Invasive *Pomacea* snails: actual and potential environmental impacts and their underlying mechanisms

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Abstract

Apple snails are large freshwater snails belonging to the family Ampullariidae that inhabit tropical to temperate areas. The South American apple snails *Pomacea canaliculata* and *Pomacea maculata* have been introduced to other continents where they have successfully established and spread. Our review aims to analyse the mechanisms of the impacts that these invasive *Pomacea* provoke or may provoke. Nine basic mechanisms were identified: grazing/herbivory/browsing, competition, predation, disease transmission, hybridisation with native species, poisoning/toxicity, interaction with other invasive species, promotion of collateral damage of control methods on non-target species and when acting as prey. The most important impacts are those related to their grazing on aquatic macrophytes, algae and rice and their competition and predation on other aquatic animals, mostly macroinvertebrates, including other apple snails. Invasive *Pomacea* are also responsible for outbreaks of an emergent parasitic disease (human eosinophilic meningitis). Their great abundance in invaded areas, their bioaccumulation of pollutants and their natural toxicity may impact on their predators and on trophic webs through apparent competition, trophic cascades and biomagnification. The biota from man-managed and natural wetlands may be unintentionally affected by mechanical, chemical and biological control against invasive *Pomacea*. Their capacity to hybridize may affect the distinctiveness and ecological traits of native *Pomacea* in invaded regions of America. Established populations of these invaders may either facilitate or resist the establishment of other exotic species. Field surveys and more realistic experimental approaches with multiple interacting species are needed to better understand the environmental impacts of invasive *Pomacea* and their underlying mechanisms.

Keywords: Golden apple snail, Biological invasion, Pest, Plague, Risk

Review Methodology: We searched the following databases with 31 December 2018 as deadline: Scopus, Scielo, PubMed, Agris and CAB Abstracts. The following combination of terms was used for searching in tittles, abstracts and keywords: ((pomacea) OR (apple AND snail) OR (ampullaria) OR (ampullariidae) OR (ampullariid) OR (ampularid) OR (ampullarid) OR (caracol AND manzana) OR (ampularia) AND (impact) OR (risk) OR (threat) OR (menace) OR (damage) OR (danger)). Wildcards were used when necessary (e.g. damag*).
A total of 430 articles were retrieved using the search options mentioned above. A few of these (53) did not bear a relationship with apple snails, being the result of coincidental homonymy, or lack an available abstract. Many articles (210) mentioned impact-related terms in their title, abstract and keywords but upon closer examination they probed to contain no new evidence or knowledge about impacts.
The remaining 167 articles, even if the authors did not aim to evaluate impacts explicitly, contained information that was considered relevant to the aims of the present review. Most of these articles belong to studies performed in Southeastern Asia (58.7%), mainly China (32.7%), Philippines (18.4%) and Japan (8.2%), followed by studies in the Americas (32.9%) and Europe (2.4%). Except for most papers from Argentina and Brazil, the native range of invasive *Pomacea*, these numbers reflect the distribution of present impacts and the concerns about future impacts around the world. Most relevant articles dealt with *P. canaliculata* (55.7%) or *P. maculata* (5.4%) and a few with two or more *Pomacea* spp. (21.6%). Most studies were performed in rice fields (31.7%) followed by laboratory microcosms (22.2%) and those based on field experiments or mesocosms (16.8%).

Introduction

Apple snails (Ampullariidae) are a diverse and widespread group of freshwater snails with very peculiar features such as an aerial–aquatic respiratory system, the largest sized shells among freshwater snails and, in some genera, cleidoic eggs with calcareous eggshells [1, 2]. A few species of this family, notably the South American *Pomacea canaliculata* and *Pomacea maculata*, have been transported intra- and inter-continentally and attracted much basic and applied scientific interest, mostly due to their invasion and impacts in wetlands and aquatic crops [3–8]. The present review aims to analyse the diverse mechanisms of the multiple impacts that *P. canaliculata* and *P. maculata* (from now on referred as invasive *Pomacea*) have provoked or may provoke in temperate to tropical regions around the world. Most information belongs to *P. canaliculata* but our conclusions may be extensive to *P. maculata* and perhaps to other species of the genus.

Mechanisms Underlying Impacts of Invasive *Pomacea*

The present review will focus on actual and potential environmental impacts, i.e. significant changes of ecological properties or processes, regardless of actual or perceived value to humans [9, 10], including impacts on human-managed ecosystems and human beings but not those on human society and economy. About a dozen different basic mechanisms are considered responsible for most of the impacts of invasive species [10]: grazing/herbivory/browsing, competition, predation, disease transmission, hybridisation with native species, poisoning/toxicity, interaction with other invasive species, parasitism, bio-fouling, increase in vegetation flammability, rooting/digging and trampling (disturbances on stones, logs and soil or damage to plants and animals caused by the activities or footsteps of big tetrapods). It is noteworthy that except for the last five, three of which are intrinsically terrestrial, all other mechanisms can be related to the impacts of invasive *Pomacea*. In addition, there are other mechanisms which also seem important in the case of invasive *Pomacea*, for example, when acting passively as prey or as promoters of the collateral damage of control methods on non-target species. The information retrieved from the databases will be presented in this framework as well as the bioecological traits related to each mechanism and their main outcomes. The magnitude of the impacts of invasive *Pomacea* has been related to their biomass [7, 11], which may be high due to their large sizes and high densities.

Grazing/herbivory/browsing

The most widely recognized impacts of invasive *Pomacea* are related to their ability to scrape and graze on live aquatic plants, including vascular ones, an ability that is uncommon among freshwater snails [12]. They have strong jaws and radular teeth and a muscular and cuticularized gizzard [13–15]. *Pomacea canaliculata* has also powerful sets of digestive enzymes, including autogenously and endosymbiotically synthetized proteases and cellulases [16–19]. This apple snail is able to detect the preferred aquatic macrophytes from a distance [20] and it can use ingested lithic particles to increase the mechanical digestion of food and its growth efficiency [21]. Invasive *Pomacea* also have higher feeding rates than other non-invasive snails [22–24].

Many studies reported their ability to ingest various species and types of plants, from aquatic to semi-aquatic or even terrestrial, but also showed great differences in their palatability and nutritive quality for apple snails [22, 24–33], even among plants with the same life form (e.g. submersed macrophytes [34]). Palatability is inversely related to physical and chemical defences and low nutrient content which impair apple snail fitness, reducing growth, fecundity and survival [28, 30, 35]. Different parts or organs of each macrophyte may have different palatability and can be affected differentially by *Pomacea* spp. [26, 36, 37]. The best predictor of macrophyte palatability to *P. canaliculata* is the ratio between nitrogen and phenolic content [33], although other factors may be important. For instance, *P. canaliculata* grazing induces macrophyte chemical defences that depress its feeding and growth [38] and the palatability and nutritive quality of macrophytes can increase, decrease or remain unchanged after their senescence [30]. Moreover, the actual feeding rate on an aquatic macrophyte, and hence the impact on it, depends also on the relative palatability of the other macrophytes available in the same waterbody [31, 34]. The most preferred macrophytes are consumed and eradicated first but then the apple snails feed on the less preferred ones [25, 34]. Field studies have shown that the abundance of invasive *Pomacea* is negatively correlated to the abundance and richness of preferred types of aquatic macrophytes [39, 40]. The feeding preferences of invasive *Pomacea* for different aquatic macrophytes need to be considered in restoration projects as they may affect their success [27, 35, 41].

Although *P. canaliculata* has been usually and generally regarded as macrophytophagous due to its strong impacts on aquatic vegetation and crops, it also consumes other diverse trophic resources [42, 43]. Benthic, filamentous and periphytic algae can be heavily depleted by *P. canaliculata* grazing [26, 34, 36]. This species can also survive and grow collecting organic material from the water surface, including floating plants and other neustonic organisms, with its forefoot [44, 45]. It heavily consumes vegetal detritus [46–49], usually the most important trophic item in its digestive contents in waterbodies from both the invaded and native range (but for exceptions see [50]). The detrital biomass from submersed macrophytes can be reduced to almost one-third (36%) by *P. canaliculata*, a reduction even stronger than the 42% observed for live biomass [34]. In rice fields, *P. canaliculata* is able to grow consuming only rice straw and acts as an active decomposer that accelerates nutrient cycling [51, 52] and, like other *Pomacea* species [53], may also contribute to the breakdown of leaf litter from riparian vegetation.

The herbivory of invasive *Pomacea* releases nutrients to water [54] that may result in eutrophication due to its uptake by phytoplankton [34, 39]; their role as detritus decomposers may also contribute to eutrophication [51, 52]. Even if there is no increase in productivity, phytoplankton-specific composition can be strongly affected [36]. Eradication of submersed macrophytes may also facilitate sediment resuspension and a consequent increase in water turbidity that lessens their recovery chances and promotes a transition from clear- to turbid-water states [39].

Invasive *Pomacea*, especially *P. canaliculata*, are regarded as major pests of aquatic crops such as rice, taro and lotus [3, 4, 6, 55–57]. Although many of these plants are quite unpalatable, in monocultures they are almost the only trophic option. In rice, damage is mostly related to water management and cultural practices that allow the snails to attack the most vulnerable stages, as seedlings and very young plants [57–62]. *Pomacea canaliculata* can also deplete rice field weeds and farmers promote it as a weed biocontrol agent through cultural and water management practices that impede at least in part the attack to rice [63–66].

Competition

Several traits of invasive *Pomacea* such as their large size [2], high trophic flexibility [42, 43], high feeding rate [22, 67] and high fecundity [68–71] indicate that they may be strong competitors of other snail species [72]. Their tolerance to abiotic stressors such as hypoxia, high salinity, desiccation and extreme temperatures [73–80], their life-cycle plasticity [81–84] and their endurance to starvation [85] may also contribute to their competitive dominance. Invasive *Pomacea* have been associated with the decline of native apple snails in Southeastern Asia [86–88] since many localities formerly inhabited by *Pila* spp. are now occupied only by *P. canaliculata*. In laboratory experiments, *P. maculata* depresses the growth of the Florida apple snail *Pomacea paludosa* [89–91], probably through depletion of shared trophic resources combined with behavioural or chemical interference. *Pomacea canaliculata* impairs growth and survival of the viviparid snail *Bellamya ferrugineus* due to an alteration of water physicochemical quality [54], whereas avoidance of contacts with it, or its mucous trails and faeces, restrains habitat use in three small snails [72]. Besides, *P. canaliculata* grazing induces chemical defences in aquatic macrophytes [38] which could reduce their palatability to other macroinvertebrates feeding on them.

Recent studies showed that detritus is usually the most important trophic item in the digestive contents of *P. canaliculata* from natural wetlands in its invaded and native range [46, 47, 49]. Even in the presence of palatable submersed macrophytes, its intense detritivory can heavily deplete this trophic resource [34] and hence could result in strong resource competition with other detritivorous macroinvertebrates, mostly arthropods and other snails, and promote bottom-up trophic cascades (PRM, unpub. results). *Pomacea* spp. also feed on fresh and partially rotten carrion from vertebrates and invertebrates [42, 43, 92] and may compete with macroinvertebrate scavengers, particularly insects, which are not very specialized in this feeding mode [93].

Predation

Invasive *Pomacea* are opportunistic predators that will prey on any animal too small or too slow to avoid contact, capture and ingestion. Even though they seem unable to detect them from a distance, their wide foot, long cephalic and labial tentacles and their relatively high crawling velocity probably facilitate the encounters with this kind of prey [94]. Their prey are usually other invertebrates but predation on amphibian egg masses has been reported in China and North America [95, 96]. Among invertebrates, bryozoan colonies [97], oligochaete worms [92] and other snails have been reported. Egg masses, hatchlings and adults of snails, especially pulmonates, are usually predated by *Pomacea* spp. in laboratory settings [72, 92, 94, 98, 99], constituting a case of intraguild predation (i.e. a combination of predation and competition). Biocontrol field experiments showed strong declines and even extirpation of schistosome-bearing snails after *Pomacea* spp. introduction [100–102] but these effects may be a combination of intraguild predation and habitat alteration [101, 102] (PRM, unpub. results).

Disease transmission

Although in their native range, *Pomacea* spp. harbour many commensals, parasites and pathogens [103, 104], none of them seems to have been reported in invaded areas. This suggests that they may have been transported mostly as eggs, the most axenic life stage, and that enemy release, especially from pathogens and parasites, may explain in part their success in invaded areas. Probably due to their complex immunological defences, which include molecular and cellular components and as well as barrier organs [105–107], invasive *Pomacea* are susceptible to infestation by only a few parasites from invaded areas, notably the rat lungworm *Angiostrongylus cantonensis. Pomacea* spp. and other snails host the third stage larvae, which may be acquired through ingestion by rats, the definitive host, but also by people eating raw or insufficiently cooked snails [108, 109]. *Pomacea canaliculata* recently become one of the main vectors responsible for an emergent parasitic disease (human eosinophilic meningitis) caused by this worm in Southeastern Asia [109–111]. Native apple snails like *Pila polita* are more susceptible to the rat lungworm than the invasive *Pomacea* [112] but the recent decline in the former and the increase in the latter are probably boosting the importance of exotic apple snails in this parasite transmission [110]. The rat lungworm has also reached other regions of the world and the native or introduced *Pomacea* spp. may contribute to the emergence of human eosinophilic meningitis in regions like Brazil and North America [106, 113, 114]. *Pomacea canaliculata* can also act as a facultative or paratenic host of another nematode (*Gnathostoma spinigerum*), which parasitize cats, dogs and humans in Thailand and Japan [115]. On the contrary, invasive *Pomacea* may be able to disrupt the life cycles of some human parasites in invaded areas. *Pomacea* spp. can act as decoys for schistosome miracidia and hence they may reduce the infestation rates of *Biomphalaria* snails with these parasites, whose adults cause schistosomiasis or bilharziasis in humans [107, 116–118]. The high densities and large sizes of invasive *Pomacea* may be especially relevant because the decoy effect increases with the number and individual body surface of non-target apple snails [116].

Hybridisation with native species

Even though *P. canaliculata* and *P. maculata* belong to different clades and are not closely related within the genus *Pomacea* [119], their hybridisation has been probed in laboratory crossings and molecular genetic evidence was also found in natural populations from the native and invaded range [120, 121]. More than 96 *Pomacea* species inhabit the Neotropical region [2] and hence the probability of co-occurrence of native and invasive *Pomacea* in the same waterbody is high. Genetic exchange may blur the distinctiveness of natives but also enhance their tolerance and biotic potential [121]. The heterospecific copulations may likewise result in a decrease of the fecundity of natives due to partial sterility or to low viability of hybrid progeny [120].

Poisoning/toxicity

The aerial eggs of *Pomacea* spp. are regarded as unpalatable to most predators and are seldom eaten by vertebrates or invertebrates, either in their native or invaded range [122, 123]. The perivitelline fluid of invasive *Pomacea* eggs shows neurotoxic, antidigestive and antinutritive properties to terrestrial and aquatic vertebrates [124–128]. Moreover, female reproductive organs involved in perivitellin synthesis have been recently shown to share these egg properties [129]. The most specialized avian predators of *Pomacea* along its native range, the Snail Kite *Rostrhamus sociabilis* and the Limpkin *Aramus guarauna*, are known to discard these organs despite the significant loss of captured biomass [130]. Some predators such as rats, raccoons and storks learn to discard these organs in the invaded range [131–133], but perhaps other naïve native predators from invaded areas may be unable to identify the toxic organs and may be affected negatively by this very unusual trait.

Invasive *Pomacea* are especially tolerant to diverse pollution types [134–136] and are able to strongly bioconcentrate several toxic chemicals that naturally or anthropogenically occur in their habitats, ranging from heavy metals [135, 137, 138] and synthetic compounds [139–141] to uranium [137] and cianotoxins [142]. The potential dangers of these bioaccumulated chemicals to humans and aquaculture or farm animals have been already put forward [137, 143] but there are also potential effects on wild predators attracted by the abundant invasive *Pomacea*. For instance, a cyanotoxin accumulated by *P. maculata* may produce avian vacuolar myelinopathy in the already endangered Snail Kite in Florida [142].

Pesticides used against invasive apple snails may also result in negative effects on organisms feeding on them. For instance, organic pesticides used against *P. canaliculata* in rice fields reduced the number, biomass and diversity of scavenger flies emerging from apple snail corpses with likely consequences in other trophic levels [144].

Interaction with other invasive species

Multiple invasions are increasingly common and facilitation among invaders may enhance the chances of establishment, spread and impacts, provoking invasional meltdown [145, 146]. For instance, the differential grazing of the invasive *P. maculata* may favour the growth of an invasive aquatic macrophyte over native ones in North America, although without beneficial effects for the apple snail [147]. The populations of the native *P. paludosa* were associated with native macrophytes in a Florida lake, whereas *P. maculata* ones were associated with the invasive *Hydrilla verticillata*, suggesting at least a unilateral facilitation through enhanced propagule dispersal and grazing on native competing macrophytes [148]. Conversely, an established invader may help to impede or slow the establishment of new potential invaders [146] and contribute to the biotic resistance of the community. Such a role has been suggested for apple snails as they seem to prefer exotic over native macrophytes [31]. The grazing of *P. canaliculata* and of an unidentified *Pomacea* species in Brazil reduces the growth and propagule production of *H. verticillata* and may exert biotic resistance [37, 149], since at least *P. canaliculata* seems to prefer the invasive macrophyte over natives [150, 151]. The biotic resistance potential of *P. canaliculata* against other snails depends on their reproductive and morphological traits: small pulmonate snails that lay gelatinous egg masses are the most affected whereas big snails that give birth to their offspring are barely affected, irrespective of their native or exotic status [72, 94].

Collateral damage on non-target species

The attempts to control invasive *Pomacea* spp. are mostly limited to rice fields and other aquatic crops (but for exceptions see [152, 153]). Most control measures, mechanical, chemical or biological, may also have effects on non-target species inhabiting or visiting the fields or irrigation channels and the last two may also impact nearby natural wetlands [59, 144, 154]. Control measures like inundation of rice fields with seawater may affect both their production and biodiversity [155]. Several chemical molluscicides are effective against apple snails but not very specific and may affect invertebrates and vertebrates as well [156–159]; this prompted the development of new environmentally-friendly molluscicides with low or no toxic effects on non-target freshwater biota [160]. Biocontrol agents tried against invasive apple snails may also be effective but are not very specific either and may significantly impact on other aquatic fauna and flora [161, 162]; biotechnologically developed all-male predatory prawns used for inundative biocontrol of apple snails may still have undesired impacts but are not expected to persist and will be localized [163]. Even hand-picking, one of the most environmentally-friendly control methods, may impact on native apple snails if farmers are not able to distinguish them from invasive ones [154].

As prey

Pomacea spp. are a valuable trophic resource for many predators [2] and the density and biomass of invasive *Pomacea* may reach higher values than those of their native counterparts [148, 164]. In the invaded range, many native and exotic predators take advantage of *Pomacea* snails. Generalist predators soon learn to capture, handle and eat the novel and abundant trophic resource [39, 165–169] which may alter trophic webs provoking bottom-up cascades. Diverse changes in the populations of more specialized predators are also to be expected. For instance, the establishment of dense populations of invasive *Pomacea* led to range expansion and use of new habitats as foraging and nesting grounds by Snail Kites and Limpkins in South and North America [164, 170–172]. In Southeastern Asia, the malacophagous Open-bill stork (*Anastomus oscitans*) has similarly modified its migratory routes and foraging sites after the establishment of *P. canaliculata* populations [132, 173]. However, some invaded wetlands may become ecological traps for specialized predators if an abundant invasive prey differs in subtle ways from native staple prey [174, 175]. Notwithstanding, at least in the case of the endangered Snail Kite in Florida wetlands, the survival and breeding success increases when foraging on *P. maculata*, as its greater size and abundance provides a higher nutritional reward than the native *P. paludosa* [164]. On the other hand, the increase in geographical range or abundance of these specialized predators due to the presence of invasive *Pomacea* may contribute to the decline of other potential native prey, for instance *P. paludosa* in Florida and *Pila* spp. in Southeastern Asia, due to apparent competition (i.e. negative effects due to a shared predator).

Conclusions

Some of the multiple recognized impacts of invasive *Pomacea* have been studied frequently but others remain to be confirmed and explored with more detail. With the exception of studies in rice fields, many impacts of invasive *Pomacea* may be regarded as potential as most studies were performed in laboratory microcosms with only one other species at a time to interact. Field surveys and more realistic experimental settings like mesocosms or enclosures with several interacting species are needed to obtain sound evidence about the environmental impacts of invasive *Pomacea* and their underlying mechanisms.

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