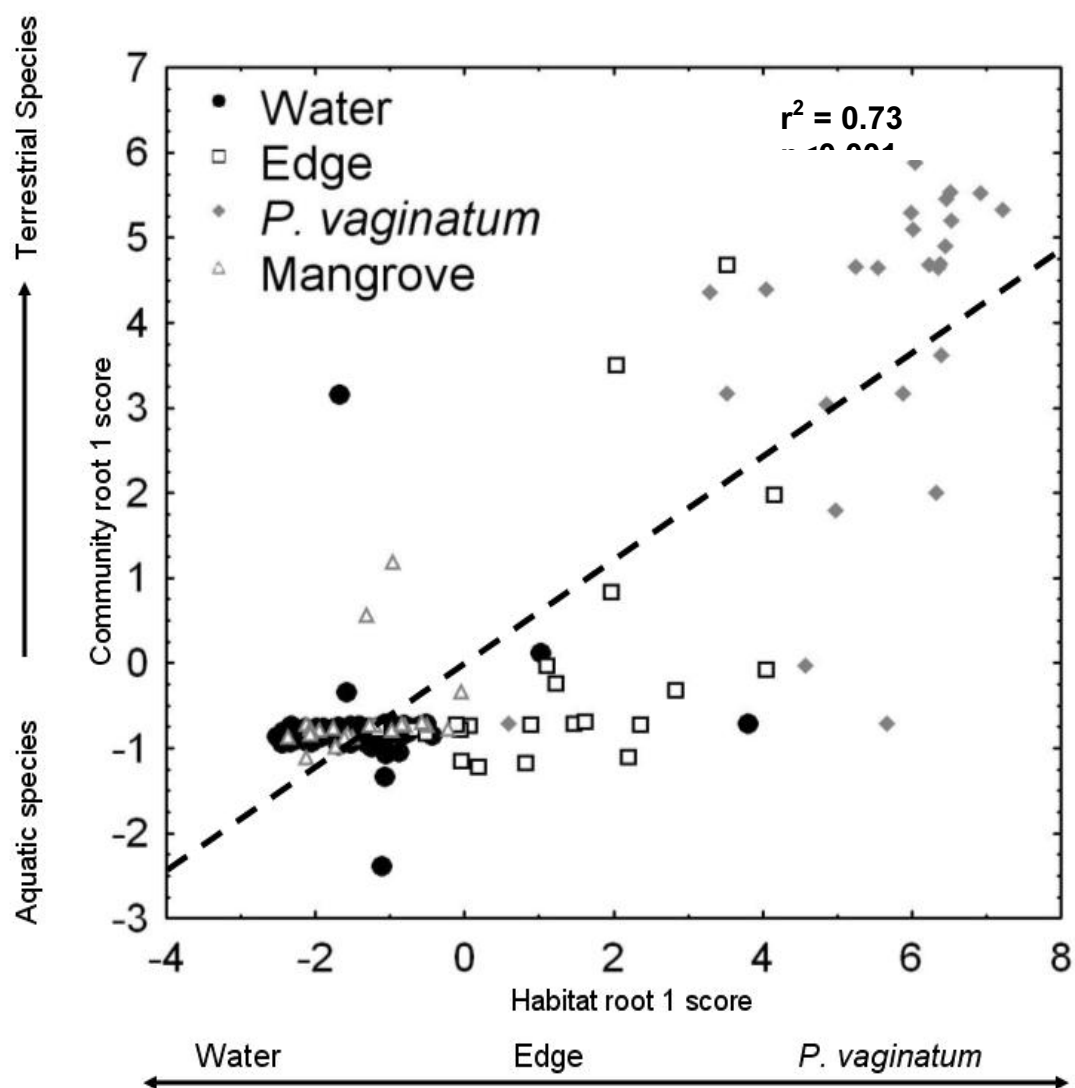


Figure 2.8 Regression of invertebrate community canonical root 1 scores versus habitat canonical root 1 scores. Dashed line shows estimated linear relationship.

Table 2.6 Bird counts by habitat

Bird species	Habitat			
	mangrove	<i>P. vaginatum</i>	mud	water
white cheeked pintail	1	0	14	56
flamingo	116	5	1	86
gallinule	18	34	25	20
black-necked stilt	3	0	3	8
whimbrel	0	2	8	0
semipalmated plover	0	0	7	0
great blue heron	5	2	0	0
yellow-crowned night heron	1	0	0	0
lava heron	1	1	0	0
cattle egret	20	16	0	0
great white egret	2	1	0	0
Total	167	61	58	170
				456

\* Note that relative abundances in this table don't incorporate amount of each habitat available.

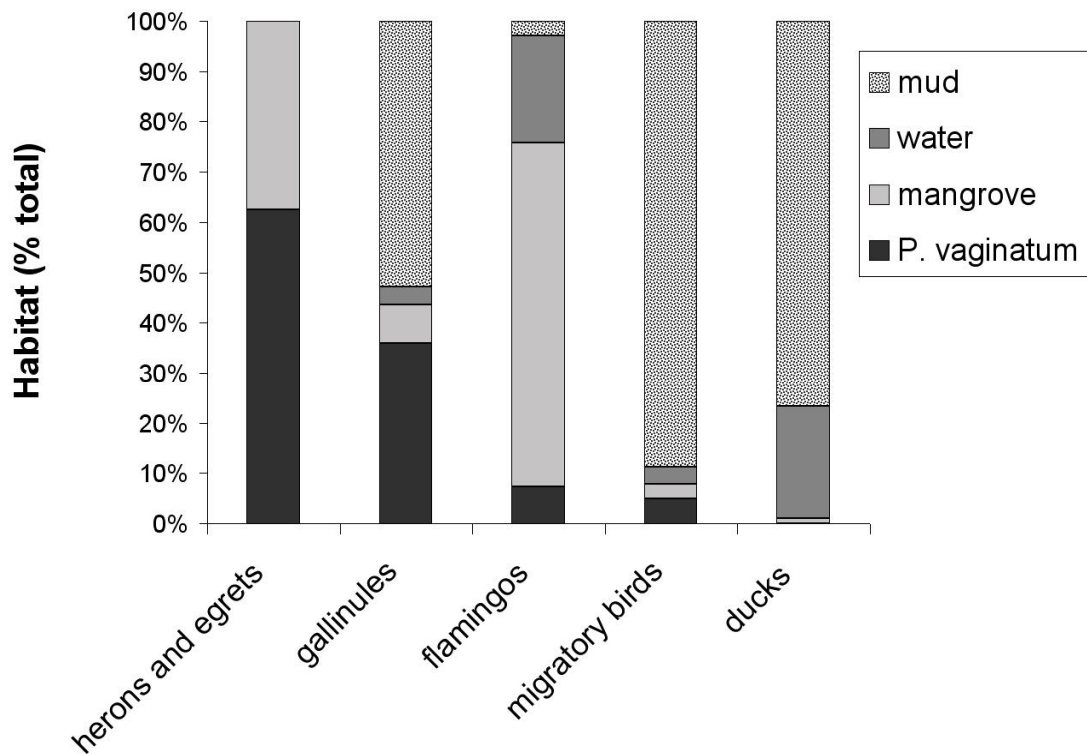


Figure 2.9 Proportion of habitat type (%) associated with bird observation categories. Habitat proportions displayed are normalized according to the actual habitat available [ *P. vaginatum* (10%), Mangrove (25%), mud (5%), and water (60%)]. See “*Bird observation statistical analysis*” section (page 41) for an explanation.

*vaginatum* were herons and egrets (62%). The remaining herons and egrets were encountered in mangrove. Flamingos, however, had the highest association with mangrove habitat (35%) and slightly less so with open water (22%). My observations include a flamingo nesting colony on a mangrove dominated island in the middle of Diablas lagoon (Figure 2.9). I observed 17 juvenile flamingos and 5 adult caregivers in the nesting site. The migratory waders were predominantly associated with muddy shorelines (88%); however, 8 of the 14 black necked stilts observed were wading in open water, and 2 whimbrels were observed in *P. vaginatum* (Table 2.6). Ducks preferred the muddy shore (76%) and open water (23%) habitat (Figure 2.9). The birds appeared undisturbed by my presence suggesting my observations accurately document their behavior. As an aside, six of the flamingos I observed in the lagoon Diablas were dead; however these birds were not included in the statistical analysis.

#### *Assessment of P. vaginatum impact on bird feeding attributes*

The invasion of *P. vaginatum* represents an overall negative impact on the feeding ecology of flamingos, white cheeked pintail ducks, and herons. *Paspalum vaginatum* reduces food resources, presents undesirable habitat, and likely interferes with feeding mechanisms for these birds (Table 2.7). However, terrestrial birds and the common gallinule may benefit from *P. vaginatum* since it doesn't affect their feeding mechanism or habitat. Furthermore, *P. vaginatum* harbors their preferred food resources. The impact of *P. vaginatum* on migratory bird feeding ecology is mixed. Their feeding mechanisms will unlikely be affected by *P. vaginatum*; however, the habitat it presents is unlikely desirable to migratory birds (Table 2.7). Also, while there was a negative effect on open water invertebrates targeted by some migratory birds, *P. vaginatum* does harbor some species that are generally desirable to migratory

Table 2.7 Assessment of *P. vaginatum* potential impact on bird feeding attributes  
(habitat, mechanism and food resource)

Bird (species or group) ^	Feeding Characteristic		Food Resource		Effect of <i>P. vaginatum</i> ** Φ		
	Habitat	Mechanism	General ^^	Invertebrates from this study*	Habitat	Mechanism	Resource §
terrestrial birds	Mangroves	picking snatching	Insects	TA, SY, OD, CH (adult forms)	0	0	+++
flamingo	Open water	filtering water	Aquatic invertebrates zooplankton	CH, TR, OS	-	-	---
white cheeked pintail	Open water	filtering water	Aquatic invertebrates zooplankton	CH, TR, OS	-	-	---
common gallinule	shoreline	pecking probing	Invertebrates aquatic plants	OD, HA, HL, PI	+	0	+++
herons and egrets	shoreline open water	diving probing	fish	n/a	-	-	-
migratory birds	shoreline open water sediment	pecking probing	Invertebrates aquatic plants	PO, TA, SY, OD, HA, PI, CH, ME, TR	-	0	+++ ---

^ Only bird species that may interact with *P. vaginatum* included

^^ Only food items that may be found in lagoons included

\* Only abundant invertebrate species included (see Table 2.8 for key)

\*\* Assumes high *P. vaginatum* density.

Φ Impact value +/-0 is relative to open water resources

§ Multiple impact values (+/-0) correspond to "invertebrates from this study" column

Table 2.8 Key to Invertebrate codes in Table 2.7

Code	Invertebrates from this study
OS	Ostracoda
TR	<i>T. rediculata</i>
CH	Chironomidae
ME	Mesoveliidae
PI	Pleidae
HA	Hydrophilidae adults
HL	Hydrophilidae larvae
TA	Tabanidae
OD	Odonata
PO	Polychaeta
SY	Syrphidae

birds (Table 2.7). A key to the invertebrate codes used in the Table 2.7 is listed in Table 2.8.

#### *Assessment of P. vaginatum potential spread*

All of the lagoons except Las Diablas, Salinas, Baltazar, and Puerta del Jelí have the potential to be entirely invaded by *P. vaginatum*. Las Diablas has low salinity, but 10 % of this lagoon is greater than 1 m deep. Similarly, 20 % of Baltazar is too deep to be invaded. Although fringed by *P. vaginatum*, Salinas experiences extreme salinity events that periodically kill *P. vaginatum* and is therefore uninvasive. A large portion of Puerta del Jelí (about 40%) is very close to the ocean and, like Salinas, cannot be invaded due to high salinity levels. After excluding Salinas and uninvasive portions of Baltazar, Diablas, and Puerta del Jelí, I calculated that 84.42 of the 92.5 ha (90.6%) SIW habitat is potentially invasive by *P. vaginatum*.

## DISCUSSION

Invasion of *P. vaginatum* into the Southern Isabela Wetlands of the Galápagos Islands has a clear and dramatic impact on lagoon invertebrate community structure. Compared to other habitats, the invertebrate community in *P. vaginatum* was characterized by increased species richness, altered community composition, and similar overall biomass. Increased species richness in *P. vaginatum* is likely due to increased habitat complexity leading to increased available invertebrate niches. Many studies have documented an increase in invertebrate species richness in vegetation due to added refuge (Watkins et al. 1983; Murkin et al. 1992) and structural habitat

complexity (Cantrell 1985). The altered invertebrate community composition across habitats was clearly driven by different abiotic conditions within each habitat, as indicated by the significant association between habitat and invertebrate community composite variables (Figure 2.8). Compared to edge, open-water, and mangrove *P. vaginatum* habitat had low oxygen and low amounts of water. Invertebrates found primarily in the grass (polychaetes, syrphid, and tabanid larvae) are known to tolerate anoxic conditions (Merritt and Cummins 1984; Moore and Dillon 1992). Similarly, invertebrates excluded from *P. vaginatum* (primarily *T. reticulata*, and Ostracods) are less tolerant of anoxic conditions and prefer unobstructed water or only partially vegetated conditions (Batzner and Resh 1992; Murkin et al. 1992).

Invertebrate biomass usually varies across habitats due to fluctuations in population growth rates and life cycles (Cummins and Merritt 1984). Indeed, I found that the relative contribution of each species to the overall invertebrate biomass in each habitat did change across season. However, all habitats across both seasons produced the same overall invertebrate biomass (Figure 2.4 A). This suggests that the invasion of *P. vaginatum* does not affect annual average invertebrate production *per se*; rather the relative contribution of each species to the overall biomass. Whereas within the *P. vaginatum* habitat, invertebrates occurred at lower densities, had greater mass, and were found within the sediment fraction of the sample, invertebrates originating from water samples were densely distributed, had less individual mass, and were present in the water fraction. This redistribution of biomass across species and space is likely the most substantial impact on the invertebrate community associated with the *P. vaginatum* invasion.

The lack of seasonal variation in total invertebrate abundance and biomass was probably due to a relatively insubstantial (only 15 %) increase in water-levels in January. Such a small increase in water level over a period of a few months was probably not sufficient to cause restructuring of invertebrates associated with the

dilution of mineral and nutrient resources associated with rapid flooding (Smith and Collopy 1995), or creation of new aquatic habitat (Stinson et al. 1997). An increased species richness in January 2002 could be due natural fluctuations in phenological schedules; however, I cannot rule out the possibility that it is in part due to improved sorting efficiency rather than seasonal differences in habitat conditions (the additional species encountered in January 2002 were rare (Table 2.3) and may have been overlooked in the initial sampling effort). Irregardless, the additional species found had negligible influence on overall biomass or abundance.

Similar invertebrate biomass across habitats does not preclude the possibility that ecosystem production is increased in *P. vaginatum*. Concurrent with the decreased % water cover, I observed an increase in sediment associated with cores from *P. vaginatum* habitat. In shallow lentic systems such as lagoons, sediment accumulation is normal (Kjerfve 1994). However, sedimentation rates increase in the presence of emergent vegetation due to anaerobic conditions that slow mineralization, and promote accumulation of plant detritus (Schleyer and Roberts 1987). Anaerobic conditions can halt the formation of detritivore communities that utilize the organic substance. Indeed, few organisms other than anoxia-tolerant deposit-feeders (like those found in this study) can access and utilize anoxic sediments (Schleyer and Roberts 1987). Through this mechanism, production associated with *P. vaginatum* may be filling the lagoons with organic sediment rather than moving plant energy up through the food web and ultimately benefiting birds. Further research measuring productivity and differential speeds of sediment accumulation across habitats may provide evidence in support of this “terrestrialization” hypothesis.

Because this study is limited to one site, it is possible that my results have limited applicability to other SIW lagoons, as they vary greatly in size and salinity. Although it is well known that salinity gradients are important in structuring invertebrates (Merritt and Cummins 1984), local invertebrate populations are

regulated by fluctuating availability of specific habitat and associated resources rather than their osmoregulating capacity (Verschuren 2000; Lin et al. 2003). Baltazar has an invertebrate community representative of all of the lagoons (Gelín and Gravez 2002; Appendix II) and the species I observed will likely have a similar interaction with *P. vaginatum* regardless of the lagoon. Furthermore, a study that compared invertebrate communities across three lakes of varying salinities found that the relative distribution of invertebrate biomass among habitat types was similar (Wolheim and Lovvorn 1996).

My assessment of *P. vaginatum*'s impact on lagoon bird feeding ecology showed that the shift in invertebrate community and physical habitat changes may have largely a positive effect on terrestrial birds, but an overall negative effect on aquatic birds (Table 2.7). Terrestrial birds such as smooth billed anis extract dipteran and odonate larvae directly from the grass (Castro and Phillips 1996), while adult forms of Syrphidae, Tabanidae, Odonata and Culicididae (some originating from *P. vaginatum*) are preyed upon by yellow warblers and mangrove warblers (Castro and Phillips 1996). This provides another example of a possible “terrestrialization” as invertebrate biomass produced by *P. vaginatum* is likely being exported to the terrestrial environment, potentially improving terrestrial bird food resources.

Also likely to improve due to *P. vaginatum* are gallinule feeding habitat and food resources (Table 2.7). My frequent observation of gallinules pecking in and pulling at the *P. vaginatum* is not surprising since gallinules are known to be adept at navigating dense and tangled vegetation (Perrins and Middleton 1985; Castro and Phillips 1996). They are likely feeding on the Hemiptera (water scavenger beetle, Hydrophilidae, and also the pigmy backswimmer, Pleidae) which I found associated with the grass surface.

However, *P. vaginatum* will have a negative effect on open water food resources accessed by some migratory birds such as black necked stilts, lesser

yellowlegs and phalaropes (Table 2.5). Although these birds also utilize mudflats where they feed on many of the same invertebrates extracted from *P. vaginatum* (polychaetes, tabanidae larvae syrphidae larvae), the relative value of *P. vaginatum* compared to muddy shoreline cannot be evaluated because data on SIW mudflat invertebrates are presently not available. Regardless, *P. vaginatum* probably has a negative effect on their feeding habitat because, as predicted by optimal forage theory (Krebs and Kacelnik 1991; Zwarts 1996), it is unlikely migratory birds will search for invertebrates in the *P. vaginatum* (the energy exerted in searching and handling within the dense, tangled and unstable *P. vaginatum* is unlikely equal the energetic rewards offered by grass). Indeed, of the 31 migratory birds I observed only two whimbrels were in *P. vaginatum*. These whimbrels were probably searching for fiddler crabs (Zwarts and Blomert 1990; Ribeiro et al. 2004), which have a negative association with high density *P. vaginatum* (Chapter 1)

*P. vaginatum* probably also has a negative effect on heron and egret feeding habitats and mechanism. Although in my bird observations there was a substantial proportion of herons and egrets associated with the *P. vaginatum* (Figure 2.9), the birds appeared to be using the *P. vaginatum* as a convenient resting perch, not as forage or nesting habitat. The striated and lava herons I observed were fishing from the shore perched on sticks or rocks, as the open water is too deep for wading. For these short-legged birds, *P. vaginatum* is likely degrading feeding habitat by preventing access to open water from shoreline.

*Paspalum vaginatum* has a negative effect on all aspects of Galápagos flamingo feeding ecology. It completely transforms flamingo open water feeding habitat and suppresses flamingo food resources: *T. reticulata* and ostracods (Tindle and Tindle 1978). *Paspalum vaginatum* will also interfere with flamingos feeding mechanism, since they need unobstructed water to sweep their specialized beaks through the water and filter microscopic prey (Baldassarre et al. 2000). An inability to

access the invertebrates in the grass can explain why I observed no flamingos in *P. vaginatum*.

Much like the flamingo, *P. vaginatum* also has an overall negative effect on the white cheeked pintail duck feeding ecology since they also feed primarily on *T. reticulata* and ostracods in the open water. Although it is feasible given their beak morphology they could pick at invertebrates in the grass, none of the 71 ducks I observed were within 5 m of *P. vaginatum*.

This study strongly suggests that *P. vaginatum* degrades waterbird food resources and habitat in the SIW. Currently *P. vaginatum* may not represent a significant threat to bird populations as it remains confined to the lagoon shore and small bays and probably affects only 1-3% of SIW habitat. However, it is spreading (Appendix II) and has the potential to invade 90.6% of the SIW open water habitat (see “assessment of *P. vaginatum* impact” section of this work). Loss of 90.6% of the SIW habitat would be especially problematic for the Galápagos flamingo population, whose small population may be at risk of extinction if they experience any further reduction in numbers. Increased risk of extinction in small populations is often due to processes such as environmental catastrophes (e.g. El Niño), demographic stochasticity, inbreeding depression, and loss of genetic variation (Lande 1998). A study that evaluated extinction rates of bird species as a function of population size on the California Channel Islands provides relevant bird data that allows an accurate estimation of risk associated with actual population sizes (Jones and Diamond 1976). In particular, of populations on islands with between 10 – 100 breeding pairs, 10% went extinct over an 80 yr period, while only 1 population numbering between 100 and 1000 breeding pairs went extinct (Jones and Diamond 1976). The Galapagos flamingo is naturally near the 10-100 breeding pair risk category at 166 breeding pairs and loss of the SIW habitat (25% of the flamingo population) would bring it even

closer by reducing its number to 125. Therefore, loss of SIW bird habitat due to *P. vaginatum* invasion may increase risk of Galápagos flamingo extinction.

In conclusion, shifts in aquatic invertebrate communities associated with the invasion of *P. vaginatum* represent a degradation of water bird foraging habitat and loss of food resources. It is possible that *P. vaginatum* may eventually occupy 90.6 % of the SIW, potentially reducing population sizes and threatening the long term viability of flamingo populations. Clearly with almost complete loss of its aquatic habitat, the SIW would no longer sustain the required 1% of the white checked pintail duck to merit recognition by the Ramsar treaty. Control of *P. vaginatum* may therefore be necessary to prevent loss of water bird habitat and maintain SIW's status as an Internationally Important Wetland.

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## APPENDIX I.

### VARIATIONS IN PASPALUM VAGINATUM GROWTH RATE IN THE SOUTHERN ISABELA WETLANDS, GALÁPAGOS.

#### INTRODUCTION

The invasion of *P. vaginatum* into the Southern Isabela Wetlands (SIW) of the Galapagos Islands has the potential to negatively impact the lagoon ecosystem. Knowing the rate of its spread into lagoons and along shore-lines would help managers gauge the urgency of this threat. However, no studies have attempted to quantify its invasion rate. Small scale measurements, such as the rate of stolon elongation over a short period of time, will provide a useful measure of its potential to spread; however, substantial ecological impact is more likely felt at the invasion front (as a mat of vegetation advances across the surface of the water) which represents a larger spatial and temporal scale. Therefore, the objective of this study was to measure *P. vaginatum* expansion at these two spatial and temporal scales.

#### MATERIALS AND METHODS

##### *Study species*

Please see Chapter 2 for a description of the biology and behavior of *P. vaginatum*.

### *Study design*

I measured the rate of stolon growth in Baltazar lagoon (Figure 1.1). Please see Chapter 2 for a description of the study site. I measured a *P. vaginatum* stolon as it grew parallel to the shore line on saturated soil. I measured elongation rate by noting the location of 6 stolon tips at the beginning and the end of a 5 day time interval (from January 6<sup>th</sup> to January 11<sup>th</sup>, 2003). I then measured the difference between these two points in cm. Each stolon measured originated from a single parent-stolon and I marked the location of the stolons tips using wooden sticks.

I measured the advancement of the *P. vaginatum* invasion front as it extends into the open water in the lagoons Diablas, UNE, and Manzanillo (Figure 1.1). I measured the location of the invasion front as the distance from a permanent land marker to the end of the *P. vaginatum* growth along a line perpendicular to the shore. I measured this distance and noted the angle of this line with a compass in July 2002. This measure can form a baseline for future comparisons. I repeated these measurements in January 2003 being careful to use the same angle as in July 2002. On both dates I recorded salinity (SeaTest, Marine Depot, Anaheim, CA) and water depth at the invasion front.

## RESULTS

Stolons grew 6 to 27 cm, with an average of  $16.24 \pm 2.8$  cm [ $\pm$ SE] (2.7 cm/day). The measured salinity in Baltazar was on average  $13 \pm 1$  ppt [ $\pm$ SE].

The *P. vaginatum* invasion front in Manzanillo lagoon grew 2.8 m toward the center of the lagoon over the 5 months between the two monitoring dates for a growth rate of 0.56 m/month. The invasion fronts in UNE and Diablas did not move. Water depth in UNE, Diablas, and Manzanillo dropped between July 2002 and January 2003

Table 3.1 Lagoon characteristics and *P. vaginatum* growth at invasion front monitoring sites

Site	<i>P. vaginatum</i> growth (m)	salinity (ppt)	Depth of lagoon at leading edge (cm)		
			Jul-02	Jan-03	
Manzanillo	2.8	0	10	9	
UNE 2	0	7	23	20	
Diablas	0	9	45	41	

(Table 3.1). Manzanillo had fresh water and was the shallowest lagoon, while UNE and Diablas were slightly deeper with intermediate salinities (Table 3.1).

Furthermore, in UNE and Diablas, the floating *P. vaginatum* appeared sparser in January 2003 compared to 2002.

## DISCUSSION

Growth rate of *P. vaginatum* was highly variable for both individual stolons and at invasion fronts of different lagoons. Although all stolons were branching from one parent stolon, their elongation varied at least 4 fold. UNE and Diablas had no growth and displayed loss of plant vigor, while at Manzanillo and Baltazar the invasion front and stolons advanced rapidly and the grass looked healthy. Lack of growth in UNE and Diablas may be due to higher salinity since *P. vaginatum* grows best in fresh water (Graeme and Kendal 2001). In addition, water depth may have played a role in lack of growth in Diablas and UNE, as these lagoons were deeper than Manzanillo. However, repeated photos in Diablas showed that an invasion front near the one I monitored grew substantially (estimated at 2 m from July 2002 to January 2003). These results suggest that while *P. vaginatum* has the potential for very rapid spread, its growth is variable and dependant on local conditions. Therefore, further efforts to quantify *P. vaginatum* growth should include sufficient replication to span gradients of abiotic conditions (lagoon size, salinity, and depth). Monitoring should also be sufficiently long term to incorporate the influences of annual variations in growing conditions. While this study cannot generate a reliable estimate of average *P. vaginatum* growth rate, rapid stolon growth in Baltazar and invasion front expansion in Manzanillo point to its potential for continued rapid invasion into the lagoons. Potential impact of this spread on natural lagoon ecosystem function should be evaluated.

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## APPENDIX II.

### A COMPARISON OF THE AQUATIC INVERTEBRATE COMMUNITIES IN 8 LAGOONS IN THE SOUTHERN ISABELA WETLANDS OF THE GALÁPAGOS ISLANDS, ECUADOR

#### INTRODUCTION

The Southern Isabela Wetlands (SIW) of the Galápagos Islands are recognized for their biodiversity of local and global significance (Ramsar 2002). This recognition is due primarily to the documented presence of endemic and threatened shore birds, such as flamingos and white-cheeked pintail ducks (Vargas 1995). Although many of these birds depend on the lagoons for invertebrate food resources, very little is known about aquatic invertebrate diversity and abundance (Gelín and Gravez 2002). Baseline aquatic invertebrate community data from invaded lagoons (approximately 12 lagoons and at least 20 small ponds, Figure 1.1) is limited to two lagoons: Diablas and Salinas (Gelín and Gravez 2002). Not only do aquatic invertebrates serve as food sources for higher trophic levels (Schneider 1983), they are excellent indicator species as their abundance and distribution responds rapidly to habitat alteration (Pik et al. 2002). For example, the grass *Paspalum vaginatum* Sw. is invading the lagoons, growing along lagoon shoreline and forming mats of floating vegetation. Habitat alteration from the *P. vaginatum* invasion may result in aquatic invertebrate shifts that will impact their avifaunal predators. Documenting the diversity and abundance of aquatic invertebrates in the SIW is critical for understanding lagoon ecosystem function as well as higher-level trophic consequences to habitat change. Therefore, the objective

of this study was to characterize the abundance and diversity of aquatic invertebrates across a range of lagoons in the SIW.

## MATERIALS AND METHODS

The Southern Isabela Wetlands (00°57'S 90°58'W) cover an area of about 211 ha and contain 17 lagoons (Vargas 1989). These lagoons vary in size (1 to 79 ha), depth (20cm to 3m,) and salinity (average salinity 10‰, but ranges from fresh to hyper-saline 74‰ (Gelín and Gravez 2002)).

I sampled 8 lagoons (Figure 4.1) that represented the range in SIW size and salinity. I sampled within shore-line vegetation as well as open water in order to capture the diversity of invertebrates present. Using a hand-held net (mesh size= $1 \pm 0.04$ mm [mean $\pm$ SE]), I sampled by creating a figure-8 pattern (repeated 10 times) within each habitat. I did not attempt to quantify ostracods, but did note their presence. Within 4 hrs after sampling, I picked live invertebrates from the samples using soft forceps and conserved them in 70% EtOH. I also measured water temperature, salinity (using a hydrometer, Marine Depot, Anaheim, CA) and depth (with a 3 m PVC pipe marked with 1cm increments). Invertebrate sampling and abiotic measurements took place from 1-4 July 2002. Preserved specimens were transported to Cornell University for identification. I utilized Merritt and Cummins (1984) and consulted with Tom Poulson (Charles Darwin Research Station), who specializes in Galápagos aquatic invertebrates, for invertebrate identification.

## RESULTS

I encountered 11 morphospecies belonging to 5 orders: Odonates (Libelulidae and Aeshnidae), 2 dipteran larvae (Chironomidae and Tabanidae) and an unknown dipteran pupa, 2 Hemiptera (Corixidae and Mesoveliidae), and 2 Coleoptera (Hydrophilidae and Hydraenidae). I noted the presence of diving beetles (Dytistidae) in Manzanillo, however they did not appear in my samples. Ostracods were noted in 4 of the lagoons: Manzanillo, Baltazar, Puerta del Jeli, and UNE.

Water temperature did not vary substantially across lagoons (Table 4.1). Water depth at sample stations was highest in Baltazar and lowest in Salinas (Table 4.1). Depth at sample site and size of the lagoon had no apparent relationship to invertebrate composition or abundance.

Table 4.1. Abiotic characteristics of selected Isabela lagoons

Lagoon	Size (ha)	Salinity (ppt)	Depth at sample station (cm)	Temp. (°C)
Diablas	59	7	56	27
Salinas	2	>40	20	29
Baltazar	1	11	87	30
Manzanillo	1.9	0	32	32
Laguna Verde	2	40	43	28
Puerta del Jeli	0.7	37	23	29
Poza Redonda	0.4	30	25	28
UNE	0.1	9	36	31

Salinity appeared to affect invertebrate species richness and abundance with an increased invertebrate abundance but decreased species richness with increasing salinity (Figure 4.1). The corixid *Trichocorixa reticulata* was highly abundant (Figure 4.2) and the predominating species (Figure 4.3) in the saline lagoons. Samples from the highest salinity lagoons (Salinas, Poza redonda, and Laguna verde) contained only *T. reticulata*. In lagoons with lower salinities (<11 ppt), there was a dramatic drop in overall invertebrate abundance coupled with an increased prevalence of dipteran larvae and odonates (Figure 4.2). Manzanillo and UNE both were characterized by a high level of odonate nymphs (figure 4.3). Diablas was characterized by low invertebrate abundance comprised primarily of chironomids and mesoveliidae. At the intermediate salinity of 11 ppt, Baltazar's invertebrate community was comparable to most of the other lagoons, having relatively abundant *T. reticulata* while also boasting high species richness with representatives from both saline and fresh lagoons (Figure 4.3). Puerta del Jelí provided an exception to the salinity-species richness relationship having high morphospecies richness (8 species) while at a high salinity of 37ppt (Figure 4.1); however, like the more saline lagoons, *T. reticulata* were highly abundant and odonates were excluded from Puerta del Jelí.

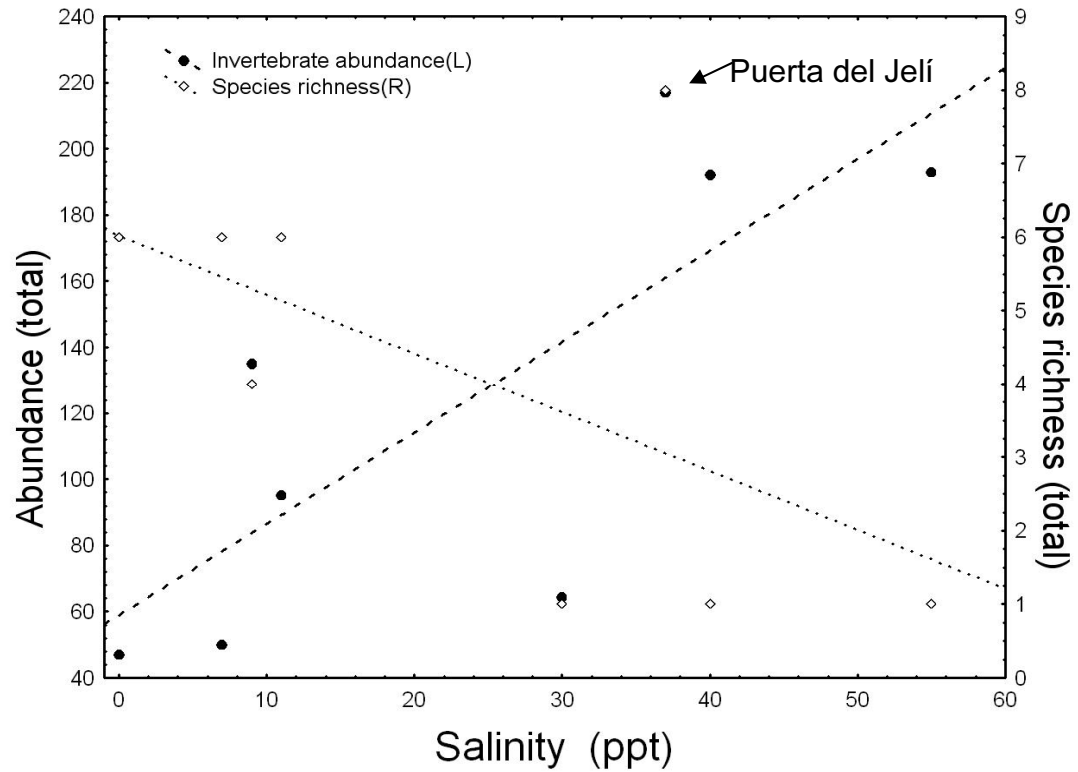


Figure 4.1 Relationship between lagoon salinity and invertebrate abundance (left y axis) and morpho-species richness (right y axis). In this figure, the reported July salinity (from Gelín and Gravex 2002) from Salinas (55ppt) was used.

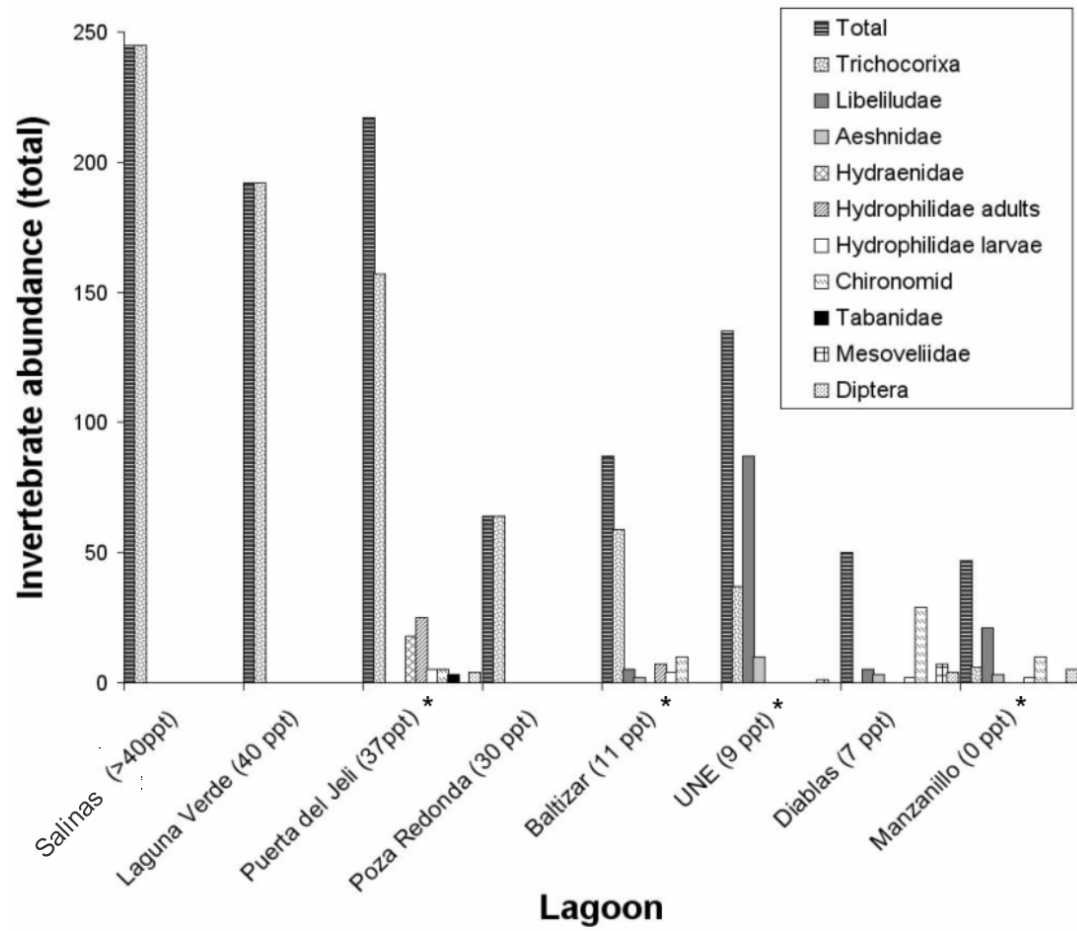


Figure 4.2. Total abundance of each invertebrate group found in each lagoon. Lagoons are ordered according to decreasing salinity. (\*) indicates ostracods are present.

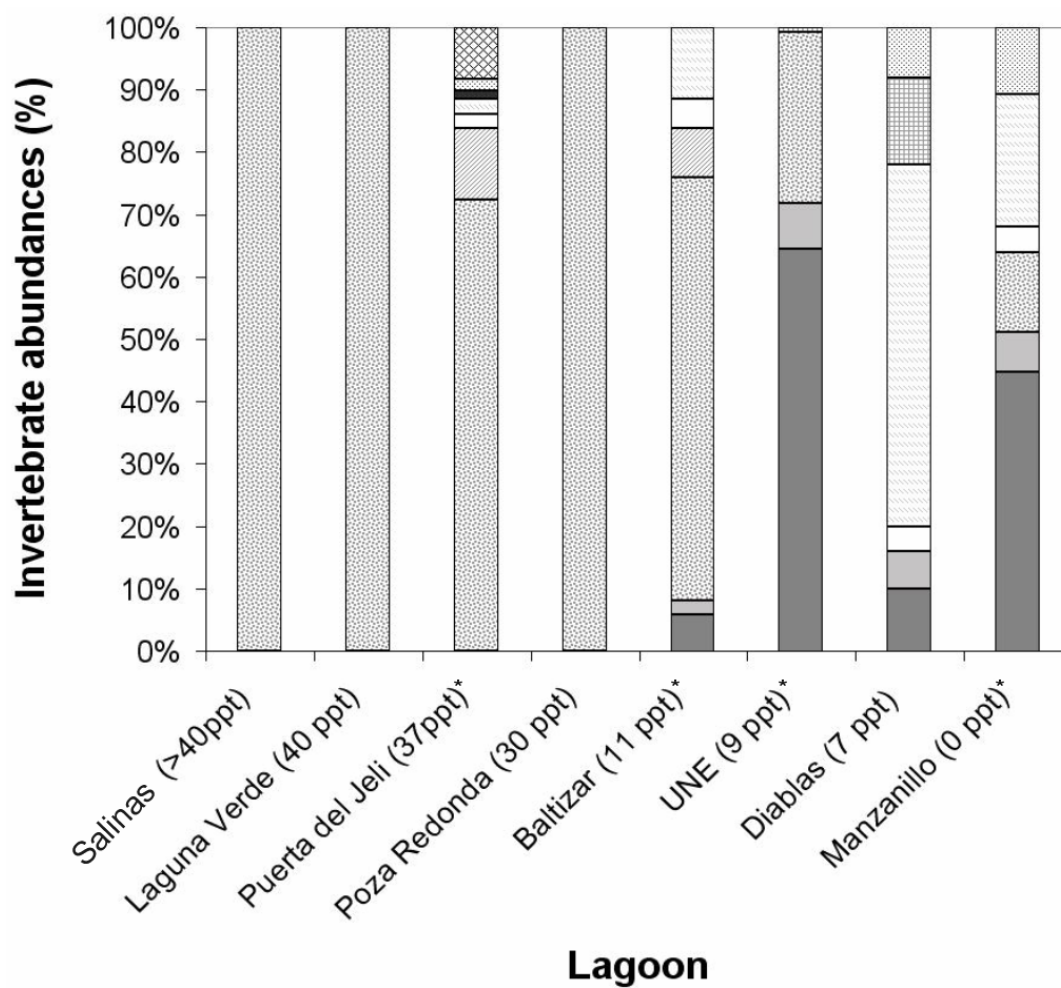


Figure 4.3. Relative abundance (%) of invertebrates encountered in each lagoon. Lagoons are ordered according to decreasing salinity. (\*) indicates ostracods are present. Fill patterns follow figure 4.2.

## DISCUSSION

These data result from a cursory survey of shoreline-associated invertebrates using a one-time sample. Therefore, the invertebrate community reported here does not incorporate possible seasonal or spatial variation in abundances. Furthermore, because I sampled with a coarse-mesh sweep net, very small invertebrates (<1mm) are not representative, nor are fast swimmers such as (Dytiscidae) who can escape the figure 8 motion. However, given these limitations, sampling methods remained consistent and data are useful for snap-shot comparisons of abundance and diversity across lagoons.

The patterns of diversity across the lagoons are consistent with and much previous work identifying the role of salinity gradients in structuring invertebrate communities. Saline lagoons tend to have comparatively low species richness (Verschuren 2000; Lin et al. 2003) and my samples from very saline lagoons often contained only the Corixid *T. reticulata*. Likewise, an increase in species richness in the fresh water lagoons was expected because fewer insects tolerate saline conditions (Merritt and Cummins 1984).

Although my data show a decrease in invertebrate abundance is associated with decreasing salinity, this trend may also be a reflection of changes in trophic status. Lagoons near the village of Puerto Villamil (including Salinas, Baltazar, and Puerta del Jelí) receive substantial anthropogenic pollution such as phosphates associated with cleaning products as well as human waste (Chávez 2002). These lagoons also had a greater invertebrate abundance, possible as a response to this increased nutrient input. This may help explain the high species richness in Puerta del Jelí despite its high salinity.

Community composition reported here is consistent with the results of Gelín and Gravez (2002), however, they encountered much higher levels of diversity in

Salinas, including: Corixidae: *T. reticulata*, Dixidae, Culicidae, Tabanidae: *Tabanus vitiger*, Syrphidae, Hydrophilidae: *Enochrus waterhousei*. This increased species richness may be a function of increased sampling effort by Gelín and Gravez (2002) who sampled a wider range of salinity levels. The invertebrate community in Puerta del Jeli is notable for its high diversity, including specimens of the endemic moss beetle: *Hydraenidae ochthebius*. Baltazar lagoon is notable for having high diversity, including representatives from both hyper saline (*T. reticulata*) and fresh water (Odonata) habitats.

The presence of *T. reticulata* in the saline lagoons is not surprising and agrees with previous SIW surveys (Tindle and Tindle 1978; Gelín and Gravez 2002), since it is well known that this species tolerates high levels of salinity (Merritt and Cummins 1984). As the primary prey for the Galápagos flamingo (Tindle and Tindle 1978) and carnivorous fish (Gelín and Gravez 2002), this abundant Corixid represents one of the most important links in the lagoon food web.

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### APPENDIX III

#### HISTORY AND STATUS OF PASPALUM VAGINATUM ON THE GALÁPAGOS ISLANDS, ECUADOR

The origin of *P. vaginatum* is in dispute, with Europe (Edgar and Conner 2000), Central and South America (Duble 1996), and South Africa (Duncan and Carrow 2000) all mentioned as native ranges of *P. vaginatum*. The confusion about its origin may be partially due to the difficulty in identifying *P. vaginatum*; on the Galápagos it had been initially identified as Kikuyu grass, *Pennisetum clandestinum* (Laegaard 2003, pers. comm). The debate over its origin extends to the Southern Isabela Wetlands, Isabela Island. On the Galápagos archipelago as a whole, *P. vaginatum* is listed as a native species (Wiggins and Porter 1971). However, because populations are defined at the island, not the archipelago level, there is reason to doubt its native designation also applies to Isabela Island. Verbal testimony combined with herbarium records suggest *P. vaginatum* was deliberately introduced to Isabela Island in the early 1900s, but did not expand its range into the lagoons until the late 1970s. Although the SIW area was extensively surveyed by botanists during the 1850's (Andersson 1858) this effort did not produce any record of the species, suggesting it was not present in the lagoons in the 1850s. In fact, *P. vaginatum* herbarium records from Isabela only date back to 1977. Long time residents of Puerto Villamil report that *P. vaginatum* had been present in Isabela since at least the 1930s, when it was used as cattle fodder (Pers. com. Don Gustavo Jaramillo; Vargas 1995) but that it was not purposefully introduced into the SIW area until the 1950's (Vargas 1995). While these reports suggest *P. vaginatum* arrived as a purposeful human introduction, probably around the turn of the century, further studies are needed determine the mechanism of *P. vaginatum*'s arrival to Isabela.

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