

Apple snails as agricultural pests: their biology, impacts, and management

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What are Apple Snails?

Ampullariidae are freshwater snails predominantly distributed in humid tropical and sub-tropical habitats in Africa, South and Central America and South-East Asia. They include the largest of all freshwater snails (*Pomacea urceus* (Müller) can attain a shell height of 145 mm - Burky, 1974; *P. maculata* Perry can exceed 155 mm - Pain, 1960) and frequently constitute a major portion of the native freshwater mollusc faunas of these regions. Among the seven to ten genera usually recognized, the two largest are *Pomacea* Perry, with about 50 species, and *Pila* Röding, with about 30 (Berthold, 1991). Snails in these two genera particularly are frequently known as 'apple snails', because many species bear large, round, often greenish shells. They have also become known as 'mystery snails', 'miracle snails', 'golden snails', among other common names ('kuhol' in the Philippines, 'bisocol' in the Filipino community in Hawaii).

There are a few instances of ampullariids causing damage to crops, predominantly paddy rice, in their native ranges. More significantly, a number of species have been introduced outside their native ranges in recent years and have become serious agricultural pests. In this review I will summarize relevant aspects of the snails' biology, focusing on the pest species; I will then outline the agricultural problems they are causing and the control measures that have, generally unsuccessfully, been implemented; and finally I will make suggestions for future approaches and needs in order to address the problems.

Classification, Diversity and Natural Range

Ampullariidae (= Pilidae of some authors; Cowie, 1997a) are operculate snails. They are most closely related to the Viviparidae, together with which they form the superfamily Ampullarioidea in the orders or superorders (depending on classification) Mesogastropoda of earlier authors and Caenogastropoda of more recent authors (Ponder and Warén, 1988; Berthold, 1989; Bieler, 1992).

Traditional subdivision of the family, by various authors, has been into seven to ten genera, with the form of the siphon and the operculum considered diagnostically significant (e.g., Michelson, 1961). Pain (1972) briefly reviewed the history of taxonomic work on the family. More recently, Berthold (1991: pp. 245-250) recognized ten genera (and three subgenera) with approximately 120 species. His detailed anatomical account treated representative species from each of these generic groupings. He divided the family into two subfamilies: the Afropominae (containing just a single Recent African species in the genus *Afropomus* Pilsbry & Bequaert); and the Ampullariinae, which he subdivided into the tribes Sauleini (one genus, *Saulea* Gray, containing two African species, one Recent, one fossil) and Ampullariini (the remainder). He further subdivided the Ampullariini into the groups Heterostropha and Antlipneumata, but these divisions and names have been criticized by Bieler (1993), who reanalysed Berthold's data using cladistic techniques. Bieler's reanalysis showed that the various groupings of genera remained more or less similar to those of Berthold, but the relationships among these groups were inconsistent. Given these inconsistencies, it seems unwise to force the various clades into a traditional hierarchy of family-group names. One of the ten genera recognized by Berthold (1991), *Pseudoceratodes* Wenz (African, fossil only), was included in the family only tentatively. Of the remaining nine genera, six contain fewer than four species each: *Afropomus* and *Saulea* are African; *Asolene* d'Orbigny, *Felipponea* Dall, *Pomella* Gray and *Marisa* Gray are South American. The three genera *Lanistes* Montfort, *Pila* (*Ampullaria* Lamarck and *Ampullarius* Montfort are junior synonyms; Cowie, 1997a) and *Pomacea*, containing 21, about 30, and about 50 species, respectively, comprise the great majority of species in the family. *Lanistes* (distinguished by its hyperstrophic and hence superficially sinistral shells) is African (including Madagascar). *Pila* is African and Asian. *Pomacea* is South and Central American.

Berthold (1991) hypothesized a Gondwanan origin for the family, specifically an origin in that part of Gondwana that was to become Africa. The group is assumed to have spread and diversified onto the South American and Indian plates, but failed to reach the Australian plate prior to its split from Gondwana. An alternative scenario, although less favoured by Berthold (1991), involved extinctions on the Antarctic/Australian plate. As the plates moved to their present positions, the group probably spread and diversified within the humid tropics and subtropics (in particular from the Indian plate into South-East Asia) to their physiological/ecological limits, defined approximately by the 10°C minimum annual temperature isotherm and the 600 mm annual precipitation isohyet. The limit of their distribution in South-East Asia (genus *Pila*) corresponds closely with Wallace's line, despite New Guinea and parts of northern Australia apparently being suitable climatically. Wallace's line corresponds essentially with the boundary between the Asian and Australasian plates; ampullariids simply have not yet reached Australasia.

The genus *Pomacea*, which is the main focus of this review as it contains the majority of the pest species, is found

throughout most of South and Central America and the Caribbean, with a single species, *Pomacea paludosa* (Say), extending into the south-east of the USA. The genus is divided into two subgenera, *Pomacea sensu stricto* and *Pomacea (Effusa)* Jousseau. But the relationships among these two subgenera and the genus *Marisa* are not well resolved (Bieler, 1993) and, at least in terms of shell morphology, the three taxa intergrade (personal observations).

Biology

A thorough understanding of relevant aspects of the biology of pest species is important if effective management strategies are to be developed. With knowledge of the snails' ecology, behaviour and certain aspects of their physiology, it may be possible to manipulate their environment to reduce reproductive output, to provoke behaviour that facilitates mechanical control, to apply pesticides at appropriate points in the life-cycle, and so on.

Unfortunately, detailed knowledge of the biology of ampullariids is sparse and scattered. *Pomacea* is the best known genus, and various species have been the subject of basic studies of systematics, anatomy, physiology, genetics, distribution, behaviour, and so on. *Pila* has been investigated to a lesser extent. *Marisa* has attracted interest, often because of the perceived value of *Marisa cornuarietis* (Linnaeus) in controlling other snail species that are vectors of schistosomes (e.g., Demian and Lutfy, 1966; Robins, 1971; Demian and Yousif, 1975; Peebles *et al.*, 1972; Pointier *et al.*, 1988, 1991). The basic biology of the other genera is hardly known (Berthold, 1988).

Certainly, however, there have not been studies directly focusing in detail on aspects of the biology of the pest species that might be most relevant to the development of control measures. In the sections that follow, I have attempted to summarize what is known in these areas, mostly regarding species of *Pomacea*. I have not attempted to review areas of less relevance, such as embryology (e.g., Demian and Yousif, 1973, 1975), anatomy and histology (e.g., Andrews, 1964, 1965a, b; Keawjam, 1987), karyology (von Brand *et al.*, 1990), genetics (Fujio and von Brand, 1990; Keawjam, 1990), biochemistry and physiology (Little, 1981).

Habitat

Ampullariids are freshwater snails. Some may be able to tolerate low levels of salinity (Prashad, 1925a; Hunt, 1961; Fujio *et al.*, 1991a; Santos *et al.*, 1987), but they generally do not live in brackish water habitats. Most species are amphibious, able to spend significant lengths of time out of water breathing air. Many species, especially species of *Pomacea*, *Marisa*, *Pila* and *Lanistes*, inhabit slow-moving or stagnant water in lowland swamps, marshes, ditches, lakes and rivers (e.g., Pain, 1950a, 1960; Andrews, 1965b; Robins, 1971; Louda and McKaye, 1982; Keawjam, 1986). Some species could be considered pre-adapted for living in rice paddies, taro patches, and other similar artificial habitats in which aquatic crops are grown. There may be differences in habitat among closely-related species. For instance in Argentina, Scott (1957) reported that *Pomacea canaliculata* (Lamarck) inhabited relatively still water, while the almost indistinguishable *P. insularum* (d'Orbigny) was found in rivers. In Lake Malawi, five species of *Lanistes* occupy marshy areas and the lake edges, with the lake edge species being generally found at slightly different depths (Louda and McKaye, 1982). In Thailand, the five native species of *Pila* have overlapping distributions but slight differences in habitat preferences (Keawjam, 1986). The Asian genus *Turbinicola* Annandale and Prashad (treated as a synonym of *Pila* by Berthold, 1991) is found in fast-flowing hill streams, and shows trends towards a more fully terrestrial existence than other ampullariids (Prashad, 1925b; Andrews, 1965b; Berthold, 1991; Keawjam, 1986). *Limnopomus* Dall, a sub-group of *Pomacea* treated as a distinct genus or subgenus by some authors but synonymized by Berthold (1991), also inhabits swiftly-flowing mountain streams (e.g., Pain, 1950a, b, 1960).

Reproduction, growth and demographics

Breeding system. Ampullariids are dioecious, internally fertilizing and oviparous (not reciprocally-fertilizing hermaphrodites as stated by Chang, 1985). There is evidence that females are larger than males, at least in some species (Prashad, 1925a; Robins, 1971; Keawjam, 1987; Marwoto, 1988; Lum-Kong and Kenny, 1989; Cazzaniga, 1990a; Perera and Walls, 1996; Wada, 1997; Estebenet and Cazzaniga, 1998). The extent of dimorphism may vary among populations within species: it may be slight (Cazzaniga, 1990a) or dramatic (Fig. 1); and it is possible that this has caused considerable nomenclatural and taxonomic confusion. Preliminary study of *P. canaliculata* in Hawaii found no size dimorphism and an approximately 1:1 sex ratio in the wild, although in the laboratory females grew faster than males under certain feeding regimes (H. Ako and T. Nishimura, Honolulu, 1997, personal communication). In addition to size dimorphism there appears to be some slight dimorphism in shape of the aperture and operculum. In *Pomacea canaliculata*, females have a broader mouth (Cazzaniga, 1990a) and a concave operculum (convex in males) (Adalla and Morallo-Rejesus, 1989; Anon., 1989; Guerrero, 1991; Schnorbach, 1995) (H. Ako, Honolulu, 1997, personal communication, says it is the other way round: females have convex opercula). In *Marisa cornuarietis*, the shell aperture of males is said to be more round compared to the more oval shape in females, and males are said to produce thicker, more heavily ridged shells (Robins, 1971). Species of *Pila*, and perhaps *Pomacea*, have been reported to change sex (Keawjam, 1987; Keawjam and Upatham, 1990). The sex change is from male to female (protandry) and takes place during aestivation (*Pila*) or without aestivation (*Pomacea*). The larger size of females in *Pila* has therefore been attributed to continuing growth following this change (Keawjam, 1987). The

ubiquity and significance of this phenomenon needs further investigation; it was not reported by Andrews (1964) in her detailed account of the functional anatomy and development of the reproductive system in *Pomacea canaliculata*, nor by Estebenet and Cazzaniga (1998) in their study of dimorphism in the same species.

Mating, oviposition, eggs and fecundity. Breeding in many species is seasonal and related to latitude, temperature and rainfall (Andrews, 1964). In equatorial regions, many species aestivate during the dry seasons as their habitat dries up (see below), breeding in the rainy season; in subtropical regions, they may only breed during summer, once temperatures reach a certain level (Scott, 1957; Andrews, 1964). Local variation in reproductive regime may be related to local climatic variation, especially availability of water (Bourne and Berlin, 1982).

Species of *Pomacea* generally lay their eggs above water on the exposed parts of vegetation, rocks, etc., perhaps to avoid aquatic predators or in response to low oxygen tension in their often near-stagnant aquatic habitats (Snyder and Snyder, 1971). The eggs are enclosed in a calcium carbonate shell, which may or may not be used as a source of calcium for the developing embryo (Andrews, 1964; Tompa, 1980; Turner and McCabe, 1990). The eggs of *Pomacea scalaris* (d'Orbigny) have been reported to lack the calcareous shell and to be laid under water (Scott, 1957). In fact, as for other species of *Pomacea*, they are laid out of water and do have a calcareous coating; they are salmon-pink (A. Castro-Vazquez, Mendoza, Argentina, 1997, personal communication).

The eggs of *Pila* spp. are also laid out of water, but in depressions made by the snails on banks or mudflats (Michelson, 1961; Andrews, 1964; Keawjam, 1986). They have a calcareous coating (Prashad, 1925a; Keawjam, 1986). In India, laying begins at the start of the rainy season (Prashad, 1925a; Andrews, 1964). The eggs of *Turbinicola* have a calcareous coating and are laid out of water attached to stones (Prashad, 1925b). Those of *Marisa*, *Lanistes* and *Asolene* lack the calcareous coating (Keawjam, 1986) and are deposited under water on submerged vegetation or other surfaces (Michelson, 1961; Robins, 1971; Albrecht *et al.*, 1996).

In *Pomacea canaliculata*, and other species (e.g., *P. dolioides* (Reeve): van Dinther, 1956; *P. haustum* (Reeve): Guimarães, 1981a, b; *P. paludosa*: Perry, 1974), oviposition (above water) takes place predominantly at night, or in the early morning or evening (Andrews, 1964; Chang, 1985; Halwart, 1994a; Schnorbach, 1995; Albrecht *et al.*, 1996), about 24 h after copulation (up to two weeks after mating, according to Chang, 1985). Andrews (1964) and Albrecht *et al.* (1996) described copulation in *P. canaliculata* in detail; it occurs at any time of day or night (Naylor, 1996; personal observations), although there may be some diurnal rhythm, and it takes 10-18 h. Copulation takes place about three times per week (Albrecht *et al.*, 1996). On each oviposition occasion, a single clutch is laid, of highly variable egg number (Table 1). The interval between successive ovipositions has been reported as 12-14 days (Chang, 1985) and about five days (Albrecht *et al.*, 1996) for *P. canaliculata* and 8-16 days for an unidentified '*Ampularius* sp.', presumably *P. canaliculata* (Lacanilao, 1990). Hatching generally takes place about 2 weeks after oviposition, but this period varies greatly (Table 1). Newly hatched snails immediately fall or crawl into the water. One snail can produce an average of 4375 (maximum observed 8680) eggs per year (Mochida, 1988a, 1991), which, if clutch size is about 200 (Table 1), translates into about 22 clutches (see also Anon., 1989, which gave an even higher figure of up to 1200 eggs per month). Development is highly dependent on temperature (e.g., Robins, 1971; Demian and Yousif, 1973; Aldridge, 1983; Mochida, 1988a, b; Estebenet and Cazzaniga, 1992; Schnorbach, 1995), and therefore locality, which probably largely accounts for the variability in the data for *P. canaliculata* in Table 1. The eggs of *Marisa cornuarietis* take 8 days to hatch at 25-30°C and 20 days at 15-20°C; those of *Pila globosa* (Swainson) take 10-14 days at 32-38°C and 3 weeks at 21-27°C (Demian and Yousif, 1973).

A very different strategy is adopted by *Pomacea urceus* (Burky, 1973, 1974; Lum-Kong and Kenny, 1989). This species mates towards the end of the rainy season. Females then bury into the muddy substrate and aestivate as their marshy habitat dries out. Snails living in permanent rivers also aestivate, burying into the river banks above the water level. Eggs are laid at the start of the aestivation period and are maintained within the shell, between the operculum and the aperture. Development takes place during the dry season, within the female's shell (even if she dies). The young snails hatch but remain and aestivate within the female's shell until the start of the rainy season. Burky *et al.* (1972) argued that this strategy protects the newly hatched juveniles from high (possibly lethal) temperatures and water loss during the dry season. *P. urceus* is the only ampullariid known to adopt this strategy.

The eggs of most species of *Pomacea* are brightly coloured, perhaps as a warning of unpalatability since the eggs appear to be distasteful, at least to vertebrates although perhaps not to invertebrates (Snyder and Snyder, 1971; Kushlan, 1978). They are various shades of pink, orange and red in *Pomacea australis* (d'Orbigny), *P. bridgesii* (Reeve), *P. canaliculata*, *P. dolioides* (possibly a synonym of *P. lineata* (Spix) but considered distinct by Geijskes and Pain, 1957), *P. hanleyi* (Reeve), *P. insularum*, *P. lineata*, *P. megastoma* (Sowerby), *P. paludosa* and *P. sordida* (Swainson) (van Dinther, 1956, 1973; Snyder and Snyder, 1971; Thiengo, 1987, 1989; Winner, 1989, 1996; Keawjam and Upatham, 1990; Thiengo *et al.*, 1993; Perera and Walls, 1996). The eggs are green in *Pomacea glauca* (Linnaeus), *P. pyrum* (Philippi), *P. decussata* (Moricand) and *P. nais* Pain (Pain, 1950b; van Dinther, 1956, 1973; Snyder and Snyder, 1971; Perera and Walls, 1996). Snyder and Snyder (1971) hesitated to consider green eggs to have evolved for camouflage because they generally remained distinctly visible, at least to humans. The eggs of *P. falconensis* Pain and Arias, *P. flagellata* (Say), *P. gossei* (Reeve), *P. fasciata* (Roissy) and *P. cuprina* (Reeve) are white (Andrews, 1933; Snyder and Snyder, 1971; Perera and Walls, 1996). Eggs of *P. urceus* are reported as either white (Burky, 1973; 1974), orange (Lum-Kong and Kenny, 1989), or to vary from orange to pale green (Perera and Walls, 1996); those of *P. haustum* have been reported as both green (Winner, 1989, 1996) and red/pink (Snyder and Snyder, 1971; Guimarães, 1981a); in both cases this may represent taxonomic confusion. Comfort's

(1947) report that the eggs of *P. glauca* are red is based on a misidentification of a species (perhaps *P. canaliculata*) from Argentina. Egg colour may change somewhat as the egg surface dries following oviposition and subsequently as the dark-coloured embryo develops inside (Snyder and Snyder, 1971).

The eggs of *Pila* and *Lanistes* are not brightly coloured. The colour of the eggs of *Asolene* have not been reported. Those of *Marisa* (at least *M. cornuarietis*) are orange when laid but soon lose this colour (Michelson, 1961); they were reported as 'grayish-white' by Robins (1971).

Growth and longevity. Little is known of these aspects of the biology of ampullariids (Table 1; and see Estebenet and Cazzaniga, 1992). A number of studies have investigated growth in the laboratory (Table 1) but it is difficult to relate these studies to growth in the wild, which is probably dependent on season, food availability, temperature, etc. One laboratory study, on *Pomacea canaliculata* in its native Argentina (Estebenet and Cazzaniga, 1992), did however demonstrate the crucial role of temperature in growth and reproduction. At a constant 25°C, snails matured in 7 months and then bred continuously for a single 'season' of about 4 months, then died. In contrast, under seasonally fluctuating temperatures (7-28°C), the snails took 2 yr to reach maturity; they then bred for two distinct annual breeding seasons, for a life-span of about 4 yr. In the wild in Argentina, *P. canaliculata* breeds only during the summer (Scott, 1957), and the life-cycle under the fluctuating laboratory temperature regime may indeed reflect the life-cycle in the wild. Under semi-artificial conditions in Japan (an outdoor pond but with food provided), *Pomacea canaliculata* grew to maturity in less than two months (Chang, 1985). In tropical regions of South-East Asia, release from the seasonality of its natural range may be at least one reason why *P. canaliculata* is so prolific; rapid growth and breeding, and hence rapid succession of generations, are permitted year round (Naylor, 1996), leading to rapid population expansion and high population densities. A short life might then be predicted, but longevity in the wild under such conditions has not been reported.

A multitude of other biotic and abiotic factors may influence growth. For instance, growth rate of *Pomacea dolioides* in its native South America is determined by food availability, as well as by the quantity of water and the duration and intensity of the dry season (van Dinther, 1956, 1962; Donnay and Beissinger, 1993). And, as for other species of snails (Cameron and Carter, 1979), population density (Cazzaniga and Estebenet, 1988) and both inter- and intra-specific competition may be important.

Maximum size varies greatly among populations (e.g., Keawjam, 1986; Estebenet and Cazzaniga, 1992; Donnay and Beissinger, 1993) and may be related to a number of environmental factors, including habitat size (Johnson, 1958), microclimatic variation and differing water regimes (Donnay and Beissinger, 1993), and population density (as it is in other species of snails: Williamson *et al.*, 1976). Maximum size of *Pomacea canaliculata* in Hawaii is about 30 mm, but in Asia it can reach at least 65 mm (Schnorbach, 1995) or even 90 mm (Heidenreich *et al.*, 1997).

Population dynamics and densities. Few studies have addressed ampullariid population dynamics directly. It is clear, however, that seasonal changes in water availability are important. In Florida, recruitment of *Pomacea paludosa* was dramatically enhanced during years when the water table remained high, allowing the snails to remain active instead of having to aestivate; larger snails were also thought to be more able to withstand dry periods (Kushlan, 1975). *P. urceus* will only enter aestivation once a shell length of 85 mm has been reached (Burky *et al.*, 1972). In Venezuela, habitats with more permanent standing water (rice fields, as opposed to natural wetlands) allowed *Pomacea dolioides* to grow larger and achieve higher population densities, essentially because the period spent in aestivation (no growth) was shorter; densities ranged from three per 100 m² in natural wetlands to 33 per 100 m² in rice fields (Donnay and Beissinger, 1993). In Hawaii, densities of *P. canaliculata* in taro patches have been recorded over 130 m⁻² (12.9 ft⁻²; Tamaru, 1996; Tamaru and Hun, 1996). Densities of *P. canaliculata* in rice paddies in the Philippines generally are 1-5 m⁻² but densities up to 150 m⁻² have been reported (Halwart, 1994a; Schnorbach, 1995). Anderson (1993), perhaps mistakenly, reported '1,000 mature snails per square metre' in the Philippines. In rice in Japan, studies have reported 3-7 m⁻² (Okuma *et al.*, 1994) and 12-19 m⁻² (Litsinger and Estano, 1993). Clearly, in irrigated systems with water present longer than would naturally be the case, snails can reach maturity in a shorter period. Fluctuations in population density in *Pomacea haustrum* in Brasil (maximum 215 m⁻²) were reported by Freitas *et al.* (1987), although the underlying reasons for the fluctuations were unclear. Again, numerous other biotic and abiotic factors may be involved, e.g., vegetation type (Bryan, 1990), food availability, temperature, water hardness (Perera and Yong, 1990). Over the reproductive season in Florida, *Pomacea paludosa* populations were estimated to produce 1.2-1.5 million snails per ha (= 120-150 m⁻²) (Hanning, 1978).

Marisa cornuarietis, introduced to Florida has been reported at densities over 200 m⁻² (20.9 ft⁻²; Robins, 1971). *Lanistes nyassanus* Dohrn is found at densities of about 1 m⁻² in Lake Malawi (Louda and McKaye, 1982). It is listed as an endangered species by IUCN (1996).

Clearly, following hatching, densities in the immediate vicinity of the clutch will be high. However, few of the above reports are sufficiently detailed to assess the impact of survivorship on density, although clearly some species, especially when introduced, are able to achieve remarkably high adult population densities.

Natural enemies

Predators. Perhaps the best known predator of New World ampullariids is the kite *Rostrhamus sociabilis* d'Orbigny

(in Florida, known as the Everglade Snail Kite and considered endangered in the USA), which has a long, slender hooked bill adapted for extracting snails, its almost exclusive prey (Pain, 1950b; van Dinther, 1956; Snyder and Snyder, 1971; Kushlan, 1975; Beissinger *et al.*, 1994). In Florida, the kite's natural prey is *Pomacea paludosa*; in South America it preys on a number of other species: *Pomacea lineata*, *P. dolioides* (possibly a synonym of *P. lineata*), *P. papyracea* (Spix) and *Marisa cornuarietis*. Another important New World avian predator is the limpkin (*Aramus guarauna* d'Orbigny), a large wading bird similar to an ibis. Limpkins are found virtually throughout the New World distribution of ampullariids, which constitute a major part of their diet (Peterson, 1980). Caiman lizards (*Dracaena guianensis* Daudin) feed almost exclusively on ampullariids; their teeth have evolved into rounded knobs for crushing snails (Perera and Walls, 1996). Other predators include slender-billed kites, boat-tailed grackles, white ibises, crocodilians, various fish, turtles, crayfish and aquatic insects (Robins, 1971; Snyder and Snyder, 1971; Kushlan, 1975; Donnay and Beissinger, 1993). However, insufficient work has been done to evaluate whether any of these predators impact snail population dynamics significantly (Donnay and Beissinger, 1993). In Africa, species of *Lanistes* are a major food resource of various species of fish, which may exert significant selection pressure on shell morphology (Louda and McKaye, 1982), but their impact, if any, on snail population dynamics is unknown.

Some species (*Pomacea paludosa* and to a lesser degree *P. glauca* and *P. dolioides*), exhibit an alarm response on detecting chemical stimuli in the water from predators (turtles), the juices of damaged conspecifics (Snyder and Snyder, 1971), and in response to mechanical disturbance of vegetation they are sitting on (Perry, 1974). The snails drop to the substrate (if they are not already on it) and bury themselves into it.

Parasites and pathogens. Little has been published in this area. Various ampullariid species, including *Pomacea canaliculata*, are vectors of *Angiostrongylus cantonensis* (Chen), the rat lungworm (Wallace and Rosen, 1969; Keawjam, 1986; Chao *et al.*, 1987; Mochida, 1991; Naylor, 1996). They may also harbour schistosomes (Hanning and Leedom, 1978; Leedom and Short, 1981) and flukes (Keawjam, 1986). Three species of trematode flatworms are reported living symbiotically in the mantle cavity of species of *Pomacea* and *Asolene* in South America (León, 1989). Whether any of these parasites cause harm to the snail host is unknown. There appears to be no knowledge of natural microbial pathogens in apple snails, although other snails, especially land snails, are known to be associated with microorganisms, especially protozoa, both as parasites and as symbionts or commensals (Godan, 1983). Again, whether any of these parasites or pathogens play (or could play) a role in population regulation is unknown.

Food and feeding

The feeding habits of ampullariids are microphagous, zoophagous, and macrophytophagous, none being mutually exclusive (Estebenet, 1995). Ciliary feeding on particulate matter on the water surface has been described for some species (McClary, 1964). Some species will feed on insects, crustaceans, small fish, etc., mostly as carrion but not always so (McLane, 1939; Estebenet, 1995). Some species (e.g., *Marisa cornuarietis*, *Pomacea canaliculata*) will attack other snails and their eggs (Demian and Lutfy, 1966; Robins, 1971; Aldridge, 1983; Cedeño-León and Thomas, 1983; Cazzaniga, 1990b). The predominant habit, however, is macrophytophagous, which from an agricultural pest standpoint is also the most significant. Andrews (1965a) described the feeding behaviour of *Pomacea canaliculata* in detail. *P. canaliculata* shows preferences among different food plants; its rate of growth correlates with its feeding on the preferred plant; and it is able to detect its food plants from some distance using chemical cues in the water (Estebenet, 1995), as can *Pomacea paludosa* (McClary, 1964). However, despite exhibiting such preferences, *P. canaliculata* appears relatively generalist and indiscriminate (e.g., Schnorbach, 1995), and, as suggested for *Marisa cornuarietis* by Robins (1971), it may be 'more pertinent to determine what the animal does not eat than what it will eat'. In fact, anecdotal comments suggest that *Pomacea canaliculata* is particularly voracious compared to other ampullariids (Neck, 1986).

Respiration

Many ampullariids are amphibious, both in physiology and behaviour. The mantle cavity contains both a ctenidium ('gill') and a portion modified as a pulmonary sack or 'lung' (Andrews, 1965b). In *Pomacea urceus* in Venezuela (Burky and Burky, 1977), ventilation of the lung by extending the siphon to the water surface occurs periodically, and more frequently under conditions of low oxygen tension. Ventilation of the lung, as well as being used for respiration, is also used to adjust buoyancy levels, such that snails can float at the water surface under periods of low oxygen tension. Burky and Burky (1977) reported similar patterns of ventilation for *Pomacea falconensis*, *P. luteostoma* (Swainson) and *Marisa cornuarietis*, smaller snails (including juvenile *P. urceus*) ventilating more frequently than larger snails, probably reflecting relative differences in lung capacity to total body weight in relation to metabolic rate. Lung ventilation is obligatory, but the snails can nevertheless survive extended periods without ventilation: up to 6 h in *Pomacea lineata* (van Dinther, 1956). Similar respiratory behaviour has been described for other ampullariids (McClary, 1964; Freiburg and Hazelwood, 1977), with differences among species in the relative significance of aerial and aquatic respiration (Andrews, 1965b). Work on respiration rate and its relation to temperature and oxygen tension has been reviewed by Aldridge (1983) and Santos *et al.* (1987). The ability to use the ctenidia and the 'lung' for respiration allows many ampullariids to survive significant periods out of water and to disperse significant distances over land. This is clearly of adaptive value for species that live in marshy or other habitats that dry out

periodically, but it also means that when introduced to new habitats, such as rice paddies or taro patches, the snails may be difficult to contain within circumscribed areas as they may easily cross the raised burms between paddies (although this has been reported as not occurring; Eversole, 1992).

Aestivation

Many ampullariids aestivate during dry periods (Lum-Kong and Kenny, 1989). When the snails' habitat dries out, they bury themselves into the mud. Some species (e.g., *Pomacea urceus*) bury only superficially, with part of the shell remaining above the surface of the hardened mud (Burky *et al.*, 1972); others bury up to 1 m deep (e.g., *Pila ampullacea* (Linnaeus), *P. pesmei* (Morelet); see Keawjam, 1986). They can survive in this state in some cases for extended periods (in laboratory experiments) far longer than are likely to be necessary in the wild: e.g., 8 months for *Pomacea glauca* (van Dintter, 1956), 13 months for *P. lineata* (Little, 1968), 17 months for *P. urceus* (Burky *et al.*, 1972), at least a year for *Pila ampullacea* and *P. pesmei* (Keawjam, 1986) and 25 months for *Pila globosa* (Chandrasekharam *et al.*, 1982). *Pomacea canaliculata* is only reported to survive buried in the earth up to 3 months (Schnorbach, 1995). They can withstand significant loss of soft tissue weight during aestivation; in *Pomacea lineata* up to 50% (Little 1968) and in *P. urceus* up to 62% (Burky *et al.*, 1972). *Pila virens* (Lamarck) and *Pila globosa* lose considerably less weight (5%) but can nevertheless aestivate for at least 6 months; the shell and operculum appear to be effective barriers to water loss, especially as the operculum is sealed in the shell opening with dried mucus (Meenakshi, 1964). Metabolism during aestivation is anaerobic in *Pila virens* and *P. globosa* (Meenakshi, 1964; Aldridge, 1983), but aerobic in *Pila ovata* (Olivier) and *Pomacea urceus* (Burky *et al.*, 1972). *Pila virens* and *P. globosa* (and other species of *Pila*) aestivate buried very deep in the ground; their anaerobic aestivation metabolism may be an adaptation to this, in contrast to the aerobic respiration of the shallow burying *Pomacea urceus*. Metabolism during aestivation in *Marisa cornuarietis* has been described by Horne (1979); this species only tolerates anaerobic conditions for about 48 h. However, adult *M. cornuarietis* can withstand at least 30 days out of water in 20% relative humidity, or 120 days at 80% relative humidity, although juveniles have little resistance to desiccation (Robins, 1971).

Physiology

Lethal temperatures. During aestivation, *Pomacea urceus* regulates its body temperature below 41°C, in part through evaporative cooling, and has an upper lethal temperature between 40 and 45°C (Burky *et al.*, 1972). Adult *P. urceus* are more tolerant of high temperature than are juveniles (Burky *et al.*, 1972), perhaps because adults can afford to lose more water through evaporative cooling (cf. Cowie, 1985). In both *Pomacea paludosa* and *Marisa cornuarietis*, 40°C is lethal when snails are exposed for 1-4 h. (Freiburg and Hazelwood, 1977), although Thomas (1975) reported that they could withstand temperatures up to 45°C. Robins (1971) gave 39°C as the 'upper limit of short-term heat tolerance' for *M. cornuarietis*, with juveniles more tolerant than adults at 37°C, and both adults and juveniles feeding normally between 33.5 and 35.5°C; eggs did not develop normally at 35-37°C. Mochida (1991) reported for *P. canaliculata* that mortality is high at water temperatures above 32°C (35°C in Mochida, 1988b, and Eversole, 1992). *Pila virens* and *Pila globosa* cannot survive 2 days at 40°C (Meenakshi, 1964). *Pomacea lineata* survived 1 h exposure at 40°C (Santos *et al.*, 1987).

Regarding low temperature tolerance, Robins (1971; see also Neck, 1984) reported that *M. cornuarietis* could survive over 24 h at 11°C (although egg development ceased at this temperature) but succumbed in 5 h when exposed to 8°C, although Thomas (1975) reported that it could withstand 6°C. *Pomacea paludosa* can survive exposure at 5°C (Freiburg and Hazelwood, 1977). Mochida (1991) reported for *P. canaliculata* that the snails can survive 15-20 days at 0°C, 2 days at -3°C but only 6 h at -6°C (see also Neck and Schultz, 1992; Wada, 1997). *Pomacea lineata* survived 1 h exposure at 5°C (Santos *et al.*, 1987). *Pila virens* and *Pila globosa* cannot survive 4 days at 20°C and die within 1 day at 10°C (Meenakshi, 1964).

Differences among species in both their upper and lower lethal limits may reflect adaptation to their natural climatic environment. There appears to be less variability in the upper limit, which in general appears to be around 40°C for many aquatic organisms. Comparability among the studies mentioned above is poor, largely because experimental procedures, especially exposure time, differed. Nevertheless, *Pomacea canaliculata*, of more temperate habitats (Argentina), seems to have a lower limit than other more tropical species such as *Pomacea urceus*, *Marisa cornuarietis* and the two *Pila* species. Lower limits seem more variable, with *P. canaliculata* able to tolerate freezing temperatures, in marked contrast to the *Pila* species, which are unable to survive at 20°C for extended lengths of time. These differences probably have significant consequences for the potential establishment, reproduction, growth and population dynamics of apple snails when they are introduced to new regions with climates differing from those in their natural ranges.

Salinity tolerance. *Marisa cornuarietis* can withstand up to about 30% salt water (Hunt, 1961; Robins, 1971; Santos *et al.*, 1987). *Pila globosa* can 'live in salt water of low salinity' (Prashad, 1925a). Fujio *et al.* (1991a) indicated differences in salinity tolerance among three 'strains' of *Pomacea canaliculata*. Preliminary observations in Hawaii suggest that *P. canaliculata* is sufficiently tolerant of sea water to survive long enough to be carried by currents from one stream mouth to another, thereby expanding its distribution (F. and N. Reppun, Hawaii, 1997, personal communication). However, although exhibiting some tolerance of salinity, ampullariids generally live only in fresh water, and brackish water may limit the spread of newly introduced species (e.g., *Marisa cornuarietis*; Robins, 1971).

Dispersal

Adult *Pomacea lineata* travel several meters an hour (van Dinther, 1956). *Lanistes nyassanus* moves an average 2.8 m per day (Louda and McKaye, 1982). *Pila globosa* makes long excursions on land both for going from one source of water to another and for the purpose of laying eggs (Prashad, 1925a). Short-term dispersal activity, however, does not necessarily translate into long-term, long-distance dispersal. There is little documentation of the spread of ampullariids from a focus of introduction. In a canal in Florida, an introduced population of *Marisa cornuarietis* expanded by at least 1.5 km downstream in 6-8 months (Hunt, 1958), and by 1970 was distributed in virtually the entire freshwater canal system in the Miami area, dispersal being predominantly by floating downstream on vegetation (Robins, 1971). Floating downstream (unattached to vegetation) has been seen in Hawaii and no doubt facilitates rapid dispersal, but crawling upstream is also possible (H. Ako, Honolulu, 1997, personal communication). However, the rapid dispersal of *Pomacea canaliculata* to most parts of the Philippines (and within other countries in South-East Asia) following its initial introduction has been predominantly human mediated.

Introductions

Distribution as a food item

A number of ampullariids are used as human food in their native ranges. For instance, *Pomacea urceus* is eaten in Trinidad (Lum-Kong, 1989; Lum-Kong and Kenny, 1989) and in times of food scarcity in Guyana (Pain, 1950b). In India, *Pila globosa* is eaten (Thomas, 1975), as are *Pila conica* (Wood) in Malaysia (Johnson, 1958), *Pila luzonica* (Reeve) in the Philippines (Palomino and Juco, 1983) and native species of *Pila* in Thailand (Keawjam, 1986, 1990). Elsewhere in South-East Asia, they may be only a minor part of the local diet (e.g., in Cambodia; Cowie, 1995a). In Africa, *Pila congoensis* Pilsbry and Bequaert was eaten, although only by older people because eating snails was thought to cause 'infecundity' (Pilsbry and Bequaert, 1927).

In both Guam (first reported 1984) and Hawaii (first recorded 1966) *Pila conica* was introduced without authorization, either accidentally or deliberately as a food item (Smith, 1992; Cowie, 1995b). It was introduced to Palau in 1984 or 1985 but was thought to have been eradicated by 1987 (Eldredge, 1994).

Between 1979 and 1981 a species of *Pomacea*, usually referred to as *Pomacea canaliculata*, was introduced to South-East Asia, initially from Argentina to Taiwan (e.g., Mochida, 1988a, b, 1991; Cheng, 1989 [as '*Pomacea lineata*']). The initial introduction to Taiwan was illegal (Cheng, 1989). The purpose of the introduction was both for local consumption and for development for export to the gourmet restaurant trade, with the expectation of high profits (Acosta and Pullin, 1991; Naylor, 1996). Prior marketing research had not been undertaken. The subsequent spread of these snails, distributed for the same purposes and still with no market research, has been summarized by Mochida (1991), Litsinger and Estano, (1993), Halwart (1994a), Naylor (1996) and Vitousek *et al.* (1996). In 1981 they were taken from Taiwan to Japan (they were present in Okinawa by at least 1984; Fujio *et al.*, 1991a; Wada, 1997), and by 1983 about 500 snail businesses had opened up all over Japan (Wada, 1997). In either 1980 or 1982 they were introduced from Taiwan to the Philippines (Mochida, 1991; Anderson, 1993; Halwart, 1994a), and introductions to the Philippines continued from various sources (and possibly including more than one species; Mochida, 1988b) as snail-farming was promoted by both governmental and non-governmental organizations (Anderson, 1993). Later the snails were taken to China (1985), Korea (probably 1986), parts of Malaysia (Sarawak and Peninsular Malaysia, 1987), Indonesia (Java and Sumatra, 1989), Thailand (1989), Vietnam (1988 or 1989) and Laos (1992). They have also been introduced to Hong Kong (Laup, 1991), Cambodia (Cowie, 1995a), Singapore (Ng *et al.*, 1993), Guam (from Taiwan - Smith, 1992; Eldredge, 1994), Papua New Guinea (from the Philippines - Laup, 1991 [as '*Pomacea lineata*']; Anon., 1993; Eldredge, 1994) and Hawaii (Cowie, 1995b).

However, the snails' economic potential seems to have been over-estimated and no major aquaculture operations have developed (Acosta and Pullin, 1991). In Taiwan, failure of the local market was said to be because consumers did not like the 'tough meat and repulsive taste' (Chang, 1985; see also Cheng, 1989; Naylor, 1996; Vitousek *et al.*, 1996). In addition, developed nations maintain stringent health regulations that largely precluded its importation (Anderson, 1993; Naylor, 1996). Snails escaped or were deliberately released from captivity and have since become widespread and abundant in many countries. Expansion of their distribution has been assisted by, among other things, floods and typhoons, movement of infested soil during new paddy preparation, deliberate release of snails for weed control, and use of snails for fishing bait (Anderson, 1993; Wada, 1997).

Distribution by the aquarium trade

Ampullariids are popular domestic aquarium snails (Perera and Walls, 1996) and a number of species have been introduced to many parts of the world via the aquarium trade. *Marisa cornuarietis* of northern South America has been introduced to several countries (e.g., the USA) by aquarists (Hunt, 1958; Robins, 1971; Neck, 1984; Perera and Walls, 1996). *Pomacea bridgesii* of South America became established in Florida, either accidentally or through intent, probably introduced in the early 1960s (Clench, 1966). The shell of *P. bridgesii* is usually dark greenish-brown with or without spiral

banding patterns. However, when a bright yellow shell colour variant was discovered, it was selectively bred by the aquarium trade and subsequently transported to many parts of the world. Bright yellow, orange and other shell colour variants have also been found in other species of *Pomacea*. These brightly coloured forms are favoured by the aquarium trade and the market for ampullariids for aquaria has expanded since their discovery (Perera and Walls, 1996); they have become established or have been intercepted by customs officials as far from their natural range as Singapore (Chan Sow-Yan, Singapore, 1996, personal communication; Bishop Museum collections) and Australia (P. Colman, Sydney, 1994, personal communication; Bishop Museum collections). *Pomacea canaliculata* (including brightly coloured forms) has recently been reported in California (Cerutti, in press). The promulgation of these brightly coloured varieties has unfortunately led to the use of the terms 'golden snail', 'golden apple snail', 'golden mystery snail', as if referring to a single, particular species. Indeed the terms 'golden apple snail' and 'golden snail' have become the most frequently used common names for the major pest species in South-East Asia, which has been distributed almost entirely for use as food (above) rather than via the aquarium trade. Use of these common names has led to immense confusion and misunderstanding, both within the aquarium trade and, more seriously, among managers, politicians and other non-biologists trying to cope with the agricultural problems that have arisen as these snails have escaped or been released into the wild far beyond their natural range.

Keawjam and Upatham (1990) considered the *Pomacea* spp. known in Thailand to have been imported by the aquarium trade, but it is also probable that they were introduced for food, as elsewhere in South-East Asia. In Hawaii, *Pomacea canaliculata*, as well as being introduced for food, has been available in aquarium stores. Purchase in aquarium stores followed by release for culture as food items appears to have been one reason for the spread of *P. canaliculata* in Hawaii (H. Ako, Honolulu, 1997, personal communication). *Pomacea lineata* has been introduced to South Africa (Berthold, 1991), perhaps via the aquarium trade.

Introduction for biological control

As a snail competitor/predator. Ampullariids have been introduced in attempts to control the snail vectors of schistosomes, either by out-competing them and/or by predation (especially on eggs and juveniles). In Guadeloupe, introduced *Pomacea glauca* and *Marisa cornuarietis* caused the decline of *Biomphalaria glabrata* (Say) through competition (Pointier *et al.*, 1988, 1991). In Puerto Rico, *Marisa cornuarietis* caused a decline in *B. glabrata* and *Lymnaea columella* Say through predation (Robins, 1971; Peebles *et al.*, 1972). *M. cornuarietis* is said to have had a similar effect in the Dominican Republic (Perera and Walls, 1996) and in Egypt (Demian and Kamel, cited by Cedeño-León and Thomas, 1983; Berthold, 1991).

For aquatic weed control. Ampullariids such as *Marisa cornuarietis* are voracious feeders on aquatic plants; this is partly the reason for their reported success in controlling other snail species: they reduce the available food supply (Perera and Walls, 1996). They have therefore been used or suggested for control of aquatic weeds. For instance, in Florida and Puerto Rico, *Marisa cornuarietis* has been deliberately introduced in attempts to control aquatic plant nuisances (Robins, 1971; Simberloff and Stiling, 1996a); *Pila globosa* in India has been tested as a control agent for the aquatic weed *Salvinia molesta* Mitchell (Thomas, 1975); and in Japan, introduced *Pomacea canaliculata* has been suggested as a possible agent for weed control (Okuma *et al.*, 1994; Wada, 1997).

Ampullariids as Agricultural Pests

Pests in their native range

In general, ampullariids are not serious agricultural pests in their native ranges. A major exception is in rice-growing areas of Surinam (van Dinther, 1956, 1962, 1973; van Dinther and Stubbs, 1963). Here, since the development in the 1930s to 1950s of large scale rice farming involving mechanized sowing, *Pomacea dolioides* (also referred to as *Pomacea lineata*, a probable synonym, although considered distinct by Geijskes and Pain, 1957) in particular, but also *P. glauca*, have caused serious problems. The seeds, planted directly into the irrigated fields, are attacked by the snails as they germinate. Prior to the development of direct sowing as the preferred crop establishment method, seedlings were germinated in nurseries and transplanted in the field. Although some damage occurred in the nurseries and after planting out, larger seedlings were more able to withstand attack.

In El Salvador, 'snails' (presumably ampullariids) necessitated treatment of rice with pesticides (Efferson, 1968). Damage has also been reported in Barbados, Bolivia, Brasil, Columbia, Guadeloupe and Trinidad (Litsinger and Estano, 1993; Bombeo-Tuburan *et al.*, 1995;), but no details are available. Some of these reports may be of non-native species. In Africa, *Lanistes ovum* Peters and *L. carinatus* (Olivier) have been reported damaging seedlings (Van Dinther, 1973). *Pila* has occasionally been implicated as an agricultural pest. In Burma, *Pila pilosa* has been reported to damage paddy rice (van Dinther and Stubbs, 1963). *Pila globosa* has been reported as a paddy pest in India (Singh and Agarwal, 1981), although Thomas (1975) stated that this species did not feed on rice. Van Dinther (1973) mentioned *Pila globosa* and *Pila polita* (Deshayes) in India and Burma.

Pests when introduced

In Puerto Rico, *Marisa cornuarietis*, native to northern South America and a voracious feeder on rice (Thomas, 1975), has been reported destroying seedlings (van Dinther, 1973); and species of *Pila* have been introduced outside their natural range and have become pests (e.g., *Pila conica* in Hawaii; Cowie, 1995b). However, it is species of *Pomacea* that have become by far the most serious ampullariid pests, attacking a wide range of crops, with their most serious impacts being on rice in South-East Asia.

Rice. The history of the introduction of non-native apple snails into South-East Asia (above) and the damage they cause to rice farming have been reviewed by Halwart (1994a) and Naylor (1996), among others. One or more species of *Pomacea* (usually identified as *Pomacea canaliculata*) have become pests of paddy rice in many countries including Thailand, Vietnam, parts of Malaysia and Indonesia, China, Taiwan, Japan, but probably most seriously in the Philippines.

In Taiwan, where *Pomacea* was first introduced between 1979 and 1981, 17,000 ha of rice and other crops had been infested by 1982, increasing rapidly to 171,425 ha by 1986 (Mochida, 1991). In the Philippines the spread of *Pomacea* has been even more rapid, from 9500 ha of rice in 1986 to over 400,000 ha in late 1988, 500,000 ha by 1989, and occurring in most provinces (Adalla and Morallo-Rejesus, 1989; Mochida, 1991; Olivares *et al.*, 1992; Anderson, 1993; Litsinger and Estano, 1993) and 800,000 ha by 1995 (Palis *et al.*, 1996). They have now become the most important pest of rice in the Philippines (Mochida, 1988a, 1991; Cheng, 1989; Acosta and Pullin, 1991; Halwart, 1994a; Naylor, 1996; Vitousek *et al.*, 1996). In Japan, introduced in 1981, *Pomacea* had spread to 35 out of 47 prefectures by 1989 (Mochida, 1991) and by 1995 occurred in over 50,000 ha of paddy fields (Wada, 1997). Details of the snails' spread in other countries are not readily available.

Problems caused by *Pomacea canaliculata* are not totally confined to South-East Asia. In 1990/91 infestation of rice-growing areas in the Dominican Republic by a species tentatively identified as *P. canaliculata* was reported, and by 1997, 40% of this country's rice-growing areas were infested, with losses up to 75% in some areas (D. Robinson, Philadelphia, 1997, personal communication).

Other crops. Other crops reported as being attacked by ampullariids are listed in Table 2. In about 1989 *Pomacea canaliculata* was introduced to the Hawaiian Islands. Within 3 yr it been taken deliberately to most of the main islands in the archipelago and had escaped and been deliberately released into taro patches, which are similar ecologically to rice paddies, where it is now a major pest (Cowie, 1995b, 1996, 1997b). Taro is the main traditional staple for native peoples not only in Hawaii but on many Pacific islands. A number of other introduced ampullariids have been present in the Hawaiian Islands since before the arrival of *Pomacea canaliculata*, but do not seem to cause major agricultural problems (Cowie, 1995b, 1997b), although there have been no formal economic yield loss assessments.

Yield Loss and Economic Cost of Ampullariid Damage

Yield loss can be massive but variable. In rice in the Philippines (Naylor, 1996), where probably the most serious damage occurs, losses vary from 5% to 100% depending on locality and the level of infestation. Yield loss is related to the density and size of the snails. In experimental studies, one snail per m² can reduce rice crop stand by 20%, but eight snails can reduce it by over 90% (see also Olivares *et al.*, 1992; Schnorbach, 1995); a single snail eats 7-24 rice seedlings per day (Litsinger and Estano, 1993). Densities in infested rice paddies in the Philippines are generally 1-5 m⁻² but densities up to 150 m⁻² have been reported (Halwart, 1994a). In Japan, 3-19 m⁻² have been reported in rice (Litsinger and Estano, 1993; Okuma *et al.*, 1994).

However, little quantitative yield loss or economic information is available. In Taiwan, loss of rice was estimated as US\$2.7 million in 1982, increasing rapidly to US\$30.9 million in 1986 (Mochida, 1991). Huge areas were treated with pesticides (103,350 ha in 1986) at additional enormous cost. In Japan, control in just 176 ha cost US\$64,385 (Mochida, 1991). In the Philippines, between 1987 and 1990, farmers spent US\$10 million on pesticides (Anderson, 1993).

The most detailed published economic analysis so far is that of Naylor (1996), reported also by Vitousek *et al.* (1996), for the Philippines. This analysis included not only the cost of loss of rice, but also the costs of replanting, application of pesticides and hand-picking snails. Total costs in 1990 due to *Pomacea* infestation were estimated as US\$28-45 million. This was 25-40% of what the Philippines spent on rice imports in 1990. Naylor (1996) also compared the costs of control measures (pasturing ducks in the paddies, hand-picking the snails, and applying insecticides) in the Philippines with costs in Vietnam. She showed that the relative implementation of each of these techniques differed because of different costs in the two countries, but also because infestation in Vietnam had not reached the extreme levels that it had in the Philippines, and hand-picking combined with duck pasturing was relatively more feasible and effective in keeping snail numbers low. As snail populations increase and spread in Vietnam this may change. No doubt, tailoring the suite of management practices to local needs will differ both among and within the other countries impacted; research will be necessary.

Environmental Impacts

In addition to the serious agricultural problems caused by introduced ampullariids, there are also potential concerns for the natural environment, including impacts on native snail species. In Guadeloupe, Pointier *et al.* (1988, 1991) argued that

expanding populations of the artificially introduced *Pomacea glauca* and *Marisa cornuarietis* caused the decline of *Biomphalaria glabrata*, the snail host of the vector of schistosomiasis, through competition. In Puerto Rico, *Marisa cornuarietis* caused a similar decline in *B. glabrata* and *Lymnaea columella*, in this case it was argued through predation, and at the same time removed the entire plant cover in the experimental pond (Peebles *et al.*, 1972). Similar impacts of *M. cornuarietis* have been reported from the Dominican Republic (Perera and Walls, 1996) and Egypt (Demian and Kamel, cited by Cedeño-León and Thomas, 1983). While the implication is that this 'biological control' is a good thing from the perspective of schistosomiasis, it is clear that introduced ampullariids could have serious impacts on native snail populations. Already, introduced *Pomacea* have been implicated in the decline of native species of *Pila* in South-East Asia (Acosta and Pullin, 1991; Halwart, 1994a), although Ng *et al.* (1993) considered there to be little competition between introduced *Pomacea* and the native *Pila scutata* (Mousson) in Singapore. In the Philippines, native *Pila* are reported to have declined as a result of extensive application of pesticides against introduced *Pomacea* (Anderson, 1993). Cowie (1995b) and Neck (1984) warned of the possible impacts of introduced ampullariids on native snail species in Hawaii and Texas, respectively.

Although some species (e.g., *Marisa cornuarietis*) will feed on other snails and their eggs, they are predominantly herbivores and apparently voracious and rather generalist (Cedeño-León and Thomas, 1983). Invasion of natural wetlands by ampullariids could therefore have significant impacts, as suggested by Cowie (1995b) in Hawaii and Neck (1984) in Texas. In Florida, *Marisa cornuarietis*, as well as having been dumped by aquarists (Hunt, 1958), has been deliberately introduced in attempts to control aquatic plant nuisances, despite the fact that it feeds indiscriminately on many desirable native plant species, thereby not only destroying these plants but severely impacting native animals that depend on them (Simberloff and Stiling, 1996a). Other apple snail species, possibly with equally generalist feeding habits, have been suggested for aquatic weed control (above). The pristine wetlands of northern Australia seem especially vulnerable, as they lie within what appears to be a climatically favourable region from which ampullariids are absent for reasons of historical biogeography (Berthold, 1991; and above). The effects of snails on both macrophytes and epiphytes may be extremely complex (Brönmark, 1989).

Medical Concerns

Various ampullariid species, including *Pomacea canaliculata*, can act as vectors of *Angiostrongylus cantonensis*, the rat lungworm, which can infect humans if ingested and cause the potentially fatal eosinophilic meningoencephalitis (Wallace and Rosen, 1969; Keawjam, 1986; Chao *et al.*, 1987; Mochida, 1991; Halwart, 1994b; Albrecht *et al.*, 1996; Naylor, 1996). However, many other snail species can act as vectors and there is no obvious relationship between presence of apple snails and incidence of the disease (Smith, 1992). Nevertheless, an overall increase in consumption of snails could lead to an increased incidence of the disease. Thorough cooking is essential.

Ampullariids also carry schistosomes that cause dermatitis in humans (Hanning and Leedom, 1978; Leedom and Short, 1981); and they harbour an intestinal fluke, *Echinostoma ilocanum* (Garrison), that causes inflammation, ulceration, diarrhoea and anaemia in humans (Keawjam, 1986).

Thus, in addition to the agricultural and environmental impacts caused (or potentially caused) by introduced ampullariids, human health concerns associated in particular with eating them are very important and are just one of the many reasons for not introducing them.

Control Measures

In general it is extremely difficult to eradicate established populations of alien species (e.g., the land snail *Theba pisana* (Müller) in California; Gammon, 1943), and it is probably not going to be possible to eradicate apple snails from areas where they have become widely established. Use of molluscicides over large areas is expensive and often inappropriate from human safety and environmental perspectives, yet in many areas the first reaction to infestation has been to apply vast amounts of pesticides (not necessarily only molluscicides). Biological control using predators can usually only reduce pest numbers to acceptable levels, not eradicate the pest. Furthermore, biological control is increasingly seen as environmentally dangerous, in contrast to its original perception as an environmentally acceptable alternative to the use of chemical pesticides (Howarth, 1991; Civeyrel and Simberloff, 1996; Simberloff and Stiling, 1996a, b; Williamson, 1996). Cultural management practices may be able to limit damage, but cannot completely destroy entire populations of snails. Nevertheless, if new introductions are addressed before they have a chance to become widely distributed, eradication indeed may be possible and is certainly worth attempting. Eradication of a new infestation (of *Pila conica*, and perhaps some *Pomacea* sp., as pink egg masses were reported) was accomplished in Palau, where all snails were manually collected from the infested pond, which was then covered with a layer of oil (Eldredge, 1994; B.D. Smith, Guam, 1997, personal communication); and quick action to eradicate new apple snail infestations has been proposed in Papua New Guinea (Laup, 1991). It is increasingly clear that it is economically far more cost-effective to deal with potential pest species in the early phase of invasion, prior to their becoming serious pests, than to wait until they are widely established and causing significant damage (e.g., Baskin, 1996; Naylor, 1996).

However, given that, in general, the snails cannot be eradicated, methods must be developed to reduce their populations and to reduce the damage they cause. Undoubtedly a combination of methods will prove most effective (Olivares *et al.*, 1992; Litsinger and Estano, 1993), but as yet, no combination of treatments has proved entirely adequate. Rigorous quantitative assessments of this kind of integrated pest management approach are few (Litsinger and Estano, 1993). And

although many of the following measures are said to reduce snail numbers, at least to some extent, their impacts on yield losses are essentially unknown. Most of the control measures and management practices that have been tried or suggested, and that are summarized below, have been outlined in Anon. (1989) and by Eversole (1992), Olivares *et al.* (1992), Glover and Campbell (1994), Halwart (1994a), Schnorbach (1995) and Wada (1997). A bibliography specifically related to the control of ampullariid pests has been published by Acosta and Pullin (1991). New ideas that have been subject to only preliminary investigation include development of resistant varieties of rice, and development and manipulation of natural inhibitors produced by the snails themselves (Eversole, 1992).

Computer simulations of snail population dynamics and damage to rice under various management options, suggest that a number of the approaches reviewed below (transplanting older seedlings, shortening the period of irrigation, pasturing ducks, practicing rice-fish culture) have a positive effect (Heidenreich and Halwart, 1995; Heidenreich *et al.*, 1997). Their efficacy in the field requires further, rigorous testing.

Chemical control

Halwart (1994a) reviewed the main synthetic chemicals that have been used against apple snails, many of them over large areas and in vast amounts. These include copper sulphate, calcium cyanamide, sodium pentachlorophenolate, niclosamide, various organo-tin compounds, endosulphan, metaldehyde, cartap hydrochloride and isazophos. Tin-based compounds were widely used in the Philippines, but they had serious ecological consequences (bibliography in Acosta and Pullin, 1991) and have been banned there since 1989 (Halwart, 1994a). Copper sulphate was used in the 1950s in Surinam but has since been generally superseded by other pesticides, although it was used against apple snails in Hawaii in 1994. Copper sulphate is highly toxic to most invertebrates and broad scale application against apple snails has potentially serious environmental consequences (Cowie, 1994). Endosulphan is highly toxic to fish, and, along with other chemicals with high toxicity to fish, has been banned from use in rice paddies in Japan (Halwart, 1994a; Wada, 1997); endosulphan has recently been banned in the Philippines, although it is still used (Litsinger and Estano, 1993; Naylor, 1996). Sodium pentachlorophenolate has high phytotoxicity. If pesticides are being considered, a single application may not be adequate. Snails in the water will be killed, but eggs laid above water (as in most species of *Pomacea*) will not be affected and will go on to hatch after the pesticide has dissipated. A second application, perhaps a month after the first, is necessary to kill the newly hatched snails before they grow to reproductive maturity.

Many experimental studies, both in the laboratory and the field, have been undertaken to evaluate the above and other pesticides against ampullariids (e.g., van Dinther, 1956; van Dinther and Stubbs, 1963; Singh and Agarwal, 1981; Madhu *et al.*, 1982; Rao *et al.*, 1983; Cheng, 1989; Mochida, 1991; Palis *et al.*, 1996; Schnorbach, 1995). Adequate information on their environmental impacts in the context of rice paddy systems is largely unavailable, although increasingly the complexity of these systems and the need to reduce pesticide use in them are being recognized (Settle *et al.*, 1996), as are the potential problems associated with the impacts of pesticides on non-target organisms (Jepson, 1989).

As well as the environmental consequences of extensive use of pesticides, there are serious human health problems. These are incurred partly because few farmers have adequate protective clothing and many of the application sprayers are leaky (Pullin in Acosta and Pullin, 1991). In the Philippines, there have been reports of fingernails and toenails peeling off, severe headaches, nausea, shortness of breath, skin burns, blurred vision and total blindness (Anderson, 1993); and even human fatalities have been attributed to use of (now banned) molluscicides (Anderson, 1993; Halwart, 1994b). Also, when large numbers of snails are killed in situ, their sharp-edged empty shells cut the bare feet of farmers (Cheng, 1989; Anderson, 1993; Wada, 1997), leaving them open to infection.

With increasing awareness of the environmental and human health problems associated with the use of synthetic pesticides, there has been an increasing trend to search for 'natural' pesticides. A number of plant products have been evaluated (e.g., Cheng, 1989; Maini and Morallo-Rejesus, 1992, 1993; Arthur *et al.*, 1996), but none has been developed for wide use. The possibility of using a sub-lethal dose that reduces snail feeding activity has been suggested, as has the use of as yet unidentified 'pheromones' that might modify other aspects of snail behaviour (Arthur *et al.*, 1996; Taylor *et al.*, 1996). 'Natural' pesticides are often promoted as being environmentally benign. However, in many cases they may have equally serious environmental and human health effects as synthetic chemicals, especially if deployed persistently over wide areas and in high concentrations (Taylor *et al.*, 1996).

Biological control

Predators. None of the predators of apple snails in their native ranges have been shown to play a significant role in snail population regulation (above). In South-East Asia, various fish, birds, rats, lizards, frogs, toads, beetles and ants are known to feed on introduced apple snails or their eggs (Halwart, 1994a). Some of these, especially rats, also cause serious damage to rice, and introduction or promotion of others as biocontrol agents may have unknown environmental consequences. Only ducks and fish have attracted any serious consideration as potential control agents (Anon., 1989; Halwart, 1994a, b); whether any of these other predators could play a role in regulation of introduced apple snail populations is unknown.

In rice, domestic ducks can be released into the paddies prior to planting of seedlings, again once the seedlings have established (35-40 days after transplanting, otherwise the ducks may damage the seedlings), and finally, after harvest (Anon.,

1989). Significant reduction of both snail numbers and damaged rice hills can be achieved (Halwart, 1994a), although the ducks prefer, or are only able, to eat juvenile snails (Anderson, 1993). In taro in Hawaii, Cayuga ducks have been used, but again, care must be taken that they do not damage the plants, especially new plantings (Kobayashi *et al.*, 1993; Glover and Campbell, 1994). No data on reduction of snail numbers or damage to taro are available, although this approach is said to be moderately successful (H. Ako, Honolulu, 1997, personal communication).

Mochida (1988a, b, 1991) reported the release of large numbers of black and common carp in paddies in Taiwan, but gave no data on their effectiveness at controlling snails or reducing damage to the rice. Halwart (1994a, b) suggested that common carp and Nile tilapia were useful in controlling juvenile snails, and computer modelling of rice-fish culture showed an impact on snail numbers (Heidenreich and Halwart, 1995; Heidenreich *et al.*, 1997). Carp are being promoted in Vietnam for biological control of the snails (Pedini and Shehadeh, 1996). Whether reducing snail numbers will translate into increased crop yield is unknown. Use of fish may be problematic, as they will not survive periods when the paddy dries out. They therefore must be introduced at the start of each rice growing season (Halwart, 1994b). In general, the ecological consequences of introducing non-indigenous fish are unknown (Halwart, 1994b). All deliberate introductions of non-indigenous species should be carefully evaluated prior to introduction in terms of both their positive and negative potential impacts and monitored after introduction; often neither happens (Howarth, 1991).

Parasites, parasitoids and pathogens. Little is known of microorganisms associated with ampullariids (above), nor of parasitoids that attack either the snails or their eggs. Olivares *et al.* (1992) reported preliminary testing in the Philippines of 12 bacterial isolates, with seven of them effective against the snails; but gave no further details.

Competitors. As discussed above, various efforts have been made to reduce or eradicate populations of medically important species of snails by introducing other snails that displace the unwanted species. The ampullariid *Marisa cornuarietis* has been used for this purpose in the Caribbean, where it may also act as a predator of other snails. However, *M. cornuarietis* is a voracious feeder on rice (above); it is unlikely that it would out-compete *Pomacea canaliculata*, or prey on it sufficiently to reduce its numbers. In any case, deliberately introducing yet another ampullariid into South-East Asia seems unconscionable. Other snail species (*Melanoides tuberculata* (Müller)) have also been used as biological control competitors in the Caribbean (Pointier and Guyard, 1992). However, *M. tuberculata* already occurs in South-East Asia (and alongside ampullariids in Hawaii) and it is highly unlikely that it could displace the pest ampullariids.

Cultural and mechanical control

Hand-picking of snails and eggs. Collecting by hand and destroying both the snails and their eggs, although labour-intensive, is the most effective non-chemical way to reduce snail numbers. In taro on the island of Molokai (Hawaii) it is effective against introduced *Pila conica*, as of 1991 the only ampullariid on that island (Cowie, 1995b). Almost all large snails can be collected easily, and the juveniles that are missed do not grow and reproduce sufficiently quickly to become a serious problem until around harvest time. However, *Pomacea canaliculata* grows and reproduces much more quickly and hand-picking requires significantly greater and repeated effort to effect a similar level of control. Destruction of eggs can be facilitated by placing stakes in the paddy on which the snails oviposit. Stakes with eggs are then readily removed. Use of hand-picked snails as food in other aquaculture projects has been suggested (e.g., Bombeo-Tuburan *et al.*, 1995).

Ditches. If slightly deeper strips or ditches within the body of the paddy or alongside the bunds are constructed, when the paddy is drained (slowly), water remains in these strips and snails congregate there. This then facilitates hand-picking of snails, and allows more effective and localized treatment with pesticides, should this be considered appropriate. Levelling of the field, except for these ditches, is necessary to reduce alternative snail refugia.

Grills. Wire mesh grills can be constructed at the inlets to the rice paddies, taro patches, etc. These prevent at least the larger snails from moving between paddies via this route, and snails that collect in the grills can be easily collected and destroyed.

Maintenance of clean paddies. The edges, dikes or bunds that surround the rice paddies, taro patches, etc. should be neatly maintained. This reduces egg-laying sites and allows snails to be more easily seen and destroyed. It may also decrease the chances of snails moving between paddies.

Planting and seedlings. Numerous reports indicate that, in rice, susceptibility to damage declines with seedling age, and planting out seedlings that are at least 4-6 weeks old has been recommended (Anon., 1989; Mochida, 1991; Eversole, 1992; Litsinger and Estano, 1993; Halwart, 1994a; Schnorbach, 1995; Naylor, 1996; G. Jahn, Phnom Penh, 1997, personal communication). Planting method was considered particularly important by Litsinger and Estano (1993). However, most of the new varieties of rice being developed for Asia are likely to be direct seeded rather than transplanted (Naylor, 1996; Wada, 1997). Increasing the seeding rate or the number of seedlings transplanted, or replacing damaged hills, have been recommended to offset yield loss, at least at low snail infestation levels (Anon., 1989; Halwart, 1994a). However, costs of replanting may be high. A single study (Okuma *et al.*, 1994) reported that damage, even to young seedlings, did not result in

severe yield reduction, because of compensatory growth of remaining plants.

Baits. Glover and Campbell (1994) suggested the use of baits (sacks or nets filled with lettuce, cassava leaves, sweet potato leaves, taro leaves) to divert the snails from eating taro and facilitate hand-picking of snails congregating at the baits. Eversole (1992) suggested the use of papaya leaves and promotion of the growth of *Azolla*. There seems to be some success with this in Hawaii (H. Ako, Honolulu, 1997, personal communication). However, baits have to be significantly more attractive to the snails than is the crop, and it is possible that providing additional food as baits would enhance snail numbers.

Other cultural and mechanical methods. Lowering the water level or draining the paddy will not kill the snails because of their ability to survive long periods without water (above). However, snail activity seems to be reduced if the water is shallower than their shell height (Wada, 1997). Also, periodic lowering of the water level may make the snails congregate in remaining areas of water, facilitating hand-picking (above).

Raising the temperature of the water by covering the paddy/patch with black plastic sheeting on sunny days has been suggested in Hawaii but is obviously impractical on a large scale, can only be done during fallow periods, and would have to increase the water temperature probably to well over 45°C for an extended period in order to kill the snails (see temperature tolerance, above), which in any case might be able to avoid the high temperatures by burying into the mud. Normal water temperatures in rice paddies probably rarely exceed 36°C (Halwart, 1994b). However, manipulating water temperature below lethal limits might impact snail activity, growth and reproduction, and deserves further research.

Flooding coastal taro patches in Hawaii with salt water has been suggested, but the practicalities of doing this and the potential long-term damage to the fertility of the soil preclude this option. Also, the snails are tolerant of short periods immersed in sea water (above).

In Japan, use of a rototiller for land preparation, as opposed to minimum or no till, resulted in greater snail mortality (Mochida, 1988a) because of crushing and because buried snails were then thought to be exposed to cold lethal temperatures (Litsinger and Estano, 1993; Wada, 1997). Growing wheat as an off-season crop was also said to reduce snail numbers (Wada, 1997). Burning rice straw after harvest to kill snails near the surface of the mud has been recommended; and the ash reportedly repels the snails (Mochida, 1988a; Eversole, 1992).

In Hawaii, a device like an enormous vacuum cleaner has been constructed that sucks up the larger snails. Snails are well known not to cross strips of bare copper; placing copper barriers around taro patches has been suggested as a means of keeping snails out of uninfested patches (Glover and Campbell, 1994), but is obviously impractical on a large scale.

Prevention

As with all agricultural and environmental problems caused by introduced species, prevention of the spread of apple snails is the best way to avoid damage and the future costs of implementing management programs (Laup, 1991; Cowie, 1995a; Naylor, 1996; Vitousek *et al.*, 1996). Effective quarantine at ports of entry is crucial, but also important are regulations restricting the raising, sale and purchase of the snails, and movement of snails from infested to uninfested areas. Implementing quarantine programmes is highly cost-effective relative to the cost of damage once the snails have invaded. In Hawaii, planting material is often moved from area to area, and care must be taken not to transfer snails; small juveniles would be easily missed on inspection. Import of all *Pomacea* and *Pila* species to Hawaii is restricted, as is their transport between islands within the archipelago. More stringent legislation may be necessary, prohibiting transport of snails within islands and into natural waterways. Continuing attempts to develop an aquaculture industry (Tamaru, 1996; Tamaru and Hun, 1996), initially using snails hand-picked from the taro fields, seem counterproductive as they will likely encourage the further deliberate spread of the snails around the islands (Pleadwell, 1997). Public education is crucial to the success of attempts to prevent the spread of apple snails.

Threats

The lesson of destruction in many parts of South-East Asia seems not to have been learned. In 1995 snails were imported to Cambodia, which was until then free of them. As of November of that year, they were being maintained in backyard ponds and tanks and had not been reported in the wild (Cowie, 1995a). However, some of these ponds were adjacent to rice paddies and it seemed only a matter of time before the snails got into the paddies. Villagers were loathe to destroy the snails because they foresaw potential financial gain through selling them for food, and often did not accept the possibility that the snails could escape, nor that they would become serious pests in the rice paddies. A year later, the snails had indeed got into the paddies (G. Jahn, Phnom Penh, 1997, personal communication). Baker (1998) has demonstrated by climatic modelling that large parts of Asia (e.g. central China, India, Bangladesh and Burma) that are heavily dependent on rice as a staple food but that are currently free of introduced apple snails are under serious threat. Education and publicity are crucial if parts of Asia that are currently free of introduced apple snails are to remain so.

The potential problems are not confined to Asia. Australian officials are becoming increasingly aware of the potential for damage to rice, and to natural wetland habitats, should ampullariids become established (Baker, 1988). Berthold's (1991) biogeographic analysis of the Ampullariidae as a Gondwanan group originating in Africa suggested that

they are not found in Australia simply because the Australian plate split off from Gondwana before they spread to it. His ecological analysis showed, nevertheless, that northern Australia is climatically suitable for ampullariids. Baker's (1998) more detailed climatic analysis has shown that not only northern but also other parts of Australia are at risk, as well as parts north America, Africa, Europe, New Zealand and several Pacific islands.

In the Pacific, apple snails are established in Hawaii and have become a serious taro pest (Cowie, 1995b), although there have been no formal yield loss analyses. Taro is the traditional staple throughout much of the Pacific. Elsewhere in the Pacific, apple snails have been reported from Guam (Smith, 1992; Eldredge, 1994) and Papua New Guinea (Laup, 1991; Eldredge, 1994;), and from Palau where they were reported to have been eradicated (Eldredge, 1994). Most other Pacific islands are highly vulnerable. Publicity, combined with strict quarantine, is essential if they are to remain free of apple snails.

Awareness of the threat of apple snails throughout these as yet uninfested regions must be heightened, first so that quarantine measures have a better chance of preventing introduction, and second so that if the snails invade successfully, there is a chance that they can be eradicated in the early stages of establishment before their populations expand (Naylor, 1996). This lag phase, exhibited in many instances of introductions of non-native species (Crooks and Soulé, 1996), seems virtually non-existent in the case of *Pomacea* introduced to South-East Asia and other areas; authorities must therefore act quickly and decisively if they detect an introduction.

Future Directions

Apple snail management has thus far proven extremely intractable. Pest management can only be successful against a background of clear understanding of the identity and biology of the pest species. At present, it is not entirely certain what the pest species is/are, and there is little understanding of the pest species' ecology and behaviour. Achieving this basic taxonomic, ecological and behavioural understanding will permit control measures to be more reliably developed and quarantine efforts to be more effective. Similar recommendations have been made by Eversole (1992) and Halwart (1994a).

Taxonomy

Throughout this review, species names have been used as if they were definitive. However, the taxonomy of ampullariids is notoriously confused and correct identification is often extremely difficult (e.g., Alderson, 1925; Pain, 1964; Keawjam, 1986; Cazzaniga, 1987). This is certainly the case regarding the pest species (possibly more than one) in South-East Asia (e.g., Schnorbach, 1995; Wada, 1997), which has been treated variously as *Pomacea canaliculata* (Smith, 1992; Hendarsih *et al.*, 1994), *P. lineata* (Cheng, 1989; Laup, 1991), *P. gigas* (Spix) (see Guerrero, 1991), *P. 'insularis'* (see Acosta and Pullin, 1991), *Pomacea* cf. *canaliculata* (Ng *et al.*, 1993), simply *Pomacea* sp. (Acosta and Pullin, 1991), a 'hybrid [of] *Ampullaria canaliculata* and *Ampullaria cuprina*' (Anderson, 1993), and even '*Ampularius* sp. a hybrid of undetermined origin' (Lacanilao, 1990). Keawjam and Upatham (1990) recognized three species of *Pomacea* introduced in Thailand: *P. canaliculata*, *P. insularum* and an unidentified species of *Pomacea*. Mochida (1991) indicated that as well as *P. canaliculata* (which he considered frequently to have been mis-identified as *P. insularum*) two other species of *Pomacea* have also been introduced to the Philippines: *P. gigas* and *P. cuprina* (the latter possibly a misidentification of *P. bridgesii*, a species that has been carried all over the world by the domestic aquarium trade; Cowie, 1995b). In Japan, three 'strains of *Pomacea canaliculata*' have been identified, differing in shell colour and pattern, salinity tolerance, and in aspects of reproduction and growth (von Brand *et al.*, 1990; Fujio *et al.*, 1991a). In the Philippines the snails have even been identified as species of *Pila* (see Guerrero, 1991). In Hawaii, where four ampullariid species are recorded (Cowie, 1995b), snails in an aquaculture project have been reported as hybrids of *Pomacea canaliculata* and *P. paludosa* (Nishimura *et al.* in Tamaru, 1996).

Ampullariid species-level taxonomy has been heavily reliant on shell morphology, yet snail shells, and especially ampullariid shells, exhibit much intra-specific variation. The taxonomy and systematics of most species have not been adequately worked since their original descriptions. The pest species (even if it turns out to be more than one species) in South-East Asia nevertheless appears to belong to a relatively well circumscribed group of more or less closely related species from South America. However, within this group, the species and their relationships are very poorly understood. The group comprises about 15 nominal species, including *P. canaliculata*. I refer to this group as the '*canaliculata* group'. From time to time, some of the species within the '*canaliculata* group' have been formally synonymized, informally linked together, distinguished as separate species, and so on. This confusion was discussed but not resolved by Alderson (1925), the most recent author to revise *Pomacea* and *Pila* widely (referring to the two genera together as '*Ampullaria*'). He implicitly recognized most of the species in the '*canaliculata* group' as a more or less closely knit group. Within this group he further recognized a number of rather vaguely defined associations of species, for instance explicitly linking *Pomacea immersa* (Reeve), *P. amazonica* (Reeve) and *P. haustrum*, although without formally synonymizing them; and informally referring to another sub-set of the group as '*the lineata group*'. However, he did retain most species as valid. It is quite possible that, just as for the large number of Central American species synonymized under *Pomacea flagellata* by Pain (1964), many other 'species' of Ampullariidae, including those in the '*canaliculata* group', do not deserve distinct specific status (Pain, 1960; Cazzaniga, 1987). A modern revision, involving not only conchology but also internal anatomy and molecular characters, might reduce the '*canaliculata* group' to as few as three species, possibly *P. canaliculata*, *P. lineata* and *P. gigas*. Until such work is undertaken, however, the status of these various nominal species will remain obscure.

The predominant pest may indeed be *Pomacea canaliculata*. However, *P. canaliculata* is a widespread and morphologically highly variable species in South America (Cazzaniga, 1987). How distinct it really is from the various nominal South American species also reported from South-East Asia is not at all clear. In particular the distinction between *P. canaliculata* and *P. insularum* is especially unclear, despite attempts to clarify it (Scott, 1957; Keawjam and Upatham, 1990). In many populations, maximum shell size of *P. canaliculata* is around 3 cm (e.g., in Hawaii), but in other populations, females can reach 7-8 cm (Wada, 1997) and some individuals may even reach sizes over 9 cm (Estebenet and Cazzaniga, 1992). Even in populations in adjacent ponds and with one population derived from the other, there can be enormous differences of this kind (e.g., in Cambodia; personal observations). Sexual dimorphism in size (fig. 1), combined with this overall morphological variability and the existence of considerable variation in shell colour and banding pattern, no doubt confound attempts at accurate identification.

These problems of identification cast doubt on the correctness of the names applied both in the pest-related literature and in much of the ecological, physiological, behavioural and other literature on species in this group. Comparability among studies is unreliable. The problems are compounded when no precise natural provenance information is available, as is the case with studies dealing with introduced populations in South-East Asia and elsewhere.

Because the taxonomy of the 'canaliculata group' of species is so confused, it is difficult to assess natural species distributions. For instance, *Pomacea canaliculata* itself has been considered to be extremely widely distributed, from the Plata River system in Argentina to Guyana and from the easternmost tip of Brasil to Bolivia (Scott, 1957), although its presence in northern South America depended on synonymizing it with *dolioides*. Study of museum material (personal observations) suggests that it does not extend north of Brasil, and that perhaps *dolioides* (possibly a synonym of *lineata*) replaces it in Surinam, Guyana and Venezuela.

It is therefore clear that any sound attempt to develop integrated pest management of these snails requires a modern assessment of their basic taxonomy. Such resolution of their basic taxonomy would resolve the extensive confusion that currently exists, allowing control measures, quarantine regulations, etc. to be developed on a much sounder basis than is currently possible.

Ecology, behaviour, physiology

A taxonomic re-evaluation of the 'canaliculata group' would lay the foundation for study of the ecology and behaviour of the species then identified as the major, if not only, pest species in South-East Asia. Necessary ecological information as a background to implementing integrated pest management strategies would include data on life-history (life span, age at maturity, growth, fecundity, etc.), population dynamics, predators, parasites and habitat characteristics (water temperature, flow rate, etc.). Behavioural and physiological data on aestivation, thermal and desiccation relations, seasonality of growth and reproduction, dispersal, etc. would also be important. This information needs to be obtained in the native range of the pest species (South America) as well as in the localities in South-East Asia where the species has become a serious pest. In this way, changes in the snails' ecology and behaviour, for instance niche expansion following relaxation of competition, that have arisen as a result of the different ecosystems in which they now function can be understood. Ultimately such studies would focus on aspects of ecology and behaviour that can be manipulated as possible routes to eventual control. If biological control is being considered, selection of biocontrol agents must be done with an understanding of their potential to operate and remain host-specific in a novel ecological context.

Yield loss assessments

There remains far too little information on economic losses and how these can be offset by the various control measures (in different combinations). Frequently, achieving a reduction, even a large reduction, in snail numbers is assumed to lead to increased crop yield; but the relationship is unlikely to be simple. Furthermore, levels of damage are often assumed to reflect directly levels of yield loss, but compensatory effects may be important (Okuma *et al.*, 1994) and accurate yield loss assessment may be highly complex (cf. Wood and Cowie, 1988). Such analyses are almost entirely lacking for all but a few regions where apple snails have become pests. Yet detailed economic and yield loss analyses are a necessary basis for developing recommendations of the range of management options and combinations of options that are currently available and that will be developed in the future. Economic yield loss assessments also provide ammunition to convince political authorities of the seriousness of the problem and the need for funding to address it.

Control

Even with the diversity of control and management approaches that have been developed or tried, no fully adequate strategy has surfaced that can be widely recommended. Despite huge effort on the part of farmers, losses continue to be severe, especially where infestations are heavy. Control is still dominated by the use of pesticides (Halwart, 1994a), with their often extremely harmful environmental and human health effects. Biological control using predators, parasites and pathogens that occur in the native range of the snails has barely been addressed. The search for possible predators/pathogens in South America has been minimal: preliminary surveys have not identified species-specific agents that could be easily manipulated and that have the potential to impact pest populations significantly. The idea of promoting practices that might

enhance populations of native competitors and/or predators (Settle *et al.*, 1996) has not been investigated and no such competitors/predators have been identified. Research, based in a sound understanding of the pest species' biology, must then be directed towards reduction in the use of pesticides, identifying new approaches to cultural control, and combining both new and existing strategies into fully integrated pest management protocols that can be tailored to the needs of particular situations.

Prevention

It is crucial that further spread of ampullariids be minimized. Quarantine regulations need to be put in place (if they are not in place already) and applied strictly. Such measures are far more cost-effective than attempting to address the problems once the snails have invaded and become pests. But probably most important is the raising of awareness of the threat of alien species. Publicity must be directed at the general public, the aquarists, those seeking quick profit from marketing the snails for food, etc. In particular, in South-East Asia, the full import of the spread of apple snails to rice-growing areas so far uninfested must be clearly communicated to farmers in a serious and comprehensive education campaign that has the backing of politicians and agricultural managers. It is only with public co-operation and a real public understanding of the potential problems that apple snails can cause that disasters on the scale that has befallen the Philippines can be avoided.

Conclusions

Frequently there is a conflict between potential environmental harm and economic benefit when species are considered for introduction (Baskin, 1996; McNeely, 1996; Williamson, 1996). In the case of apple snails, the potential for short-term economic gain (which has not materialized) has been foremost in people's minds, while they have been blind (and in some cases continue to be so) to the potential (and realized) long-term environmental and agricultural destruction.

There is a rapidly increasing literature on invasive species: factors causing their success or failure, the dynamics of establishment, the ecological and agricultural problems they cause, and what can be done about them (e.g., Niemelä and Mattson, 1996; Williamson, 1996; Williamson and Fitter, 1996). In many cases, new invaders exhibit a lag phase before their populations expand rapidly (Crooks and Soulé, 1996), when they become pests. In the case of *Pomacea* introduced to South-East Asia and other areas, the lag phase seems virtually non-existent, giving authorities minimal time to make a decision to act.

For regions as yet not infested, prevention of the introduction of apple snails must then be the primary strategy. Awareness must therefore be raised so that officials know the potential problems that will overcome them should the snails be introduced, rather than only becoming aware of the problems when it is too late. Officials must also be prepared to act quickly if an introduction is detected. Eradication at this early stage might still be possible, but there will be only a very narrow window of opportunity.

For areas already infested and with little hope of eradicating the snails, integrated management strategies involving both existing control measures and measures developed in the future, must be implemented. These strategies will differ from region to region, depending on the levels of infestation, potential environmental consequences, the specific needs of the local farmers and the options open to them, and local economics. Development of widely implemented and successful strategies has to be based on a thorough understanding of relevant aspect of the snails' biology.

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Table 1. Reproduction and growth in ampullariids. Asterisks indicate laboratory studies. Some data have been reported without indicating whether they were obtained from laboratory cultures or from the wild. Some of the references listed undoubtedly simply reiterate data from others that are also listed. Some, at least, of the variability exhibited (especially by *Pomacea canaliculata*) may be due to taxonomic confusion (see text).

Species Longevity	Locality References	Clutch size	Hatchability	Time to hatching	Time from hatch- ing to maturity
<i>Pomacea canaliculata</i> 478 days	Argentina	120-			Cazzaniga and Estebenet, 1988
	Argentina			28	
	Argentina*			12-15	
	Argentina*		Thiengo <i>et al.</i> , 1993		7 months - 2 years 13 months - 4
years	Estebenet and Cazzaniga, 1992	mean 101			
43%	Argentina			Albrecht <i>et al.</i> , 1996	
days	Argentina*				100-150
	Estebenet and Cazzaniga, 1998				
years	Philippines	25-320		10-15 days	60 days 2-3
	Adalla and Morallo-Rejesus, 1989				
years	Philippines	25-500		7-14 days	59-84 days 119 days - >3
	Anon., 1989; Olivares <i>et al.</i> , 1992				
years	Philippines	25-500		10-15 days	60-85 days 2-3
	Halwart, 1994a				
days	Philippines*	50-400	20.9-35.0%	9-12	
			Lacanihao, 1990 (as " <i>Ampularius</i> sp.")	10-15 days	< 1
year	Philippines	50-500			
	Guerrero, 1991				
days	Philippines	25-500	80%	8-15	
			Rondon and Callo, 1991		
80%	Philippines				Bombeo-Tuburan <i>et al.</i> , 1995
years	Philippines	25-320	90-100%	8-21 days	3
	Schnorbach, 1995				
days	Taiwan*	200-300	60%	average 12.4 days	55
		Chang, 1985			
months	Japan*	average 200-700	41.9%	12 days	6
		Fujio and von Brand, 1990; Fujio <i>et al.</i> 1991a, b			
years	Japan	30-700	7-90%		2 months >2
	Wada, 1997				
1,000	Thailand	800-			
					Keawjam and Upatham, 1990
years	Asia	321 (average)	7-90%	9-37 days	2-3 months 2-5
	Halwart, 1994a Mochida, 1988a, b, 1991				
days	Asia	320	7-90%		60-90
	Naylor, 1996				
years	Asia	25-500	7-90%	8-15 days	60-90 days 4
	Heidenreich and Halwart, 1995; Heidenreich <i>et al.</i> , 1997				
years	Hawaii	200-500		7-14 days	3-4 months 2-5
	Glover and Campbell, 1994				
years	Hawaii	c. 200		3 weeks	3-4 months 3-4
	Kobayashi <i>et al.</i> , 1993				
weeks	Hawaii	350		2-3	
			Tamaru and Hun, 1996		
months	England*	100+			< 12
	Andrews, 1964				
<i>Pomacea dolioides</i> months?	Surinam	200-300 (max. 437)		13-16 days	8-12 months c. 18
	van Dinther, 1956, 1962 (as " <i>P. lineata</i> ")				
<i>Pomacea gigas</i> weeks	?			2-6	
			Köhler cited by Demian and Yousif, 1973		
<i>Pomacea glauca</i> months?	Surinam	30-90		14-17 days	8-12 months c. 18
	van Dinther, 1956, 1962				

years	Guadeloupe			13.5 months	c. 3
<i>Pomacea haustum</i>	Pointier <i>et al.</i> , 1988				
days	Brasil*		15-23 days	374-529	
days	Brasil	Guimarães, 1981a			
days	Brasil	236	9-30		
year	Brasil	Guimarães, 1981b		< 1	
<i>Pomacea lineata</i>	Brasil*	Estebenet and Cazzaniga, 1992			
days		average 100	15		
<i>Pomacea paludosa</i>	Florida, USA	Thiengo, 1987	18-28		
days		mean 26.7 (max. 141)			
days	Florida, USA	Hanning, 1978	15-20		
days		3-50, 80			
<i>Pomacea urceus</i>	Trinidad	Perry, 1974	22-30		
days*		21-93	0-84%*		
years	Venezuela	Lum-Kong and Kenny, 1989; Lum-Kong, 1989		6-7 months	2.5-3.5
<i>Marisa cornuarietis</i>	Burky, 1973, 1974		8-20		
days	Egypt*		Demian and Yousif, 1973		
days	Florida	max. 210	11-24		
<i>Pila globosa</i>	India	200-300	c. 1		
month			Andrews, 1964; Prashad, 1925a		
weeks	India		10 days - 3		
<i>Pila polita</i>	?		Ranjah cited by Demian and Yousif, 1973		
days			<14		
<i>Pila</i> spp.	Thailand		Semper cited by Demian and Yousif, 1973		at least 3
years	Keawjam, 1987				
<i>Lanistes nyassanus</i>	Lake Malawi				5-10
years	Louda and McKaye, 1982				

Table 2. Crops other than rice that are attacked by ampullariids. This is not a comprehensive list, but simply a brief compilation from some of the more accessible literature, illustrating the susceptibility of a wide range of plants.

Plant	Region	Reference
Water hyacinth (<i>Eihhornia crassipes</i> (Martius) Solms)	Hong Kong	Laup, 1991
Water spinach/swamp cabbage (<i>Ipomea aquatica</i> Forsskaol)	Hong Kong	Laup, 1991
1991	Japan	Mochida,
Tamaru, 1996	Hawaii	Nishimura <i>et al.</i> in
Lotus (<i>Nelumbo nucifera</i> Gaertner)	Hong Kong	Laup, 1991
Water cress (<i>Rorippa</i> spp., formerly <i>Nasturtium</i> spp.) Hong Kong	Japan	Mochida, 1991; Wada, 1997
Tamaru, 1996	Laup, 1991	
Taro (<i>Colocasia esculenta</i> (Linnaeus) Schott)	Hawaii	Nishimura <i>et al.</i> in
1997	Japan	Mochida, 1988b, 1991; Wada,
	Hawaii	Cowie, 1995b; Nishimura <i>et</i>
		<i>al.</i> in Tamaru, 1996
Mat rush (<i>Juncus decipiens</i> (Buchenau) Nakai)	Japan	Mochida, 1988b, 1991; Wada,
1997		
Chinese mat rush (<i>Cyperus monophyllus</i> Vahl)	Japan	Mochida, 1991
Wild rice (<i>Zizania latifolia</i> (Grisebach) Stapf)	Japan	Mochida, 1991
Japanese parsley/dropwort (<i>Oenanthe javanica</i> (Blume) de Candolle)	Japan	Mochida, 1991; Wada, 1997
Water chestnut (<i>Trapa bicornis</i> Osbeck)	Japan	Mochida, 1991; Wada, 1997
Azolla (<i>Azolla</i> spp.)	Philippines	Adalla and Morallo-Rejesus,
1989		
	Japan	Mochida, 1991

FIGURE LEGEND

Figure 1. A mating pair of *Pomacea canaliculata*, collected by the author from a domestic rearing facility in Phnom Penh, Cambodia in November 1995; female on the left, shell height 84 mm.