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INVADING HERBIVORY: THE GOLDEN APPLE SNAIL ALTERS ECOSYSTEM FUNCTIONING IN ASIAN WETLANDS

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Abstract. We investigated the effects of an exotic snail, the golden apple snail (*Pomacea canaliculata*) on biodiversity and ecosystem functioning in tropical wetland ecosystems. This large snail (up to 80-mm shell height) has invaded large parts of Southeast Asia during recent decades. A survey of natural wetlands in Thailand showed that high densities of the snail were associated with almost complete absence of aquatic plants, high nutrient concentrations, and high phytoplankton biomass, that is, a complete shift in both ecosystem state and function. A field experiment demonstrated that grazing by the snail can cause the loss of aquatic plants, a change toward dominance of planktonic algae, and thereby a shift toward turbid water. Estimates of biologically fixed nutrients released through snails grazing on aquatic plants revealed that phosphorus releases were sufficient to explain the recorded increase in phytoplankton biomass. Hence, our study demonstrates how an herbivore may trigger a shift from clear water and macrophyte dominance to a turbid state dominated by planktonic algae. This shift and the continuing aggressive invasion of this exotic species are detrimental to the integrity and functioning of wetland ecosystems, and to the services these provide in Southeast Asia.

Key words: ecosystem functioning; exotic species; freshwater; golden apple snail; herbivory; invasive species; limnology; macrophyte; Pomacea; *species richness.*

Introduction

Invasion by exotic species has been identified as one of the major threats to global biodiversity (Buchan and Padilla 1999, Chapin et al. 2000, Kolar and Lodge 2000, Sala et al. 2000, Strayer 2001), and during the last decade there has been an increasing concern about the ecological consequences of biodiversity loss (Tilman 1999, Chapin et al. 2000, Loreau et al. 2001). Moreover, both loss of native species and addition of exotic species may have dramatic effects on ecosystem functioning by altering assemblages of species-specific traits, which can influence ecosystem processes. Hence, when the strength and direction of species interactions are altered through addition or removal of species, ecosystem functioning may be affected through both direct and more indirect pathways. In freshwater systems, changes in species interaction strength and direction are often realized as trophic cascades, where lower trophic levels are affected by changes at higher levels (e.g., Carpenter et al. 1985, Hansson 1992, Carpenter and Kitchell 1993, Brönmark et al. 1997). Modifications of energy and material fluxes induced by exotic species and reduced biodiversity may also result in a loss of ecosystem services of great economic value (Costanza et al. 1997).

Here, we study the effects of an introduced invertebrate herbivore, the golden apple snail (*Pomacea canaliculata* Lamarck; Gastropoda: Ampullariidae, see Plate 1) on aquatic plants and ecosystem processes in tropical wetlands. Aquatic plants are central to all aspects of wetland functioning from maintaining biodiversity to ensuring sustained productivity and natural water purification. Herbivore–induced changes in plant biomass and plant community structure may therefore fundamentally alter wetland ecosystem functioning. In Southeast Asia, these changes could have dramatic effects on the use of wetlands as ‘‘biological supermarkets’’ where plants, fish, crustaceans, and insects are harvested as food and animal fodder, water is used for human consumption, and wastewater is biofiltered (Tripathi et al. 1991, Furukawa and Fujita 1993, Azimi et al. 2000). The aggressive invasion of the herbivorous golden apple snail quickly drew the attention of scientists and government agencies when the snail became a serious pest on rice (Anderson 1993, Halwart 1994, Naylor 1996, Yusa and Wada 1999). This aquatic snail was initially introduced to Taiwan from South America in 1980 for aquaculture, for local food consumption as well as for export (Naylor 1996 and references therein). Within five years it became abundant in Japan, southeast China, and in the Philippines, and in 2002 it had established strong populations in most Southeast Asian countries (Fig. 1). The snail has also been found in Hawaii (Lach and Cowie 1999) and the southern United States (Neck and Schultz 1992, Thompson 1997). Recent reports indicate that the snail is now invading Australia (available online)[2] and is expected to reach Bangladesh and India in the near future (Baker 1998).

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[2] URL: ⟨http://www.state.gov/g/oes/ocns/inv/cs/2312pf.htm⟩

PLATE 1. The golden apple snail may reach 80 mm in shell height and 120 grams in weight. It is a repeat invasive offender that is spreading in Southeast Asia and elsewhere. Photo credit: Nils Carlsson.

In contrast to most other freshwater snails, *P. canaliculata* is macrophytophagous, preferring submerged or floating freshwater macrophytes (Estebenet 1995, Estebenet and Martin 2002), and thereby constitutes a major threat to rice farming. A preliminary small-scale experiment indicated that the snail might also have a strong, negative effect on naturally occurring wetland plants (N. O. L. Carlsson and J. Lacoursière, *unpublished data*), suggesting serious implications for biodiversity and the functioning of natural wetland ecosystems.

To determine the effect of *P. canaliculata* on ecosystem functioning we surveyed natural wetlands with varying densities of snails. We also performed a complementary field experiment, testing the effects of increasing densities of *P. canaliculata* on macrophytes and phytoplankton, to unravel the mechanisms behind the patterns observed in natural wetlands.

METHODS

The golden apple snail can reach a wet mass of 120 g and 80 mm in shell height (N. O. L. Carlsson, *unpublished data*), corresponding to the size of a medium-sized apple. Females can spawn on average 1.4 times a week (Albrecht et al. 1996), and the egg masses are deposited above the waterline (Estebenet and Martin 2002). We surveyed 14 wetlands (average wetland area: 283 ± 133 m^2; mean ± SD) all situated within the Klong Chonprathan catchment, close to the city of Hua Hin, Thailand (12°34′ N; 99°58′ E), assessing snail density, aquatic plant communities, phytoplankton biomass, and water chemistry. In each wetland water samples were collected with a tube sampler (1.00 × 0.18 m) in the middle of the wetland and, from a pooled sample of 2.5 L, two subsamples of 0.1 L were taken for measurement of total phosphorus (TP) and total nitrogen (TN). Total phosphorus was analyzed as soluble reactive phosphorus after digestion with potassium persulphate. Total nitrogen was analyzed as nitrite after digestion with potassium persulphate and sodium hydroxide and after nitrate reduction by a copper-cadmium reductor column. All analyses were performed on a Technicon autoanalyzer II (Technicon, Saskatoon, Saskatchewan, Canada) according to Technicon protocols (SS-EN 1189 and SS-EN 11905-1). From the same, pooled sample, 0.5 L was filtered (Whatman GF/C) for chlorophyll *a* analysis as an estimate of phytoplankton biomass. The samples were frozen for later extraction in 96% ethanol, and spectrophotometric analysis (665 nm; Jespersen and Christoffersen 1987). Wetland shape was approximated to a rectangle and total area was estimated by measuring the length of the longest and shortest sides. The wetland was then divided into 2 × 2 m squares and the percentage aquatic plant cover in each square was estimated. Maximum depth was measured to the nearest centimeter. Abundances and biomasses of snails and macrophytes were assessed by random quadrat sampling (1-m^2 frame, $n = 10$ in each wetland). We retrieved all plants and snails from quadrats with a hand net (2-mm mesh size). Plant species that covered at least 10% of the total surface area were identified to genus or, when possible, to species and only these were used in estimates of plant species richness.

One of the wetlands (area 340 m^2, mean depth 0.7 m) with a low density of the golden apple snail and high coverage of aquatic plants was used in an enclosure experiment. Twenty-four wooden framed enclosures (1 × 1 × 1 m) with walls of transparent plastic

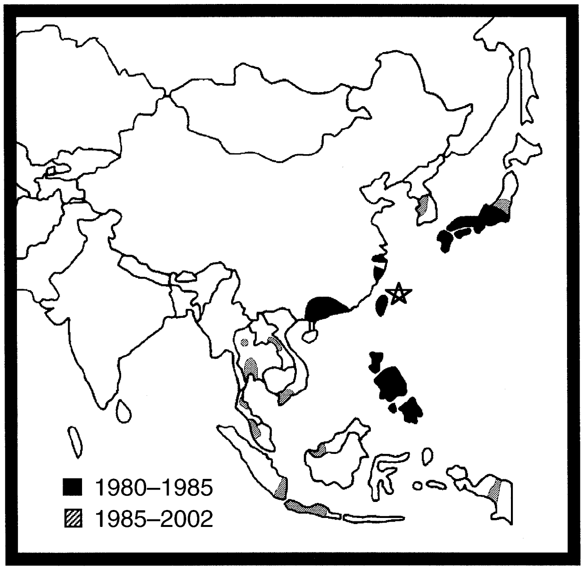

FIG. 1. Dispersal of the golden apple snail from its original introduction to Taiwan 1980. The figure is drawn after Mochida (1991), Halwart (1994), and Naylor (1996).

(1 mm) were placed in six blocks of four enclosures at a water depth of 0.6 m. The enclosures were pushed 0.2 m down into the sediment and then swept with a hand net to remove fish and snails. In addition, we placed fish traps in each corner of the enclosure to ensure that enclosures were free of fish. *Eichhornia crassipes* was a dominant macrophyte in wetlands and constituted about 75% of the total plant coverage in the experimental wetland. Other plant species were *Ipomoea aquatica*, *Lemna minor*, *Pistia* sp., *Salvinia* sp., *Ludwigia* sp., and *Typha* sp. The edibility of all plants was tested in a laboratory experiment. All species but *Typha* sp. were readily eaten by *P. canaliculata* (N. O. L. Carlsson, *unpublished data*) and, thus, edible plants refer to all species except *Typha* sp. Due to its dominance, *E. crassipes*, a free-floating macrophyte, was selected as the experimental plant and was introduced to all enclosures at a wet mass of 420 ± 7 g (mean ± SD), corresponding to natural biomass in the wetlands. *P. canaliculata* snails of medium size (25–35 mm shell height) were collected in a nearby wetland and added to enclosures at a density of 0, 2, 4, or 6 snails, respectively, with six replicates for each density. When all snails were introduced we covered the enclosures with nets (mesh size 10 mm) to avoid bird predation and snail escape. The enclosures were sampled initially and after 3, 6, 10, 15, 23, and 27 days. We measured plant biomass by lifting plants out with a hand net, weighing them, and returning them to cages. Chlorophyll *a* concentration and final snail densities were determined as in the field survey.

RESULTS AND DISCUSSION

In our survey, neither wetland area nor depth were correlated to snail abundance, macrophyte species richness and cover, or phytoplankton and nutrient concentrations ($P > 0.2$ in all cases). However, the species richness and coverage of aquatic plants were negatively correlated to the density of *P. canaliculata*. Macrophyte cover decreased when snail density exceeded two snails per square meter ($r = -0.68$, $P < 0.010$; Fig. 2) and species richness of edible plants was negatively correlated with snail density ($r = -0.50$, $P < 0.050$; Fig. 2). This analysis includes all size classes of snails, even though snails with a shell height <15 mm generally do not feed on macrophytes (Halwart 1994). If the analysis is based only on snails >15 mm, the relationship between snail density and macrophyte species number is considerably stronger ($r = -0.77$, $P < 0.002$).

The concentrations of the generally growth-limiting nutrients phosphorus and nitrogen increased with the density of *P. canaliculata* ($r = 0.79$, $P < 0.001$ and $r = 0.74$, $P < 0.001$, respectively). A positive correlation between snail density and phytoplankton biomass ($r = 0.59$, $P < 0.010$; Fig. 2) is consistent with algal blooms observed in wetlands with high snail density. At snail densities above 10 individuals/m^2 algal chlorophyll concentration generally exceeded 100 μg/L, phosphorus concentrations reached 200–1000 μg/L, and nitrogen concentrations exceeded 1000 μg/L. At the highest snail densities, wetlands were almost devoid of macrophytes (Fig. 2). Thus, the results from the wetland

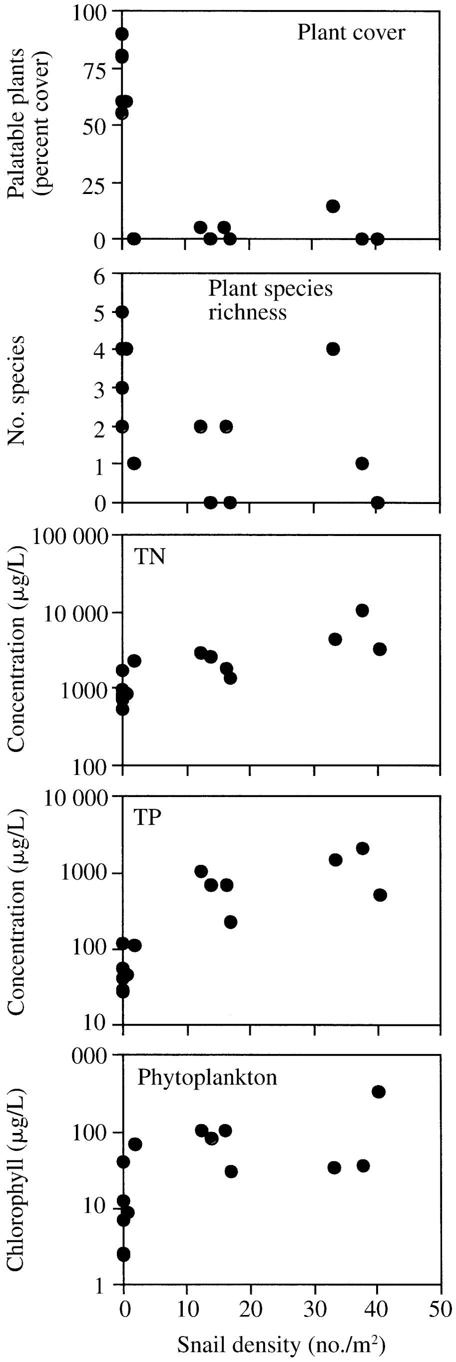

FIG. 2. Correlations among sites betweeen snail density and macrophyte plant cover, species richness, total nitrogen (TN), total phosphorus (TP), and phytoplankton chlorophyll *a* in Thailand wetlands ($n = 14$). Note the log-scale axes on TN, TP, and chlorophyll graphs.

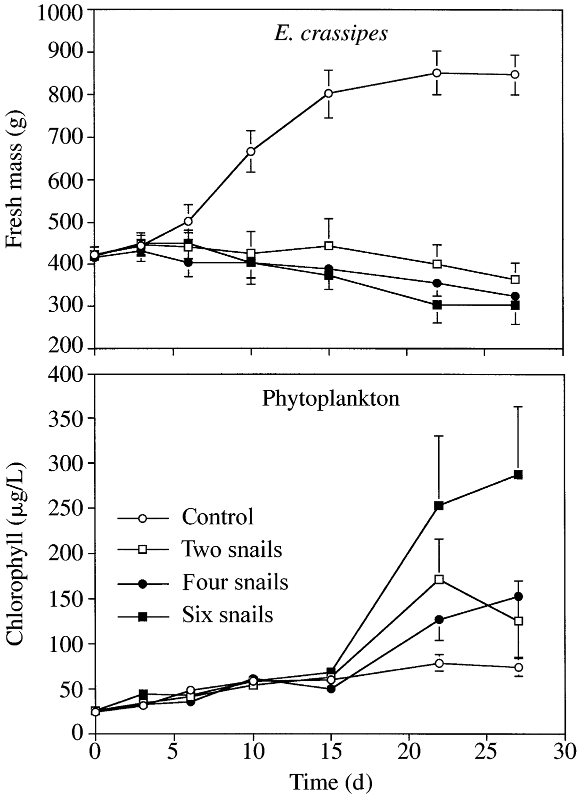

FIG. 3. Temporal developments in biomass of the dominant macrophyte plant *Eichhornia crassipes* and phytoplankton chlorophyll *a* in experimental enclosures at snail densities (no./m^2) of zero (open circles), two (open squares), four (solid circles), and six (solid squares) individuals. Mean values ± 1 SE are given ($n = 6$).

survey suggest that increasing densities of the snail *P. canaliculata* strongly modify the flux of nutrients and shift the primary production from macrophytes to phytoplankton.

The causal relationship between snail grazing, and macrophyte and phytoplankton biomass was tested in the field experiment where we found that grazing by *P. canaliculata* in experimental enclosures had a negative impact on biomass of *E. crassipes* (repeated-measures ANOVA, $F_{3,6} = 59.296$, $P < 0.001$; Fig. 3). A contrast analysis showed that there was no further effect of snail densities higher than two individuals/m^2 ($P < 0.001$; Fisher's protected least significant difference [PLSD]), suggesting that snails have strong effects on plant biomass already at very low densities (Fig. 3). The decrease in macrophyte biomass in treatments with snails was followed by severe algal blooms, so that snails had a positive effect on phytoplankton biomass (repeated-measures ANOVA, $F_{3,6} = 6.011$, $P < 0.001$; Fig. 3). The highest snail treatment had higher phytoplankton biomass than the other treatments ($P < 0.001$, Fisher's PLSD).

The average feeding rate of snails on *E. crassipes* during the experimental period was 1.01 $\text{g}\cdot\text{snail}^{-1}\cdot\text{d}^{-1}$ (wet mass), corresponding to a dry mass of 0.093 $\text{g}\cdot\text{snail}^{-1}\cdot\text{d}^{-1}$ (9.2% of wet mass; N. O. L. Carlsson, *unpublished data*). Since the phosphorus content of *E. crassipes* is 0.57% of the dry mass (Aoyoma and Nishizaka 1993), the predicted amount of phosphorus released to the enclosure (approximate volume, 400 L) at the end of the experiment (28 days) should be 37.1 $\mu\text{g}\cdot\text{L}^{-1}\cdot\text{snail}^{-1}$. Over the experimental period the phosphorus concentration increased, by this estimate, by 74.2, 148.4, and 222.6 μg/L in the treatments with 2, 4, and 6 snails, respectively. As we know the initial total phosphorus concentration (48 μg/L), we can calculate the predicted increase in chlorophyll *a* due to phosphorus excretion by snails from a log-linear relationship between total phosphorus and chlorophyll *a* ([$\log(\text{chl}) = 1.583(\log \text{phosphorus}) - 1.134$]; Dillon and Rigler 1974). Predicted chlorophyll concentrations were 148, 313, and 520 μg/L in treatments with 2, 4, and 6 snails, respectively. Our final chlorophyll concentrations were somewhat lower, reaching 125, 153, and 287 μg/L (Fig. 3), corresponding to 84%, 49%, and 55% of the predicted values. This discrepancy might be accounted for by phosphorus uptake by the snails or sequestering of released phosphorus in the sediment and in periphytic algae. However, this calculation demonstrates that phosphorus released through snail grazing on macrophytes is sufficient to cause the recorded increase in phytoplankton biomass.

The invasion of the golden apple snail results in an almost complete collapse of the aquatic plant community, leading to a shift from a plant-dominated, clear-water state, to a turbid, algae-dominated state (Scheffer et al. 1993). Recently, shifts in alternative stable states have been shown to be a common phenomenon in both aquatic and terrestrial systems (Carpenter 2000, Scheffer et al. 2001). In aquatic systems, shifts in alternative stable states have previously been shown to be mediated by high nutrient loads or high cyprinid fish abundances (Hansson et al. 1998, Scheffer 1998). Moreover, Lodge et al. (1998) suggested that macrophyte herbivory may tip aquatic systems from a clear to a turbid state. Despite several studies showing that herbivores, such as birds (van Donk 1998), fish (Hansson et al. 1987), and crayfish (Lodge et al. 1998) feed on aquatic macrophytes, such herbivores have not been shown to induce shifts in states in freshwater systems. Our study, however, demonstrates how feeding by an invertebrate herbivore can mediate a shift from clear water and macrophyte dominance to turbid water and phytoplankton dominance by making biologically fixed nutrients from macrophyte plants available for planktonic algae.

In its native South America the golden apple snail occurs at very low densities compared to invaded areas in Asia (Halwart 1994). This may be due to high predation pressure since snails from this family are regarded as key prey organisms in their native habitat (Donnay and Beissinger 1993). In Southeast Asia, efficient native predators on the golden apple snail are rare (Ichinose et al. 2002 and references herein) suggesting that lack of predation is an important mechanism in promoting the snail populations. Similar patterns have recently been shown for the snail *Littoraria irrorata* native to salt marshes in e.g., the eastern United States. When left without predators, the *Littoraria* snails completely eroded stands of the salt marsh plant *Spartina*, suggesting that snail grazing in marine salt marshes is predator controlled (Silliman and Bertness 2002).

Aquatic plants in freshwater systems provide substrate, refuge from predation, and a source of food for other aquatic organisms (Brönmark and Vermaat 1998, Diehl and Kornijów 1998, Lodge et al. 1998). Plants also affect nutrient fluxes by luxury consumption and storage of nutrients and by being a substrate for denitrifying microorganisms. Reduced biodiversity and biomass of aquatic plants have been shown to affect nutrient retention capacity of wetlands considerably (Engelhardt and Ritchie 2001). Thus, macrophyte grazing by the golden apple snail not only alters the function of wetland ecosystems; it also drastically reduces the value of ecosystem services provided by the wetland.

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