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Lethal and non-lethal effects of multiple indigenous predators on the invasive golden apple snail (*Pomacea canaliculata*)

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SUMMARY

1. We investigated the individual and combined effects of two predators (the climbing perch, *Anabas testudineus*, and the wetland crab, *Esanthelphusa nimoafi*) indigenous to wetlands in Laos, on the behaviour and survival of the invasive South American golden apple snail (*Pomacea canaliculata*). The snail is considered a pest, consuming large amounts of rice and other aquatic vegetation in the region.
2. Snail avoidance reactions to released predator chemical cues were investigated in aquaria while the effects of predators on a mixed snail population were studied in field enclosures that contained native aquatic plants (*Salvinia cucullata*, *Ludwigia adscendens* and *Ipomoea aquatica*).
3. In the aquaria experiment, neonate (2–3 mm) and medium-sized snails (8–10 mm) responded to fish chemical cues by going to the surface, whereas adult snails (35–40 mm) went to the bottom. In contrast, no size class of snails reacted to chemical cues released by crabs.
4. In the field experiment, fish reduced the abundance of neonate snails, and crabs reduced the abundance of all size classes. The effect of the combined predators could not be predicted from the mortality rate observed in single predator treatments. The survival of neonate and medium-sized snails was greater and of adults less than expected. The presence of predators did not affect egg production. Snails consumed significant amounts of plants despite the presence of predators.
5. Our findings suggest that some indigenous Asian predators have lethal and sublethal effects on *P. canaliculata* that depend on snail size and predator type. When in the presence of several predators the response of snails to one predator may either increase or decrease the vulnerability of snails to the others.

Keywords: chemical cues, freshwater snails, indigenous predators, invasive herbivory, predator avoidance

Introduction

Negative effects of introduced species on an area's economy, ecological services and native biodiversity are numerous, global and increasing (Ewel *et al.*, 1999; Mack *et al.*, 2000). General and predictive explanations of why an introduced organism becomes invasive remain elusive (Mack, 1996), but some patterns are emerging. Propagule pressure, defined as the number of individuals released as well as the number of release events, is promising as a predictor of invasion by some taxa (Kolar & Lodge, 2001). Another approach is ecological niche modelling, where the base ecological requirements of a species are extrapolated to new areas (Peterson & Vieglais, 2001). In contrast, other conceptual models relate the success of invasions to the degree of negative interactions between the introduced species and the native biota.

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These typically conform to either the 'enemy release hypothesis' or the 'biotic resistance hypothesis'. According to the first, introduced species are relieved from natural enemies in the invaded range, which allows them to proliferate (Mack *et al.*, 2000; Torchin *et al.*, 2003). According to the second, native biota could act like an immune system that lowers invader success (Elton, 1958; Kennedy *et al.*, 2002). Support for both hypotheses is accumulating rapidly, which suggests that the mechanisms affecting species invasions are complex (Mitchell & Power, 2003).

The invasion by the exotic golden apple snail (*Pomacea canaliculata*, Lamarck) in Southeast Asia is a threat to local agricultural economies (Halwart, 1994; Naylor, 1996) and the structure and functioning of wetlands (Carlsson, Brönmark & Hansson, 2004) as the snail consumes rice and naturally occurring aquatic plants. It was introduced intentionally from South America for aquaculture into a number of countries in the region in the 1980s (Naylor, 1996), so high propagule pressure preceded the invasion. Climatic modelling, where temperature and precipitation in the native range is compared with that of the invaded areas, suggests that both invaded and nearby areas (Bangladesh, India and Australia) are suitable for the snail (Baker, 1998). In addition, it has been suggested that the snail is released from natural enemies in the form of predators and competitors (Andersson, 1993; Naylor, 1996; Ichinose *et al.*, 2002 and references therein), but few studies have investigated how this invasive snail interacts with indigenous Asian predators.

Predation is one of the major factors influencing prey population dynamics and community structure (e.g. Sih, 1987; Lima & Dill, 1990). Predator behaviour can significantly influence predator impact. The outcome of predator–prey interactions in aquatic food webs containing native and exotic species is difficult to predict as we seldom know how prey responds. In some cases prey do not recognise exotic predators (Shave, Townsend & Crowl, 1994; Kiesecker & Blaustein, 1997a): in others, prey display avoidance behaviour that indirectly affects predation risk from other predators (Kiesecker & Blaustein, 1997b). Other examples indicate that, although appropriate prey avoidance behaviour may reduce predation risk substantially, predators have strong indirect effects on prey feeding and food sources (e.g. McIntosh & Townsend, 1996). Therefore, to understand the mechanisms affecting the success of invasive species it is important to study how these species respond to different types of indigenous predators and if these behaviours affect the predation risk posed by the whole predator assemblage.

In this study we tested if two co-existing predators, (the fish *Anabas testudineus*, Bloch) and the (previously unnamed) freshwater crab *Esantelphusa nimoafi* (Yeo, 2004), indigenous to shallow wetlands in Laos, affected the behaviour and survival of *P. canaliculata*. Studies involving molluscivorous fish and crustaceans suggest that these predators are selective consumers of molluscs and often prefer small size-classes of prey and snails with thin shells (Schindler *et al.*, 1994; Brönmark & Weisner, 1996; Nyström & Pérez, 1998; Smallegange & Van der Meer, 2003). Some vulnerable species and size-classes of molluscs respond to chemical cues released when predators consume conspecifics (e.g. Alexander & Covich, 1991; DeWitt, Sih & Hucko, 1999; Turner, Bernot & Boes, 2000; Rundle & Brönmark, 2001). Both the reduction in snail abundance by predators and behavioural changes of prey may indirectly affect lower trophic levels (Brönmark & Weisner, 1996; Turner *et al.*, 2000; Bernot & Turner, 2001; Trussel, Ewanchuk & Bertness, 2002). Important predators may therefore reduce the impact of the golden apple snail on aquatic plants through both lethal and non-lethal effects.

Predatory fish and freshwater crayfish sometimes have different effects on freshwater snail behaviour. In the presence of fish, snails typically seek cover whereas, in response to crayfish, they often crawl out of the water or stay close to the surface (Alexander & Covich, 1991; Turner, Fetterolf & Bernot, 1999; McCarthy & Fisher, 2000; Turner *et al.*, 2000). This suggests that predator avoidance may depend on the risk posed by particular predators in different habitats, and that the combined effects of two predators may result in behaviour and survival rates not predicted by studying a single predator (e.g. Sih, Englund & Wooster, 1998; Turner *et al.*, 2000).

In an aquarium experiment we first tested how different size classes of snails responded to chemical cues released by fish and crabs. Then, in a large-scale field experiment, we tested the effect of predators (single predators and in combination) on the survival of snails and, indirectly, on the abundance of native plants. Based on preliminary studies we predicted predator effects to be size dependent; crabs and fish crushing snails <24 and <3 mm in height, respectively. We also tested if changes in life history of snails in response to altered predation risk affected snail reproduction (e.g. Crowl & Covich, 1990).

Methods

Predators

Feeding trials showed that at least four indigenous fish species (*Clarias batrachus* L., *A. testudineus*, *Ompok bimaculatus* Bloch and *Osphronemus exodon* Roberts), the Malaysian turtle (*Malayemys subtrijuga* Schlegel and Müller) and the crab (*E. nimoafi*, Yeo) consumed snails of shell heights 2–10 mm. From these species the fish *A. testudineus* and the crab were chosen as they were numerous and were found in both rice fields and shallow wetlands with snails. The turtle (*M. subtrijuga*) was highly effective as a snail predator in the pretrials and has a native range that overlaps with the invasive snail, but it was not used because the population is threatened in Laos (Stuart, van Dijk & Hendrie, 2001).

Avoidance reactions to chemical cues

In December, predator avoidance behaviour to chemical cues released from crabs and fish was tested indoors in separate 72-L aquaria (60 × 30 × 40 cm) containing 50 L of water (50% tap water, 50% river). The temperature of the non-aerated water was approximately 28 °C throughout the experiment, and we used a light : dark regime of 12 h. Ten small (shell height 2–3 mm), 10 medium (8–10 mm) and 10 large (35–40 mm) snails that represented neonates, medium and sexually mature adults, respectively, were allowed to acclimatise for 24 h in each of 15 different aquaria (each treatment replicated five times). Their positions were recorded before, and 30 min after addition of water (0.1 L) from an aquarium that had been stocked with *A. testudineus* (fork length 80–120 mm, $n = 5$) or *E. nimoafi* (carapace width 30–40 mm, $n = 5$) for 24 h. The predators were fed snails in their holding tanks. In controls, the same volume of tap water was added. Previous observations had shown that the snail's avoidance reactions were directed either towards the surface or the bottom of the aquarium. In this study we defined a snail as using the surface habitat when it was at or above the water surface. As long as a snail had any contact with the bottom of the aquarium it was recorded as being at the bottom habitat. Thus, snails in contact neither with the bottom or the surface (e.g. on the walls) were not recorded. The movement of snails from one size class appeared independent of movements of other size classes. However, as we made multiple observations of snails both at the bottom and near the surface in the same tank, we tested the proportions of the total number of snails of a size class that were found at these positions before and after chemical cue treatment with a one-way MANOVA. The independent factors in the analysis were the different cue treatments (control, fish, and crab cue). The dependent variables in the analyses were the proportions (arcsine square root transformed) of snails of the different size classes found at or above the surface or at the bottom of the tanks. However, the number of adult snails at the surface could not be included in the analysis as they were never found at this position in any of the treatments. We therefore had five dependent variables in the analysis. A significant effect in the MANOVA would indicate that snails responded differently to predator cues. Contrast analysis (control versus crab cue, and control versus fish cue) was used to identify treatments giving significant effects in the MANOVA. Because there was no difference in positioning of snails prior to cue addition (one-way MANOVA, $F_{10,16} = 1.50$, $P > 0.22$), we only used observations after the addition of cues in the analysis when evaluating treatment effects.

Field experiment

In a field experiment conducted during the dry season (December to February) we tested if crab and fish had independent effects on the survival of different snail sizes and on reproduction. We also tested if predators indirectly influenced snail consumption of native plants. A wetland of approximately 30 × 50 m, (mean depth of 0.3 m, pH = 6.98, NH_4-N = 0.26 mg L^{-1}, Tot-P = 0.032 mg L^{-1}) situated in Ban Chomphet, Sysanatak district about 6 km south of Vientiane city (latitude 17.55°10′N, longitude 102.37°26′E) was used for the experiment.

Enclosure set-up

Thirty wooden frame enclosures (1 × 1 × 1 m) with walls of plastic net (mesh 1.6 mm) were placed in six blocks of five enclosures each in the wetland at a mean water depth of 0.3 m and driven into the sediment. A square concrete pot (15 × 15 cm) that the crabs could climb on to was added upside-down in the middle of all enclosures as we had observed that the crabs surface regularly. Before the start of the experiment all enclosures were thoroughly swept with a hand net (70 × 45 cm, mesh 1.6 mm) 10 times, or more (terminated if the last three sweeps were empty) to remove fish, crabs and snails that could interfere with the interactions tested. Each treatment was randomised within blocks. After enclosures had been stocked with experimental organisms they were covered with mosquito net (mesh 1.6 mm) to prevent the escape of snails and bird predation.

Plants

We stocked all enclosures with natural abundances of the plants *Ipomoea aquatica* Forsk, *Ludwigia adscendens* L. Hara and *Salvinia cucullata* Rox ex Bary (wet weight of 50.0 ± 1.0 g per plant species). These plants are free-floating macrophytes native to Laos. According to local residents, the two latter species have disappeared from the Vientiane wetlands since the snail was introduced in 1992. These plants were therefore gathered in wetlands 40–50 km outside Vientiane where they are farmed and actively protected from the snail. In contrast, *I. aquatica* is still present in Vientiane and could be collected in nearby wetlands.

Snails

Pomacea canaliculata snails were collected in the experimental wetland and divided into three size classes, of which only the largest (37.5 ± 7.5 mm) included sexually mature individuals (sexual maturity is reached at an approximate shell height of 25 mm (Estebenet & Cazzaniga, 1992)). To each enclosure, except controls without snails, we added one male and one female adult snail, 10 medium snails (10 ± 2 mm) and one egg batch. A normal *P. canaliculata* egg batch contains about 300 eggs (Naylor, 1996). To get equal-sized egg batches we lined up a large number of batches, still attached to an aquatic plant stem and then chose those that were of equal size. The plant stem with the egg batch was attached to the enclosure wall 150 mm above the water surface, to mimic how snails place their egg batches naturally. Eggs hatched within the first 2 weeks of the experiment and the average hatchling shell height was approximately 3 mm. At this stage, the initial density of neonates was estimated by netting (see below). The snail densities used in the experiment where within the range of those naturally found in invaded wetlands (Carlsson *et al*., 2004).

For each predator treatment we added either two crabs (one male, one female, average carapace width of 35 ± 5 mm) or two fish (average mass 30 ± 3 g, 80–120 mm fork length) or, in the combined predator treatment, two crabs and two fish of the same size as in individual predator treatments. Thus, each of the six blocks had five enclosures, one with only plants (NS), one with plants and snails (C), one with plants, snails and fish (F), one with plants, snails and crabs (CR) and one with plants, snails, fish and crabs (F + CR).

Sampling and analysis

After 2 months plants and snails were collected with a hand net (27 × 22 cm, mesh 1.6 mm) from all enclosures. Plants were shaken and gently squeezed to remove excess water and weighed according to species. Initial densities of medium and adult snails were known, whereas initial numbers of neonate snails were determined after 2 weeks. Snails were collected by scraping the walls of the enclosure and the pot as well as the top layer of the sediment with the hand net, and were then counted and measured. Eggs laid in enclosures were recorded and removed weekly. We evaluated the single and combined effects of predators (fish and crabs) on snail survival and plant biomass using a two-way ANOVA with blocks on log-transformed data. This approach is commonly used when evaluating multiple predator studies (e.g. Sih *et al*., 1998) and enabled us to test whether fish and crabs had interactive or non-interactive effects on snail survival and plant biomass. The expected snail mortality in the combined predator treatment was calculated from a multiplicative risk model (Sih *et al*., 1998). Interactive effects on snail survival would be expected if a change in the behaviour of snails in avoiding one predator increased or decreased their vulnerability to the other predator (e.g. DeWitt & Langerhans, 2003). Alternatively, interactive effects could also be expected if the foraging efficiency of one predator is affected by the presence of the second (e.g.

Soluk & Collins, 1988). The total number of egg batches laid in each treatment was tested with a one-way ANOVA with blocks.

Results

Avoidance reactions to chemical cues

There were general differences between treatments in the recorded distribution of snails at the surface and the bottom of the tanks after the addition of treatment cues (one-way MANOVA, $F_{10,16} = 6.49$, $P = 0.0005$). Contrast analyses showed that snails responded significantly to fish cues compared with the control ($F_{5,8} = 18.36$, $P = 0.0003$). This was because neonates (Fig. 1a,b) and medium-sized (Fig. 1c,d) snails increased their surface habitat use by 7.2 and 5.6-fold, respectively, compared with the controls. Adult snails, however, did not go to the surface in any treatment, but increased their use of the bottom (1.6-fold compared with controls; Fig. 1e) when exposed to fish chemical cues. Snails did not show any significant response to crab cues (contrast analysis, control versus crab, $F_{5,8} = 0.89$, $P > 0.53$, Fig. 1).

Effects of predators on snail survival and reproduction

Both predators had significant effects on the number of surviving snails. Crabs reduced all snail sizes and fish reduced neonate snails (Table 1; Fig. 2a,b). Although a few large snails were not retrieved in some controls, we found dead large snails only in treatments including crabs (Table 1; Fig. 2c). The survival of snails in the combined predator treatment differed from the expected values based on survival in single predator treatments. This was indicated by the significant fish by crab interactions (Table 1; Fig. 2). Moreover, the deviation from the expected value was different for different size classes of snails. The survival of neonate and medium-sized snails in the combined predator treatment was higher than expected, whereas the survival of adult snails was lower than expected (Fig. 2).

Snail reproduction measured as the total number of egg batches laid per enclosure, did not differ between treatments (one-way ANOVA with blocks, $F_{3,15} = 0.40$, $P > 0.75$). The total number of egg clusters ranged from 21 to 28 per treatment, which gives a mean total of four egg clusters or about 1200 eggs per enclosure for the first 3 weeks. After this period, no egg clusters were found in any enclosure.

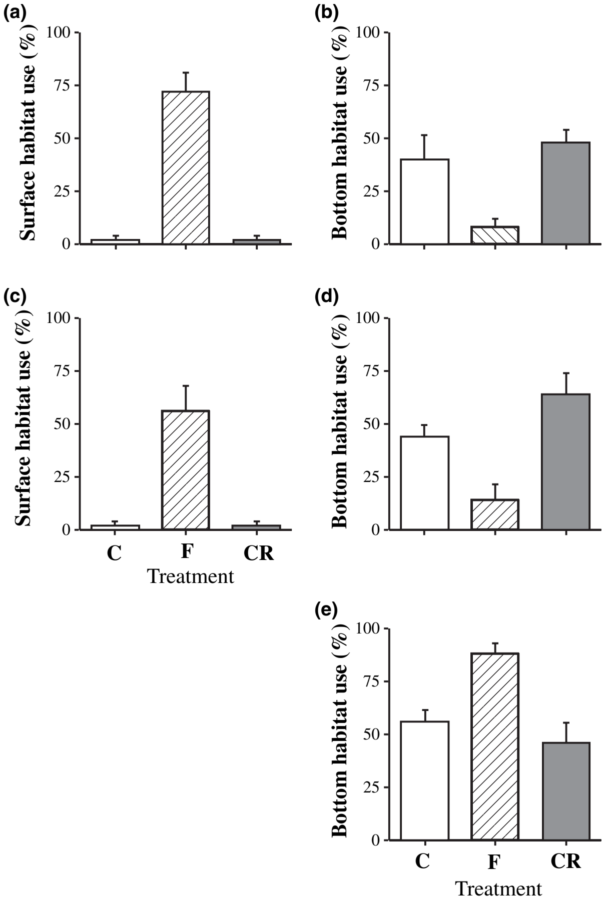

Fig. 1 The effects of chemical cues (C, control; F, fish; CR, crab) on *Pomacea canaliculata* habitat use (surface or bottom of the aquarium). The response of different size classes of snails are shown, Neonate snails (a, b), medium sized snails (c, d) and adult snails (d). There were no adult snails found in surface habitats in any treatment. Error bars denote 1 SE.

Indirect effects of predators on plant growth and biomass

Plants in enclosures without snails increased considerably in biomass, but snails had a strong negative effect on growth and biomass of all plant species regardless of predator presence (Fig. 3). Thus, neither crabs nor fish had any significant indirect effect on total plant biomass or on any of the three plant species in the enclosures (two-way ANOVA with blocks, $P > 0.14$ in all cases). Moreover, there were no

Table 1 Two-way ANOVAs with blocks for effects of fish, crabs and their interactive effects on the survival of snails of different size-classes in the field experiment. Neonates = 2–3 mm, Medium = 8–10 mm, and Adults = 35–40 mm

Source	d.f.	MS	*F*	*P*
Neonate				
Fish	1	0.47	27.03	0.0001
Crab	1	0.21	12.28	0.0032
Fish × Crab	1	0.24	14.12	0.0019
Block	5	0.01	0.57	0.72
Error	15	0.02		
Medium				
Fish	1	0.00	0.04	0.84
Crab	1	0.10	7.55	0.0150
Fish × Crab	1	0.12	9.04	0.0088
Block	5	0.01	0.42	0.83
Error	15	0.01		
Adult				
Fish	1	0.01	1.50	0.24
Crab	1	0.06	6.00	0.0271
Fish × Crab	1	0.12	13.50	0.0023
Block	5	0.02	2.40	0.09
Error	15	0.01		

significant fish by crab interactions (two-way ANOVA, $P > 0.08$ in all cases), indicating that the strong negative effects of snails on plant biomass persisted in the combined predator treatment.

Discussion

The study shows that there are indigenous predators in Laos that have both lethal and non-lethal effects on the invasive snail *P. canaliculata*. One important result was that the snail responded to chemical cues released by the indigenous fish predator, but not to the apparently more predaceous indigenous crab. The behavioural response displayed by snails in response to fish chemical cues seemed also to affect their vulnerability to crab predation. The outcomes of the interactions were either risk reduction (for neonate and medium-sized snails) or risk enhancement (adult snails). This experiment highlights the importance of investigating how invasive prey respond behaviourally to native predators, to be able to understand how multiple indigenous predators can affect the survival of invasive species. Despite the reductions in mainly neonate and medium-sized snails in predator treatments, predators had no indirect affect on plant biomass in the enclosures. The crabs are efficient predators on most snail sizes and the fact that such a small crab can handle these relatively large snails might reflect that molluscs are a part of this crab's natural diet. On the contrary, predation by the fish is limited to neonate snails, which indicates that *A. testudineus* lacks the capacity to handle larger snails.

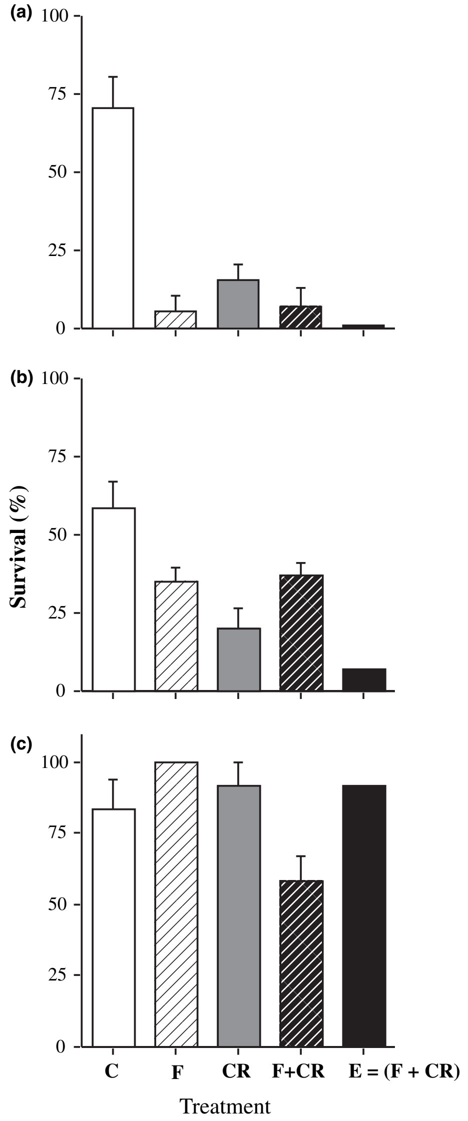

Fig. 2 Proportion of surviving *Pomacea canaliculata* at the end of the field experiment in different treatments (C, control; F, fish; CR, crab; F + CR, fish + crab). Expected survival in the F + CR treatment (E) is calculated from a multiplicative risk model using survival in single predator treatments. The survival of different size classes of snails are shown, Neonate snails (a), medium-sized snails (b) and adult snails (c). Error bars denote 1 SE.

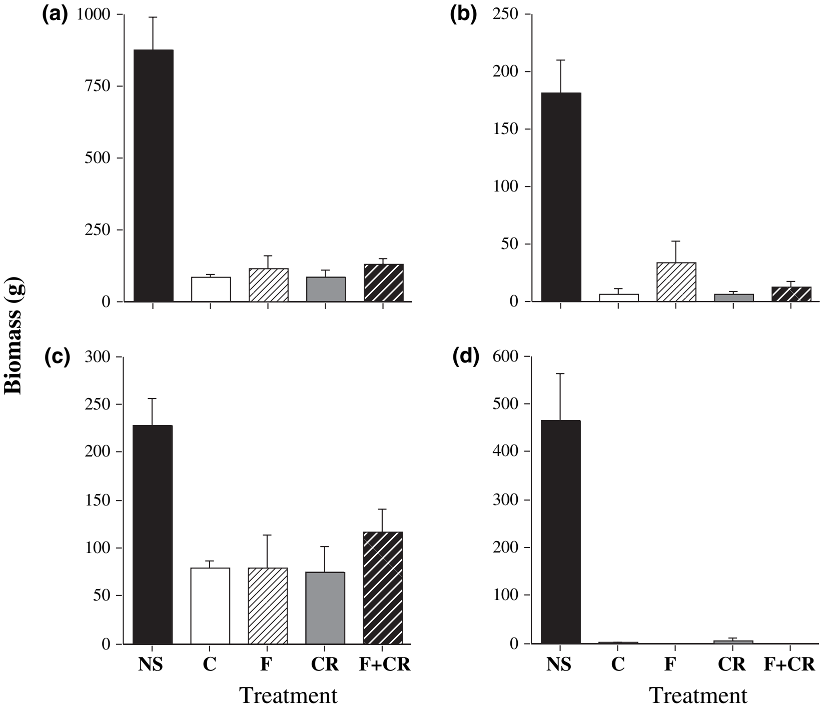

Fig. 3 Total plant biomass (a), and biomass of individual plant species, *Ludwigia adsendens* (b), *Ipomea aquatica* (c), and *Salvinia cucullata* (d), at the end of the field experiment in different treatments (C, control; F, fish; CR, crab; F + CR = fish + crab). *Pomacea canaliculata* were present in all treatments except NS, which contained only plants. Biomass is expressed in g wet-weight, and initially a plant biomass of total 150 g was added to each enclosure. Error bars denote 1 SE.

Behavioural responses of snails to predator cues

In its native South American habitat, *P. canaliculata* is considered as key prey for predators from a variety of taxa (Snyder & Snyder, 1971), and the snails subsequently display a number of predator avoidance strategies. These responses may be initiated by chemical cues released by predators and/or injured conspecifics (Snyder & Snyder, 1971). In addition, *P. canaliculata* introduced to Japan respond behaviourally to extracts from crushed conspecifics (Ichinose, 2002; Ichinose, Yusa & Yoshida, 2003). In the aquarium trials no size class of snails reacted to chemical cues associated with crabs. This indicates that crabs either are not important predators in the native habitat [predation is not mentioned in a study of *Pomacea doliodes* Reeve, and a crab that coexist in Venezuela, (Donnay & Beissinger, 1993)], or that the chemical cues released by crabs are species specific. Prey populations may experience different predation pressures with different predator types and several studies have indicated population differences in response to predator chemical cues (summarised by Kats & Dill, 1998).

In contrast, the avoidance reaction to fish odour was strong and directed towards the surface for neonate and medium-sized snails and directed towards the bottom for adult snails. Interestingly, these escapes were provoked although this snail has no co-evolutionary history with this fish species, which suggest that the snail response to fish cues could be quite general. This argument is further supported by the response shown by *P. canaliculata* to chemical cues released by the European tench (*Tinca tinca* L.). Tench is a molluscivore native to Europe and adult *P. canaliculata* responded to chemical cues from starved tench by increasing their use of the bottom habitat (Carlsson unpublished). It is not uncommon that prey show strong antipredator behaviour to fish species that have not been encountered before (e.g. Blake & Hart, 1993; Nyström & Åbjörnsson, 2000). Adult snails are outside the prey size range of this fish but they still reacted to the fish cues or to exudates from the fish neonate snail diet. Ontogenetic shifts in the avoidance reactions to chemical cues from fish predators in freshwater snails have been shown recently (Rundle & Brönmark, 2001). The same divergent size-dependent escape response that we found has also been demonstrated for a Japanese population of *P. canaliculata* exposed to extracts of crushed conspecifics. Smaller snails crawled to the water surface in response to this alarm signal and snails larger than 10 mm buried themselves in the sediment (Ichinose, 2002; Ichinose *et al*., 2003).

Multiple predator effects on snail survival

In the combined treatment with both predators, the observed effect on snail survival differed from what could be expected from single predator treatments, and depended on the size of the snails. The observed survival of neonate and medium-sized snails was higher than expected, indicating risk reduction. Risk reduction is often observed in multiple predator studies when predators interfere because of direct predation events and behavioural interactions (summarised in Sih *et al*., 1998). Although the basic ecology of the fish and crab used in this experiment is not well known, we have no evidence for strong interference between these predators, as both predators survived in the combined treatment. In contrast our results suggest that risk reduction occurred because neonate and medium-sized snails move to the surface in response to fish chemical cues, and this behaviour probably lowered their susceptibility to crabs. Fewer adult snails survived in the combined predator treatment than was expected, thus indicating risk enhancement. Again this seemed to be related to the behavioural response of adult snails to fish, i.e. to increase their use of bottom habitats. When adult snails seek refuge in the sediment in response to fish, they probably increase their exposure to crabs, as adults found dead in the combined predator treatments bore the marks of crab attack. A similar mechanism was suggested when predatory small mouth bass (*Micropterus dolomieui* Lacapede) increased the vulnerability of small fish to crayfish by forcing the small fish, *Etheostoma nigrum* Rafinesque, to seek cover under shelters occupied by crayfish (Rahel & Stein, 1988).

Indirect effects of predators on snail reproduction and plant growth

Predator-induced behavioural changes in molluscs may influence both feeding and fecundity (McCollum, Crowder & McCollum, 1998; Nakaoka, 2000; Lewis, 2001) as well as time of reproduction (Crowl & Covich, 1990). In our case, neither fish nor crabs, alone or in combination had any effect on snail reproduction. Rather, reproductive output depended on the amount of preferred plant material present, as no single egg cluster was found in any enclosure after the third week. At this point, the preferred plants *S. cucullata* and *L. adscendens* had been grazed down to very low levels and only the least preferred plant, *I. aquatica*, was still fairly abundant (results not shown). *Pomacea canaliculata* snails that feed on *Eichhornia crassipes* Mart. Solms seem not to reproduce (Estebenet, 1995). Thus, even if predators induce behavioural shifts in prey, we would expect minor effects on growth and fecundity if food sources are limited (e.g. Peacor & Werner, 2000). Even at the last sampling we encountered newly deposited egg batches on the outside of the enclosure walls, suggesting that external factors such as water temperature did not cause this halt in reproductive output. At these snail-, predator- and plant densities, the combination of direct and indirect negative effects on snail grazing have no significant positive effect on plant biomass. However, the lack of a predator effect may be because of the size structure of the snails added to the enclosures. The field experiment showed that predation was mainly directed towards the two smallest size classes of snails, while large snails were more or less in size refuge from predation. A density of only 1.5 adult *P. canaliculata* snails m^{-2} results in an almost complete absence of aquatic plants in wetlands in Thailand (Carlsson *et al*., 2004). Similar decoupling of indirect effects, because of the presence of invulnerable prey sizes, has been observed involving piscivorous pike (*Esox lucius* L) and molluscivorous tench. Although gape-size limited pike reduce the abundance of tench, the presence of a few large tench may still reduce the abundance of snails (Brönmark & Weisner, 1996).

Could indigenous predators affect the distribution of P. canaliculata*?*

Fishing pressure is extremely high in parts of South East Asia, and the densities of large predatory fish and turtles very low, supporting the ‘enemy release hypothesis’ as one important mechanism behind the successful invasion of *P. canaliculata*. Nevertheless, we have shown that there are potential predators on *P. canaliculata*, which may affect their local abundance. The potential ecosystem effects of the predators we tested should be limited, as the adult snails are in refuge from predation and both snail reproductive output and snail resource utilisation are largely unaffected by these predators. It is still possible, however, that the recruitment of younger snails might be negatively affected over generations of snails in the presence of these predators. Snail establishment typically occurs when eggs deposited on boat hulls hatch in a new area and the population is highly skewed towards the smallest size classes. If predators such as snail eating fish and crabs are abundant, the snails could be less successful. Thus, there is a need for more studies on the interactive and long-term effects of indigenous predators on the snail population dynamics in this region.

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