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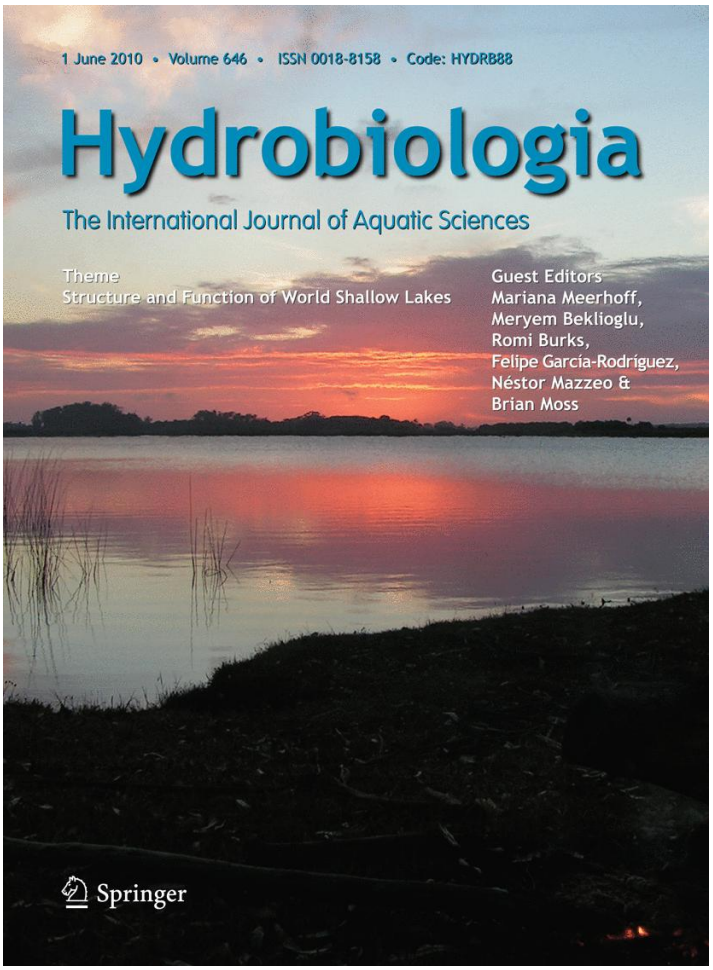

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SHALLOW LAKES

Pink eggs and snails: field oviposition patterns of an invasive snail, *Pomacea insularum*, indicate a preference for an invasive macrophyte

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Abstract Oviposition of non-calcareous or thinly shelled eggs represents an important life stage of many insects, amphibians, and several gastropods. A recently identified invasive species of apple snail, *Pomacea insularum*, exhibits alarming invasive characteristics of high reproductive rates and generalist consumption patterns. This snail takes the opposite approach to egg laying compared to most aquatic insects as adult snails crawl out of the water to place clutches on emergent, or terrestrial, substrates. As fecundity best indicates invasive potential for mollusks, control or management efforts need to understand reproductive behavior in *P. insularum* to predict, and hopefully impede, its spread throughout the Gulf Coast of the United States. Specific characteristics of wetlands and shallow lakes may facilitate the invasion process of *P. insularum* by providing females with conditions that permit successful oviposition. In order to investigate this possibility, we studied *P. insularum* oviposition behavior in an invasive population at two times during the reproductive season in Texas, USA. Based on a subsequent survey (August 2009), plants comprised 78% of the available habitat. Wild taro (*Colocasia esculenta*) and alligator weed (*Alternanthera philoxeroides*) represented 48 and 43% of that proportion, respectively. During 2008–2009, no new concrete or metal structures appeared in our sampling reach and consistent amounts of plant stands and woody debris remained dominant. Given this distribution, *P. insularum* laid disproportionately more clutches on wild taro compared to its availability and less on alligator weed and bulrush (*Schoenoplectus californicus*) than expected. Owing to limited metal and concrete substrates, we found a higher proportion of clutches on these artificial substrates than expected in both May and August 2008. However, artificial substrates comprised less than 2% of available substrates in the bayou. Our results suggest that wetlands and shallow lakes surrounded by large emergent macrophytes, particularly wild taro, likely provide ideal oviposition sites for *P. insularum*, promote egg supply, and possibly facilitate invasion into new aquatic ecosystems.

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Introduction

On both local and landscape scales, oviposition of non-calcareous or thinly shelled eggs represents a crucial, yet vulnerable life stage of many insects (Lancaster et al., 2003; Ellis, 2008a, b), amphibians (Gibbons, 2003), and some mollusks, particularly gastropods (Dana & Appleton, 2007). Although eggs unprotected by thick shells certainly display sensitivity to variation in abiotic factors (e.g., dissolved oxygen as in Hirayama & Kasuya, 2008), placing clutches underwater likely provides an environmental buffer to disturbance. While the lack of a hard shell increases the vulnerability of such eggs to desiccation, some eggs of certain species, in direct contrast to most insects and amphibians, must dry out to develop fully.

Because their eggs require exposure to air to mature, freshwater island apple snail females (i.e., *Pomacea insularum* d'Orbigny, Class Gastropoda, Family Ampullaridae) display opposite reproductive behavior to laying eggs underwater. In order to oviposit, mature *P. insularum* females climb out of their aquatic habitat and lay pink eggs in clusters (i.e., clutches) on emergent structures (Howells et al., 2006; Barnes et al., 2008). *P. insularum* clutches then dry out, and development of hatchling snails (i.e., neonates) continues for 1–3 weeks, depending on temperature and other environmental constraints (Howells et al., 2006). Whereas exposure to air and potential desiccation spells doom for aquatic insect clutches, exposure to water stress similarly decreases hatching efficiency of *P. insularum* clutches (M. K. Trawick, unpublished data) as also occurs in other *Pomacea* species (Turner, 1998; Pizani et al., 2005; Horn et al., 2008).

Given its high fecundity (average of approximately 2,000 eggs per clutch; Barnes et al., 2008) and other characteristics, *P. insularum* represents a potential threat to ecosystems when outside its native range of warm temperate South America (Rawlings et al., 2007; Hayes et al., 2008). At least two species of apple snails (*P. insularum* and *P. canaliculata*) readily consume vascular plants in contrast to periphyton resources commonly associated with other aquatic snails (Burlakova et al., 2008; Qiu & Kwong, 2009). Accordingly, now established in North America, *P. insularum* currently threatens shallow aquatic systems across the southeastern United States, including the Everglades in Florida (Rawlings et al., 2007; Conner et al., 2008; Van Dyke, 2009a).

Compared to other species, the remarkable fecundity of *P. insularum* allows for quick establishment of itself in new aquatic habitats, an acceleration of detrimental ecologic impacts, and an increased likelihood of becoming a nuisance (Keller et al., 2007; Conner et al., 2008). Thus, the life stage transition from egg to hatchling represents a critical step in the establishment and spread of exotic *P. insularum* populations (Barnes et al., 2008). For exotic *P. insularum*, egg clutches occur on different structures such as emergent plants, trees, concrete pillars, and sewer cisterns (Howells et al., 2006; Rawlings et al., 2007). Recent management plans for wetland habitats suggest that egg mortality resulting from failed hatching may reduce egg supply of this rapidly invasive snail (Van Dyke, 2009b).

Understanding of the trends in the abundance of clutches on different plant species may yield important information about *P. insularum* invasion and establishment patterns (Byers, 2002). Wild taro (*Colocasia esculenta* (L.) Schott), which humans transported to North America from Southeast Asia (Akridge and Fonteyn, 1981), commonly co-occurs with *P. insularum*. Interactions between these two exotic species could potentially produce greater ecological impacts than anticipated (Simberloff, 2006). Havel et al. (2002) previously used environmental constraints to identify potential dispersal sites for exotic invasive species. In this study, we wanted to examine whether field oviposition behavior of *P. insularum* females could provide similar information. We thus focused on identifying where, and in what proportions, exotic *P. insularum* females deposited egg clutches in relation to available substrates in Armand Bayou Nature Center (Texas, USA).

Materials and methods

Field clutch substrate census

In order to determine field oviposition substrates used by *P. insularum* females, we conducted two oviposition site surveys. Both surveys took place during one reproductive season in Horsepen Bay located in Armand Bayou Nature Center (ABNC) (Houston,

TX, USA) (29.5638°N latitude, 95.0718°W longitude). In order to gain additional perspective on behavior and impacts of temperature, we conducted one census close to the beginning of the summer (May 2008) and the other closer toward the end (August 2008).

In order to obtain a comprehensive and accurate clutch count, teams explored the banks of sampling areas via canoes and recorded the type of substrate on which any clutch occurred. Sampling days varied between 8 and 10 h on the water with a traveling distance of approximately 2-km upstream. Throughout the bayou, plentiful stands of plants existed, and our sampling stretch included two concrete bridges and two metal storm water drains. Numerous trees lined the banks and several stable, large pieces of woody debris emerged from the channel. Researchers recorded all the clutches regardless of condition, with the exception of excluding white clutch scars (i.e., no intact eggs remaining from the clutch).

During each survey, we grouped all the oviposition events into four major substrate categories: plant, wood, metal, and concrete, which represented the most abundant types of substrates found above the water's surface based on our visual observations. Furthermore, when a clutch occurred on a plant, we identified the species. We found clutches exclusively on the three most abundant aquatic macrophytes within the bay [*C. esculenta*, wild taro; *Alternanthera philoxeroides* (Mart.) Griseb., alligator weed; *Schoenoplectus californicus* (C.A. Mey.) Palla, bulrush or cord grass]. Wild taro and bulrush generally occur in narrower, less developed regions while alligator weed dominated in the wider and more impacted areas of the bayou (e.g., where people frequently mowed banks).

Field substrate availability quantification

In order to assess snail oviposition preferences in the field, we contrasted snail use of suitable oviposition substrates versus substrate availability. In each previous census, we collected and measured clutches in addition to recording location. Owing to the time involved in the collection process, we did not simultaneously document substrate availability as we recorded number of clutches in May and August 2008. On August 8, 2009, we returned to Armand Bayou and quantified the amount of each available oviposition substrate surface category (plant, wood, cement, metal) and plant species (*C. esculenta*, *A. philoxeroides*, *S. californicus*) available to *P. insularum* within our study site (m^2 of bank). No new concrete or metal structures occurred in our sampling reach. Taro invaded Armand Bayou approximately 15 years ago (M. Kramer, personal communication) and has established numerous, persistent dense stands that annually provide the dominant substrate available for oviposition. We did not observe any large change in vegetation coverage between 2008 and 2009. Consequently, we felt justified in using 2009 substrate availability data as expected values in χ^2 analyses that we used to test against our observations during May and August 2008.

In order to quantify substrate availability, a research team traveled down each bank of the bayou in a canoe marked in 1-m increments and estimated the horizontal length of regions of potential oviposition surfaces (i.e., stands of plants, areas of woody debris, etc.). We measured width of concrete structures, calculated surface area of metal storm water drains, and quantified each tree in contact with the water in our study site. An abundance of trees necessitated quantifying individual tree size from a distance by general classes using estimated diameter at breast height to divide trees into small (<10 cm), medium (10–25 cm), and large (>25 cm). We estimated the area of woody debris (i.e., dense patches of small emergent branches or sticks) by measuring length and width of debris patches visually with our canoe. We then represented substrates two-dimensionally (m^2) by assuming that snails utilized an area up to 1 m inland from the bank for egg-laying as clutches rarely occurred farther inland (authors' personal observations).

Oviposition preference analysis

Using the statistical package R, we executed χ^2 tests to test for preferences in *P. insularum* oviposition behavior for both sampling events. During our analysis, we individually tested for preferences between general substrate types (plant, wood, metal, and concrete) and specific plant species (*C. esculenta*, *A. philoxeroides*, and *S. californicus*) and then natural versus artificial substrates. In the χ^2 tests, the expected values for use of each substrate reflected the percent of the sampling site area occupied by that substrate type in 2009.

Clutch characteristics and hatching efficiency

For consistency, we only collected fresh clutches laid on taro which we identified by their bright pink color and gelatinous texture (Barnes et al., 2008). We removed clutches by cutting off the section of wild taro on which female snails deposited clutches. We did not separate clutches from plant substrates in the field. Instead, we wrapped the entire complex (clutch and taro substrate) in wax paper and placed the samples in rigid, plastic containers to minimize damage. As apple snail eggs occur in clutches where individual eggs cannot be counted easily, we examined whether we could use a whole clutch as a functional measure of fecundity. Other studies on apple snails also report number of clutches (Peña & Pocsidio, 2007; Rogevich et al., 2009) to quantify *Pomacea* reproduction. Using digital calipers (Fisher Scientific; precision to 0.01 mm), we recorded three basic dimensions (length, width, and depth) of all the clutches. In order to determine whether significant differences existed in clutch physical characteristics between our collection periods, we analyzed the three characteristics (length, width, and depth) using Mann–Whitney *U* non-parametric tests due to differences in sample size (SPSS 17.0).

We then calculated egg clutch hatching efficiency which we defined as the total number of hatchlings divided by the total number of eggs in the clutch (=unhatched eggs + hatchlings). In order to determine whether or not those physical characteristics of the clutch influenced hatching efficiency (i.e., fecundity % that yields hatchlings), we took clutches laid on wild taro that we collected during our May 2008 ($N = 20$) and August 2008 ($N = 35$) sampling trips and allowed them to hatch within our lab. Incubation of all clutches took place at 28.5°C with a 12L–12D light cycle. Clutches rested on a raised platform, allowing hatchlings to fall into spring water for collection. After the clutch had either hatched completely or stopped producing hatchlings (normal hatching duration = 10 days; Barnes et al., 2008), we preserved all new hatchlings and any unhatched eggs in 10% NaOH solution to dissolve any remaining gelatinous matrix before counting. We conducted linear regressions to determine how well clutch dimensions predicted and explained their respective clutch hatching efficiency (SPSS 17.0). In order to contrast egg clutches laid at different air temperatures, we used a Mann–Whitney *U* test to see whether hatching efficiency differed between May 2008 (monthly average ≈25.4°C) and August 2008 (≈28.9°C).

Results

Field substrate patterns

In our study, we recorded just over 1,000 independent oviposition events (May 2008 = 231 and August 2008 = 779). Our 2009 quantification of substrate availability revealed that plants comprised 78% of the available habitat followed by wood substrate which comprised 20% of overall habitat. Concrete made up 1.4%, and metal storm water drains represented 0.2% of the total substrate available for snails within our sampling stretch. A closer quantification of plant type showed that wild taro and alligator weed represented 48 and 43% of the proportion of plants, respectively. Bulrush comprised the remaining 9% of the plants. Taro, alligator weed, and bulrush provided 37, 33, and 7% of overall substrate availability, respectively.

We found a significantly higher proportion of clutches on metal and concrete substrates than expected in both May and August (Table 1; Fig. 1). However, metal and concrete together comprised less than 2% of available substrate in the bayou. Fewer clutches occurred on wood substrates than expected (Fig. 1). Available plant substrate (78.4%) in 2009 closely reflected the percentage of clutches occurring on plants in both May (77.9%) and August (76.0%).

Given this distribution, each survey from 2008 yielded significant results that *P. insularum* laid disproportionately more clutches on wild taro compared to its availability and less on alligator weed and bulrush than expected (Table 1; Fig. 2). We found overuse of artificial substrates compared to availability and underutilization of natural substrates (Table 1; Fig. 3).

Clutch characteristics and hatching efficiency

Snails laid eggs on taro stalks over a large range of height (15.24–123.19 cm). These heights above the water surface, however, did not differ between May and August 2008 (*t*-test, $t_{53} = 0.617$, $P = 0.540$; average ± 1 SE; 56.3 ± 3.8 cm; 60.0 ± 4.0 cm,

Table 1 Observed counts in May and August 2008 versus expected frequencies derived from additional 2009 survey of different substrates

Substrates	Date	χ^2 Value	*P* value
Plant	May	May 2008: 88.96	May 2008: **<0.001**
	August	August 2008: 1740.08	August 2008: **<0.001**
Wood	May		d.f. = 3
	August		
Metal	May		
	August		
Concrete	May		
	August		
Wild Taro	May	May 2008: 112.23	May 2008: **<0.001**
	August	August 2008: 207.24	August 2008: **<0.001**
Alligator Weed	May		d.f. = 2
	August		
Bulrush	May		
	August		
Natural	May	May 2008: 55.83	May 2008: **<0.001**
	August	August 2008: 369.33	August 2008: **<0.001**
Artificial	May		d.f. = 1
	August		

Degrees of freedom (d.f.) listed after *P* values. Snail "over-utilized" substrate types appearing in bold text

respectively). We observed a large variation in field clutch shape. We compiled descriptive statistics for clutch characteristics of all of our clutches (Table 2). After analysis, only depth significantly differed between collection periods (Depth: $Z = -6.019$, $P < 0.001$), increasing from May to August 2008. For the clutches taken from May 2008 ($N = 20$) and August 2008 ($N = 35$), none of the physical characteristics that we measured or estimated (length, width, and depth) effectively predicted clutch hatching efficiency (R^2-values <0.218, Table 2), although a significant relationship did exist for clutch depth (Table 2). For the May 2008 sample, clutches averaged a hatching efficiency of $43.8 \pm 5.51\%$ (1 SE), while the August 2008 clutches produced a $33.7 \pm 4.41\%$ hatching success rate. Successful hatching events ranged widely in efficiency for both samples (Table 2). Most clutches from the May sample exhibited at least some hatching. However, for reasons unknown, nine clutches from August 2008 failed to hatch when placed in the laboratory incubator. August clutches contained significantly fewer eggs than May clutches ($Z = -2.170$, $P = 0.03$). Despite this result and a 10% difference that existed in hatching efficiency, May and August

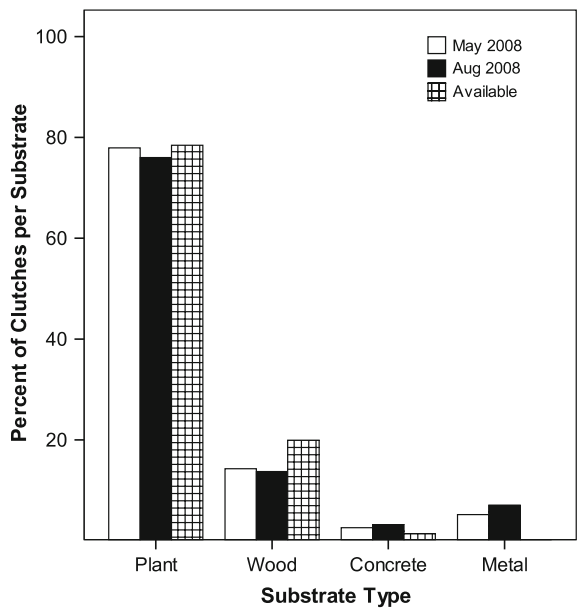

Fig. 1 Percentage of *P. insularum* egg clutches found on each type of substrate examined during May 2008 (*white bars*) and August 2008 (*black bars*) versus available substrate in August 2009 (*hatched bars*). A small quantity of available metal substrate (0.214%) explains the lack of a visible bar on the graph

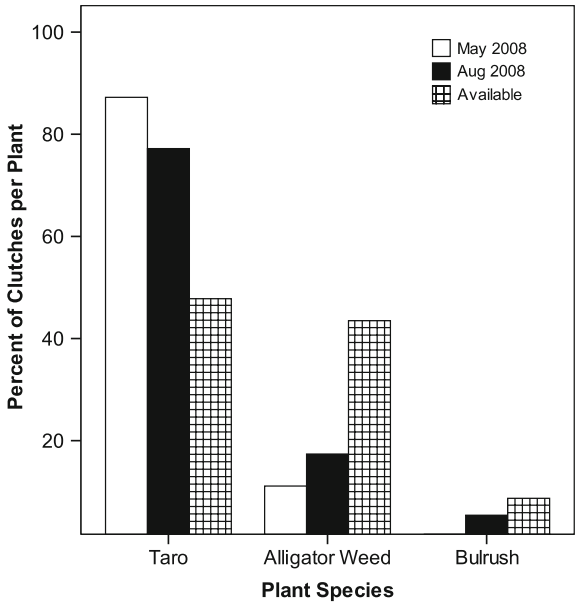

Fig. 2 Percentage of *P. insularum* egg clutches laid on specific plant species during May 2008 and August 2008 (*bars* as in Fig. 1). A small quantity of available bulrush (1.67%) explains the lack of a visible bar on the graph for May 2008

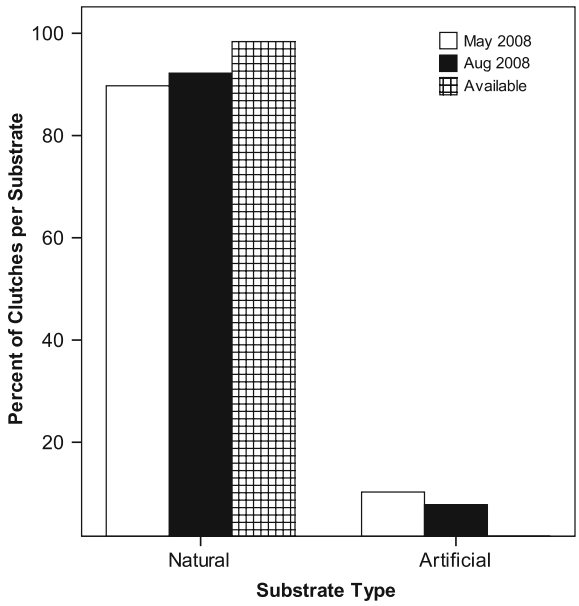

Fig. 3 Comparison of *P. insularum* oviposition on natural (i.e., plant and wood) versus artificial (i.e., concrete and metal) substrates during May 2008 and August 2008 (bars as in Fig. 1). A small quantity of available artificial substrate (1.6%) explains the lack of a visible bar on the graph

clutches still yielded the same number of hatchlings statistically ($Z = -0.404$, $P = 0.160$).

Discussion

Our field examination of oviposition trends of *P. insularum* revealed that female snails laid more clutches on wild taro than expected by the exotic plant's availability. We also unexpectedly found a higher proportion of clutches on artificial substrates than expected in both May and August. We did not anticipate this result based on the sheer abundance of emergent plants surrounding the bayou. Artificial substrates comprised less than 2% of available substrates in the bayou and usually stood isolated from other surveyed substrates. The vast majority of clutches found on artificial substrates occurred in one stretch of bayou (approximately 100 m) that suffered heavy impacts from human activity in the form of bank mowing and vegetation control.

Disturbances, such as mowing or herbicide use, that limit persistent of emergent plants may impact snail abundance indirectly. However, given their cryptic nature, we do not have density estimates of adult snails in this stretch of mowed plants versus stretches dominated by taro. When concrete and wild taro occurred in close proximity to each other, we observed clutches in taro stands and an absence of clutches on concrete substrate (authors' personal observations). Therefore, the structure of our sample region and extremely low amount of artificial substrates potentially skewed our expected results. Even with this consideration, our findings indicate that *P. insularum* exhibited preferences for wild taro over other plants, yet did not refrain from utilizing artificial substrates.

In simple terms, our use of "preference" implies that a higher proportion of clutches occurred on a particular substrate than predicted from that substrate's availability. When snails failed to demonstrate particular preferences, the relative abundance of clutches reflected the relative availability of substrate as measured by our 2009 survey. Overall, when we examined number of clutches collectively placed on all the three plants, less than a 3% difference existed between our observed counts and expected counts given the general substrate

Table 2 Clutch physical characteristics for the two sampling periods (May and August 2008) and their predictive relationships to hatching efficiency

Bold text highlights single significant statistical difference in clutch charactersitics between time periods

Characteristic	Date	Mean (± 1 SE)	Range	*P* value (R^2)
Hatching efficiency (%)	May	43.8 ± 3.45%	0–83.0	Not applicable
	August	33.1 ± 4.15%	0–83.0	Not applicable
Length (mm)	May	67.72 ± 3.98	39.40–99.60	0.970 (0.001)
	August	72.86 ± 2.94	42.73–112.01	0.393 (0.022)
Width (mm)	May	21.83 ± 0.659	15.80–26.70	0.570 (0.018)
	August	22.31 ± 0.419	16.73–26.37	0.526 (0.012)
Depth (mm)	May	12.3 ± 0.33	9.60–15.90	**0.038** (0.218)
	August	19.5 ± 0.58	14.03–27.30	0.429 (0.019)
Egg number	May	1,454 ± 117.54	632–2,494	Not independent
	August	1,132 ± 80.82	522–2,457	Not independent

availability. Snails had more potential possibilities to lay clutches on wood. However, with plants comprising 78% of available substrates, we cannot assert that snails preferred plants over wood, metal, or concrete based on availability.

This pattern of clutch number reflecting substrate proportion occurred for plant substrates in general, although species-specific preferences emerged. In our study reach, wild taro and alligator weed both provided similar quantities of available substrate but bulrush made up only 10% of plant substrates. Fewer clutches than expected occurred on alligator weed and bulrush. Bulrush stems may not provide the same stability as taro because each stem shoots up from an individual stolon versus a larger, sturdier tuber (Kaufman & Kaufman, 2007). Bulrush also lacks large leaves that could protect clutches from oxidative stress (Dreon et al., 2008) or camouflage females from aerial predation that occurs in native habitats during oviposition. Although the reason for a disproportional dependence on taro requires further study, we speculate that structurally taro represents a more appealing oviposition site for *P. insularum* than bulrush due to the physical differences described for the two plants.

For alligator weed, we suggest that a different primary mechanism might explain why fewer clutches occurred than expected. Alligator weed stems spread to form dense floating mats. Although individual hollow stems can grow up to a meter long, only short stalks rising from leaf–stem joints stick up out of the water to allow pollinators to reach the small flowers (Kaufman & Kaufman, 2007). This proximity to the water of eggs laid on alligator weed possibly increases the likelihood that a clutch suffers inundation and fails to hatch. A snail's instinct to lay eggs at higher positions than possible with alligator weed may have driven gravid females to other structures. However, this study did not investigate actual mechanisms behind species-specific responses exhibited by *P. insularum*. In order to elucidate these mechanisms, experimental studies need to offer all substrates simultaneously in equal proportions.

In contrast to less use of both alligator weed and bulrush than expected, we found that *P. insularum* showed a clear, statistically significant preference for wild taro. The same trend occurred in manipulative laboratory experiments where snails deposited more clutches on wild taro despite the presence of native pickerelweed (*Pontederia cordata* L.) in equal proportions (Kyle and Burks, unpublished data). However, we do not know whether snails seek out taro specifically for an oviposition site or as a food resource. For *P. canaliculata*, Qui & Kwong (2009) found that a sole diet of taro failed to foster reproduction. As we have observed large female *P. insularum* "munching" near the bottom of taro stalks, we expect that both factors come into play. In other places, such as Hawaii, where taro represents a valued resource, positive associations between apple snails and taro spark even further economic concern (Van Dyke, 2009c). We do not want to suggest that the sole presence of an "avoided" or less-preferred plant would limit suitable oviposition sites for invasive *P. insularum*. Researchers have not yet found a plant or substrate that will effectively deter *P. insularum* oviposition.

Resetarits (1996) proposed that female choice served as a reliable mechanism for ensuring a constant environmental habitat for development and hatching of eggs. Those species with established, yet

adaptable behaviors, provide the stability necessary for natural selection to act on more commonly considered trade-offs in reproduction such as egg number, egg size, or age at maturity (Resetarits, 1996). Because we collected all of our clutches after they had been laid, we lack information regarding the age and size of female snails that deposited clutches. Instead, clutch size provides a snapshot of potential fecundity. Hatching efficiency, on the other hand, yields a better estimation of realized fecundity, or the number of new organisms introduced into the region, which makes up one component of propagule pressure that favors establishment of exotic species (Lockwood et al., 2005).

In our study, we found relatively low hatching efficiencies when we incubated clutches compared to the previous field results (Barnes et al., 2008). Sets of field clutches from 2008 more closely reflected non-incubated laboratory hatching efficiencies of 30% found in Barnes et al. (2008). Changes in environment (such as water loss in the incubator), alterations of temperature, or transportation of our clutches from the field to the laboratory could account for such differences in hatching efficiency. However, we made our best efforts not to disturb the clutches, and we did not see visible damage. Nonetheless, as one single female *P. insularum* likely produces many clutches during one reproductive season (i.e., annual fecundity), even a low hatching efficiency of just 30% still exists as a threat to shallow aquatic environment when one considers an average of 2,000 eggs per clutch (Barnes et al., 2008).

A region's vegetative composition may hold the key to understanding *P. insularum* establishment and spread in exotic habitats. While our study demonstrates that females do preferentially use stands of wild taro for oviposition, other studies indicate that snails also utilize taro as a food source (Burlakova et al., 2008; Van Dyke, 2009b). Our results suggest that wild taro's physical characteristics support and shelter snail egg clutches, and its use as a food source suggests the potential of an eventual "invasional meltdown" (Simberloff, 2006). This interaction may prove particularly important because, as of now, all established U.S. populations of *P. insularum* overlap with wild taro's current distribution within the United States (USDA, 2009). Unfortunately, females placed a higher than expected number of clutches on man-made objects, suggesting that *P. insularum* can adjust to new ecosystems and will use almost any dry emergent surface as an oviposition site when needed. Extrapolated to the larger management perspective, provision of quality oviposition sites promotes egg supply and possibly facilitates invasion into new aquatic ecosystems.

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