Fecundity of the exotic applesnail, *Pomacea insularum*

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Abstract. International trade frequently moves mollusks around the globe, thereby increasing their opportunity to cause ecological and economic damage. Recent genetic studies have confirmed the identity of South American applesnails (*Pomacea insularum*) in the southeastern US, but limited literature exists on this species. Understanding fecundity provides direct insight into the invasive potential of mollusks. Our study documents *P. insularum* fecundity in Texas and offers comparisons with the closely related global invader *P. canaliculata*. We quantified *P. insularum* clutch and hatchling physical characteristics and examined field and laboratory hatching success. Clutches contained thousands of eggs (mean = 2064 eggs), and clutch size tended to increase over the reproductive season. Clutches exhibited average field and laboratory hatching efficiencies (number of hatchlings/total number of eggs) near 70 and 30%, respectively. Notably, several clutches hatched at 80% or higher in the field. Exotic *P. insularum* deposit more eggs/clutch than the related invader *P. canaliculata*, but we do not yet know how seasonal hatching efficiencies compare. However, even with a conservative estimate of 1 to 10% survival to adulthood, the average *P. insularum* clutch yields 14 to 144 new applesnails. The high fecundity of *P. insularum* translates into considerable ecological impact because adult females can contribute >1 clutch/wk over an extended growing season in the southeastern US. The need for research has increased with the emergence of *P. insularum* populations in the fragile Florida Everglades. We advocate life-history studies like ours to help understand the invasion potential of applesnails and other invasive mollusks.

Key words: *Pomacea*, fecundity, hatching efficiency, invasive, mollusk, Florida Everglades, population.

Estimates of economic costs caused by nonindigenous invasive species (species introduced outside their native range that cause ecological or economic harm) range from $120 billion annually in the US (Pimentel et al. 2005) to hundreds of billions of dollars worldwide (Simpson 2004). Beyond economic costs, nonindigenous invasive species represent the 2nd largest contributor to global declines in biodiversity across all ecosystems (Wilcove et al. 1998, Sala et al. 2000). In aquatic systems, nonindigenous invaders might pose overwhelming challenges to biodiversity (Lodge 2001) because of their propensity to reproduce quickly, spread, and out-compete native species (Kolar and Lodge 2001). For example, Strayer (1999) suggested that invasive mollusks, such as the zebra mussel, *Dreissena polymorpha*, and New Zealand mud snail, *Potamopyrgus antipodarum*, threaten native molluscan biodiversity because of high fecundity, rapid range expansion, and superior competition for resources. International trade frequently moves snails and other mollusks around the globe (Carlton 1999, Robinson 1999), thereby increasing their opportunity to cause economic or ecological damage.

High fecundity increases the rate and intensity at which a nonindigenous invader affects its introduced range (Sakai et al. 2001). For example, in a review of life-history characteristics of nonindigenous aquatic mollusks in the US, Keller et al. (2007) used multiple statistical techniques to demonstrate a positive relationship between fecundity and nuisance status. From these

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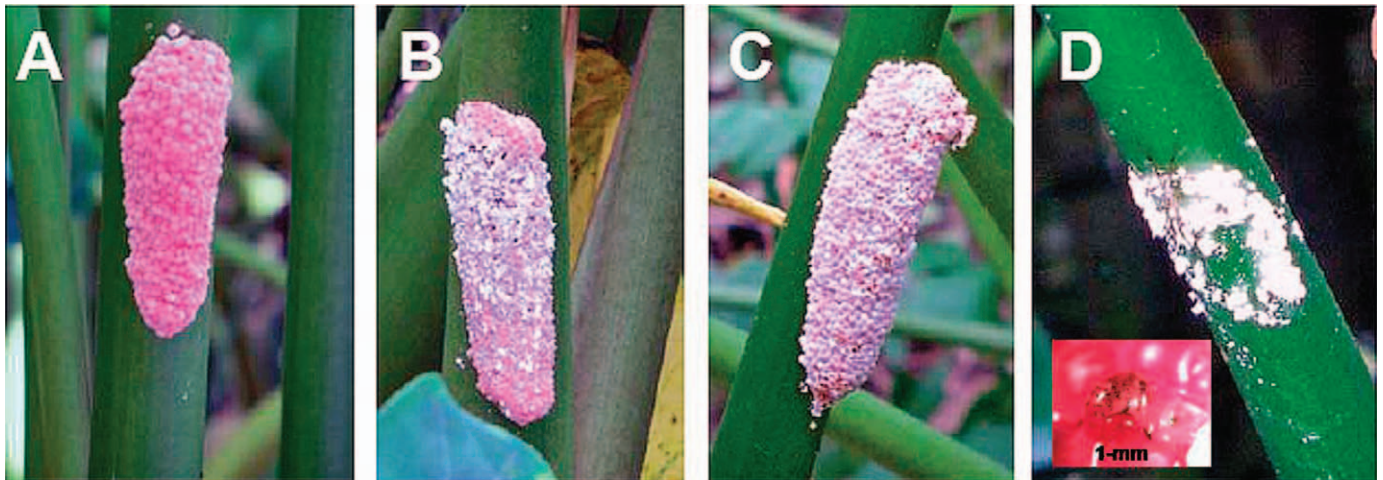[4] jenhand@sbcglobal.net

FIG. 1. *Pomacea insularum* egg clutches on macrophyte stems at different stages. A.—Newly deposited egg clutch (color is a vibrant pink). B.—An egg clutch starting to lighten. C.—Dulling egg clutch close to hatching. D.—Remnants of an egg clutch after hatching with an inset of a hatchling. Photographs by Jennifer J. Hand.

data, they concluded that high fecundity serves as the most successful predictor of molluscan invasive potential. Therefore, like the invasive *D. polymorpha* or Asian clam *Corbicula fluminea*, high fecundity of freshwater applesnails, *Pomacea insularum* and *Pomacea canaliculata*, raises legitimate concern. Snails are important algal grazers in nearly all aquatic systems (Dodds 2002). However, recent intensive examinations of macrophyte herbivory (Lodge et al. 1998) and shallow lake function (Jones and Sayer 2003, Burks et al. 2006) have suggested that the role of snails in aquatic communities should garner even more interest. The growing list of invasive snails is also testament to the important ecosystem impacts of snails. For example, *P. antipodarum* invasion has disrupted biodiversity and ecosystem function in the Greater Yellowstone Ecosystem of Montana and Wyoming (Kerans et al. 2005, Hall et al. 2006). The limited available applesnail literature provides a clear record of negative ecological and economic impacts (e.g., Cowie 2002, Sin 2003, Carlsson et al. 2004, Carlsson and Lacrousière 2005, Carlsson and Brönmark 2006, Joshi and Sebastian 2006, Boland et al. 2008) and warns that applesnails can provide vectors for the spread of human disease (Rawlings et al. 2007, Wang et al. 2007). Female applesnails generally live a cryptic benthic lifestyle, and venture out of water only to deposit egg clutches on emergent substrates above the water line. Large vibrant pink egg clutches often provide the first sign of applesnail invasion (Fig. 1A–C).

Neck and Schultz (1992) first reported a reproductive population of applesnails near the Texas Gulf Coast. In 2000, early investigators misidentified this population as *Pomacea canaliculata*. In 2004, when local officials realized that this identification was not

certain, they began to use the ambiguous title *P. canaliculata* "complex." In 2006, genetic analyses led to the identification of the Texas population as *P. insularum* (Cowie et al. 2006, Rawlings et al. 2007). Applesnails have generated increasing concern in recent years as new populations of *P. insularum* became established in the southeastern US, including regions of Florida, Georgia, and Texas (Rawlings et al. 2007, Hayes et al. 2008, S. Snow, US Fish and Wildlife Service, personal communication). The closely related nonindigenous invader *P. canaliculata* has established populations in California and Arizona (Cowie et al. 2006, Rawlings et al. 2007). Genetic analyses by Rawlings et al. (2007) labelled *P. insularum* and *P. canaliculata* as reciprocally monophyletic sister taxa. Distinguishing between these 2 species, especially when they are young, can be challenging to even the well-trained eye because of the particularly channeled suture present on shells of both species. Thus, scientists and managers urgently need information about the basic life histories of these species to understand the direction of their potential ecological or economical impacts.

Our paper provides a description of fecundity of the nonindigenous invader *P. insularum.* To our knowledge, it is the first such contribution to the literature. We focused on reproductive traits because fecundity data provide the most important predictor of invasive success in mollusks (Keller et al. 2007). Our study of *P. insularum* had 3 main objectives: 1) to investigate clutch egg number and hatching success in the field, 2) to compare hatching success between field and laboratory, and 3) to document egg and hatchling size and consider a possible trade-off between egg size and

egg number (see Godfray et al. 1991 for a review of clutch size theory). To our knowledge, no previous studies have measured *P. insularum* hatchlings. Last, based on our results, we compared our data on *P. insularum* with data published in the literature on the closely related invader *P. canaliculata* because this comparison might offer further insight into the potential of both species to cause damage.

Methods

Physical characteristics

We collected 67 intact *P. insularum* egg clutches from Horsepen Bayou in Clear Lake, Texas (lat 29.563°N, long 95.071°W), in September 2004 (23 clutches), April 2005 (24), and June 2005 (20). We haphazardly located egg clutches deposited on emergent substrates slightly above the water level near the shore. Most clutches occurred on *Colocasia esculenta* (wild taro). We selected the most recently deposited egg clutches, which seemed soft, sometimes moist, and vibrant pink (Fig. 1A). To prevent damage to the eggs and protect them during transport, we removed the section of plant to which the clutch was attached, wrapped each clutch in waxed paper, and packed each in a separate compartment of a plastic storage container.

We examined the relationship between clutch mass and egg number to develop a predictor of the number of eggs in a clutch. We weighed each clutch and then submerged it in a 1 M NaOH solution to dissolve the matrix holding the eggs together (Joshi et al. 2002). Within several minutes of submergence, this procedure left individual eggs intact for counting. We used linear regression for this analysis (all statistical analyses performed with SPSS 13.0; SPSS Inc., Chicago, Illinois) because we had counted all eggs in each clutch and wanted a predictive relationship between clutch mass and egg number. We determined whether egg size was correlated with clutch mass by randomly selecting 20 eggs from each of 7 clutches ($n = 140$ eggs total). We measured egg diameter with a dissecting stereomicroscope, digital camera, and imaging software (Image-Pro Express 4.5.1.3; Media Cybernetics, Inc., Bethesda, Maryland). We assessed this relationship with a Pearson correlation.

We placed 48 additional field-collected egg clutches above individual containers in the laboratory and collected hatchlings as they emerged to study hatchling size at emergence. We allowed clutches to hatch for 10 d after the 1st hatchling emerged. This period was sufficient for complete *P. insularum* hatchling emergence (MAB, personal observation) and falls within the average complete hatching time of *P. canaliculata* (Cazzaniga 2006). We randomly collected and measured up to 10 hatchlings d⁻¹ clutch⁻¹. We discarded any additional hatchlings that occurred each day, thereby ensuring that we collected only newly emerged hatchlings. We used a dissecting stereomicroscope and digital camera to make the measurements because of the small size of hatchlings. We chose to measure operculum width (called "greater opercular diameter" by Guedes et al. 1981 and "apertural length" by Estebenet and Martín 2003) because opercula of snails provided the only flat surface for photography, and using this flat surface maximized our confidence in our measurements (Fig. 2). Youens and Burks (2008) subsequently confirmed that this measure provided the most reliable indication of applesnail size for juveniles and adults. We measured 1453 hatchlings and calculated a linear regression to assess the predictive relationship between hatchling size and day of emergence.

Field hatching success

We used enclosures with 500-μm-pore nylon screening to determine *P. insularum* egg hatching success in the field. We individually enclosed 50 egg clutches by wrapping screen around *C. esculenta* stems and securing it tightly above and below an egg clutch. We added an additional layer of 70% UV-resistant cloth to shade 25 of these clutches. We planned to compare hatching success in the 25 shaded enclosed clutches with success in the 25 unshaded enclosed clutches to test for a relationship between temperature and hatching efficiency. Thermochron iButtons® (Dallas Semiconductor, Dallas, Texas) located on 5 shaded and 5 unshaded egg clutches recorded temperature measurements for our comparison between unshaded vs shaded enclosures. We distributed a total of 50 enclosures over 3 dates: 29 July 2006 (20 enclosures), 5 August 2006 (10), and 2 September 2006 (20). After 2 wk, we clipped each plant stem above and below the enclosure to remove the clutch in its entirety. We counted the number of hatchlings and unhatched eggs (combined total = original clutch size) in each enclosure after dissolving any remaining clutch material as previously described. We calculated hatching efficiency (the number of hatchlings as a percentage of the total eggs in the clutch). We squared hatching efficiency to normalize the data and used a 2-way analysis of variance (ANOVA) to examine effects of date and enclosure on hatching efficiency. We used Tukey's post hoc comparisons to identify significantly different dates. We calculated mean temperature over time for each treatment and used a Pearson correlation to assess any possible relationship between total egg number and hatching efficiency of all clutches.
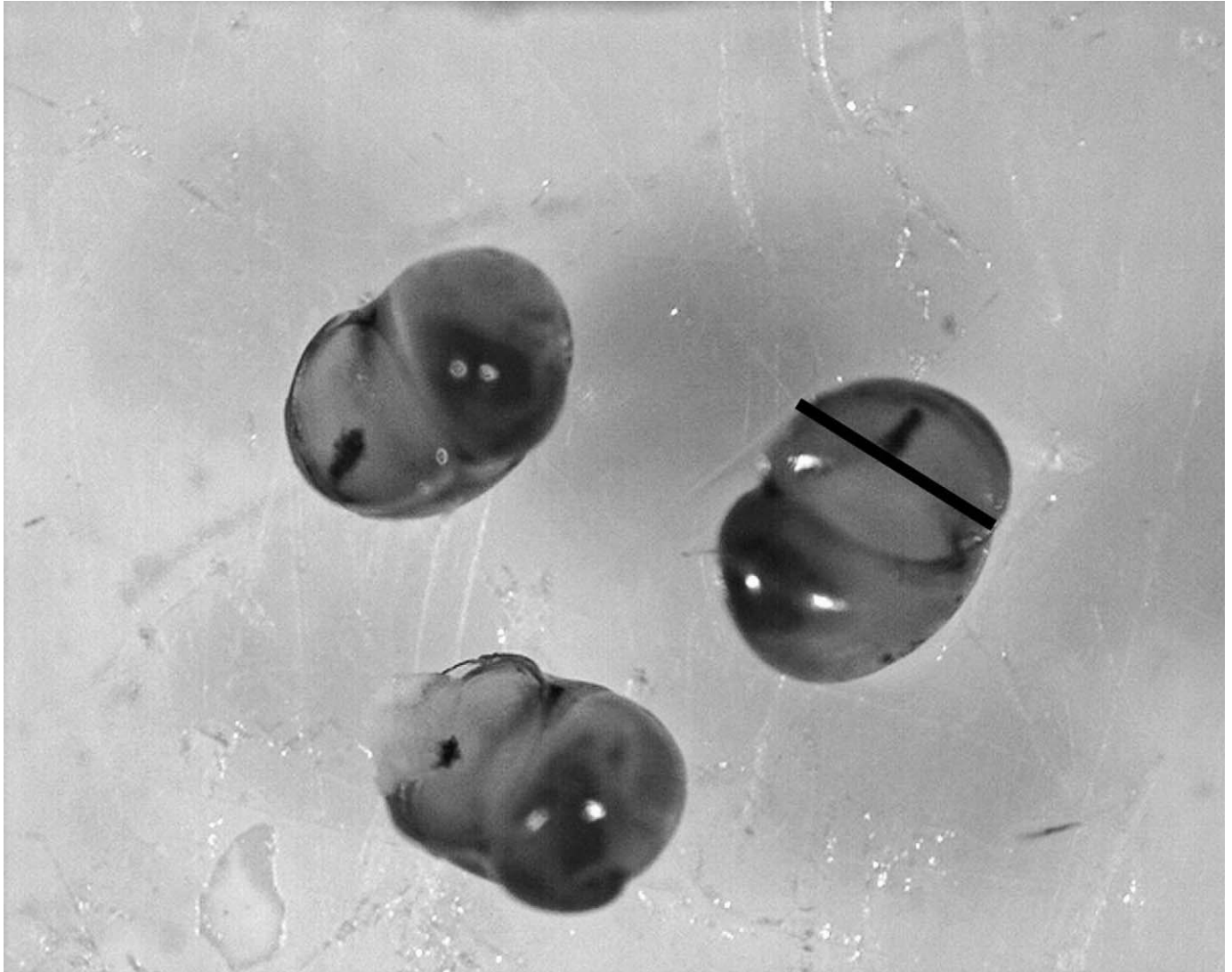
FIG. 2. Three *Pomacea insularum* hatchlings at 50× magnification. Black line indicates operculum width measurement.

Laboratory hatching success

We incubated field-collected *P. insularum* egg clutches (*n* = 48 clutches; collected May 2005) in the laboratory ~4 cm above individual water-filled containers designed to collect emerging hatchlings to analyze hatching efficiency in a controlled setting (25°C, 12:12 light:dark). After 4 wk, we determined hatching efficiency as previously described.

Results

Physical characteristics

In Horsepen Bayou, female *P. insularum* deposited large bright pink egg clutches (mean = 1626 eggs) on any hard surface above the water, especially in dense stands of *C. esculenta* (MAB, personal observation). Egg number and clutch mass were significantly positively related, but analysis of all clutches combined lacked predictive strength ($p < 0.001$, $R^2 = 0.148$; Table 1). In April, the beginning of the reproductive season, we found a strong linear relationship between egg number and clutch mass that persisted into June. Average egg number nearly tripled from April to June, but declined slightly in September (Table 1). By September, the relationship between egg number and clutch mass weakened, possibly because of the presence of very large clutches of >4500 eggs.

Mean egg size (diameter) was 1.94 mm (± 0.03 mm [SE]). Egg size and clutch mass were weakly positively correlated ($p < 0.001$, $r = 0.29$). Operculum width of emerging hatchlings did not vary (*n* = 1453, mean

TABLE 1. Variation in the relationship between egg clutch mass (x) and number of eggs/clutch (y) of *Pomacea insularum* across a summer season.

Collection date	n	Clutch mass (g)		Eggs/clutch		R^2	p	Regression
		Mean	SE	Mean	SE			
April	24	9.7	0.878	767.7	74.6	0.713	<0.001	$y = 74.6x + 71.6$
June	20	8.6	0.604	2247.8	184.8	0.654	<0.001	$y = 92.5x + 249.6$
Sepember	23	8.9	0.980	1982.0	204.2	0.306	0.006	$y = 946.5x + 116.2$
Total	67	9.1	0.489	1626.3	121.7	0.148	<0.001	$y = 754.1x + 95.8$

width = 1.14 ± 0.003 mm). Furthermore, day of hatching did not provide a reliable predictor of hatchling size ($R^2 = 0.012$).

Field hatching success

In 50 clutches observed between 29 July and 16 September 2006, total number of eggs/clutch ranged from 1187 to 4751 (2006 mean = 2651 eggs; grand mean of all clutches collected in our study = 2064). The number of eggs was not significantly different between shaded and unshaded clutches ($F_{1,49} = 0.678$, $p = 0.415$). The number of eggs varied considerably (11–4359; mean = 1907). Clutch size increased from late July to mid-September, but the change was not statistically significant ($F_{2,49} = 1.161$, $p = 0.323$; Fig. 3).

Hatching efficiencies ranged from 0.9 to 94.3% (mean = 70.8%). Several clutches failed to hatch, but most clutches produced hundreds of hatchlings. Temperature did not differ between the shaded and unshaded enclosures (mean = 27.1 ± 0.2°C), but some seasonal variation occurred, with the lowest temperatures in September. The UV cloth did not affect the temperature of the egg clutches, but it probably provided additional shelter against abiotic factors, such as light and wind. Unshaded clutches (78.4%) exhibited significantly higher hatching efficiency than shaded clutches (63.1%) ($F_{1,49} = 4.712$, $p = 0.035$; Fig. 4). Hatching efficiency did not differ significantly among dates ($F_{2,49} = 1.240$, $p = 0.299$), nor was it significantly related to the total number of eggs in a clutch ($p = 0.164$).

Laboratory hatching success

Pomacea insularum clutches deposited in the field but hatched in the laboratory exhibited an average hatching efficiency of 31.4% with considerable variation (SE = 5.04%). The high level of variation was related, in part, to the fact that 8 of 48 clutches failed to hatch. Thirty-four of 48 clutches had <25% hatching efficiency, and 5 clutches had >80% hatching efficiency.

Discussion

Between September 2004 and September 2006, we collected and counted 117 egg clutches that contained 211 to 4751 eggs each (grand mean = 2064). The largest single clutch of *P. insularum* exceeded the total estimated annual fecundity for the closely related invasive species *P. canaliculata* (4355 eggs female^{-1} y^{-1}; Keller et al. 2007). Average clutch size also greatly exceeded reported average values for single *P. canaliculata* clutches, both in exotic and native ranges. Cowie (2002) tabulated data on number of eggs/clutch from numerous studies of *P. canaliculata*, with numbers ranging from 25 to 1000, and suggested an average of ~200 eggs/clutch. Subsequent data from Malaysia (Teo 2004) recorded *P. canaliculata* clutches of 92 to 592 eggs (mean = 272). Our own preliminary studies of a native *P. canaliculata* population in Uruguay give estimates in the same range (mean = 251 eggs/clutch; RLB, unpublished data). Our work shows that the
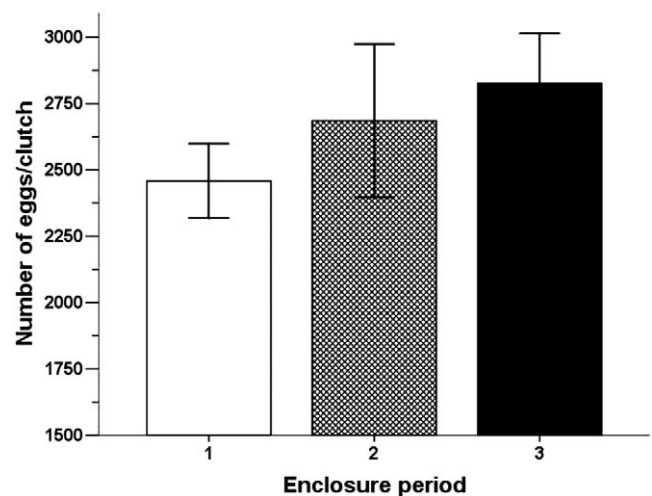

FIG. 3. Mean (±1 SE) number of *Pomacea insularum* eggs/clutch in 3 enclosure periods. Total shaded and unshaded enclosures were 20, 10, and 20 in the 29 July to 12 August (period 1), 5 August to 20 August (period 2), and 2 September to 16 September (period 3) enclosure periods, respectively.
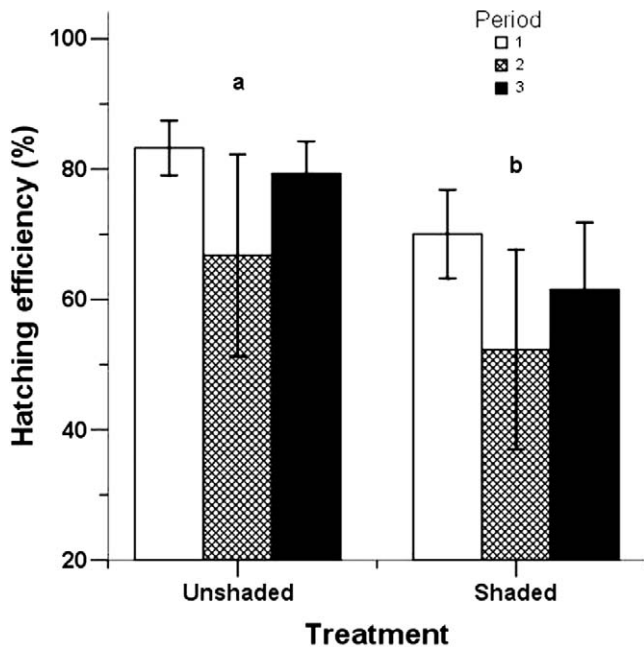
FIG. 4. Mean (±1 SE) hatching efficiency (number of eggs hatched/total number of eggs in clutch) of *Pomacea insularum* eggs in the 29 July to 12 August (period 1), 5 August to 20 August (period 2), and 2 September to 16 September (period 3) enclosure periods. Clutches were enclosed in fine mesh (unshaded) or in fine mesh and 70% UV-excluding shade cloth (shaded). Different lowercase letters above sets of bars indicate significant differences between enclosure types ($p = 0.035$).

average size of a *P. insularum* clutch greatly exceeds that of a *P. canaliculata* clutch. Keller et al. (2007) suggested that fecundity provides the strongest predictor of invasive success in mollusks. The nonindigenous gastropod *P. insularum* has occurred in Texas for >10 y (Rawlings et al. 2007), but no published studies have assessed the present population or its invasive potential. Our study provides the first quantitative examination of *P. insularum* fecundity.

However, we must be cautious not to count our snails before they hatch. *Pomacea insularum* clutches rarely experienced complete hatching success in our study. In the field, average hatching success was only slightly >70.8%. Shaded egg clutches had slightly lower success than unshaded clutches, and considerably lower hatching success occurred in the laboratory (on average, slightly >30%). Despite our best efforts to minimize clutch disturbance in transport from the field to the laboratory, the stress of transportation might have been responsible for the lower laboratory hatching efficiency. Lacanilao (1990) failed to demonstrate a temperature effect on hatching efficiency in *P. canaliculata* but did suggest that photoperiod might

affect hatching efficiency. Therefore, we speculate that the lower hatching successes under 70% UV shelter in the field and in artificial light conditions in the laboratory might have contributed to lower hatching efficiency. Future studies using incubation chambers could further examine effects of temperature and light on hatching efficiency.

Hatching success in both *P. insularum* (our data) and *P. canaliculata* (Cowie 2002, Teo 2004) is highly variable, with no consistent difference between the 2 species. Kolar and Lodge (2001) concluded that having invasive relatives increases a species' potential to be a successful invader, and we have demonstrated that egg production of *P. insularum* exceeds that of the closely related, devastatingly invasive *P. canaliculata*. Regardless of whether an innate difference in hatching success exists between the 2 species, an average *P. insularum* clutch (2064 eggs) would still produce >600 hatchlings even at a hatching efficiency of only 30%, which equals 3× the number of hatchlings produced by the average *P. canaliculata* clutch at peak hatching efficiency. If one estimates that 10% of *P. insularum* hatchlings survive to reproductive age, each clutch contributes 144 new applesnails to the population. Even with a more conservative estimate of 1% survival to adulthood, a female applesnail could contribute 14 new reproductively viable applesnails with each clutch. During warm months (16–18 wk) in the southeastern US, a female applesnail can produce a new clutch each week (RLB, personal observation), yielding a total of 252 viable hatchlings female^{-1} reproductive season^{-1}.

Populations recently have been confirmed in the Florida Everglades. Thus, the potential exists for competition with and displacement of the only native applesnail species in North America, *P. paludosa*, which is the specialized food resource of the endangered Everglades kite (*Rostrhamus sociabilis plumbeus*). Thus, the need for more research is urgent. Vibrant pink egg clutches represent the only life-history stage in which the applesnail does not hide among the benthos, and they might represent a promising target for control efforts. Ecologists have long understood the value of life-history studies and their contribution to our understanding of species population dynamics (Cole 1954). We believe our and future life-history studies will have particular importance for contributing to predictions of invasion potential of *P. insularum*, mollusks in general, and other exotic invaders.

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