

Can snails ever be effective and safe biocontrol agents?[†]

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Abstract. The use of snails as biocontrol agents against other snails and against aquatic weeds is reviewed, evaluating their success and their impacts on non-target organisms. The predatory snail Euglandina rosea (and other species), although widely used against Achatina fulica (the giant African land snail) on Pacific and Indian Ocean islands, has not been shown to control A. fulica but has seriously impacted endemic island species. The facultative predator Rumina decollata, used in California against Helix aspersa (brown garden snail), is widely considered to be environmentally benign. However, evidence of its effectiveness is weak and it will also consume native snails. Ampullariid and thiarid freshwater snails have been used as competitors (and incidental predators) of snail vectors of human schistosomes, the parasites causing schistosomiasis (bilharzia). Successful control has been reported but impacts on native biotas have been essentially ignored. Ampullariids have been used in attempts to control aquatic weeds, sometimes successfully, but again with little consideration of impacts on native biota. Most snails have generalist feeding habits. Thus they are inappropriate biocontrol agents because of their potential nontarget effects. Rarely has adequate pre-release testing of snails been undertaken and post-release monitoring of non-target impacts has always been incidental. The use of non-native snails for biocontrol purposes is poorly regulated; many introductions are unofficial and sometimes illegal. Use of snails as biocontrol agents, if implemented, must be based on adequate pre-release testing, post-release monitoring and genuine concern for preservation of native biodiversity.

1. Introduction

Biological control (or biocontrol), once hailed by many as an environmentally friendly panacea for solving pest problems, has more recently attracted criticism because of the potential for biocontrol agents to permanently harm or even cause the extinction of native non-target species (Howarth, 1983, 1991; Miller and Aplet, 1993; Cowie and Howarth, 1998). Proponents of biological control argue that these negative impacts have been exaggerated and that, given the important agricultural and economic need for environmentally friendly pest control, and with adequate testing demonstrating the specificity of biocontrol agents on the pest species, biological control should be considered an important part of an integrated pest management strategy (e.g. Waterhouse and Norris, 1987; Messing, 2000). The debate has been reviewed by Miller and Aplet (1993), US Congress, Office of Technology Assessment [OTA below] (1995) and Simberloff and Stilling (1996a, b), with further discussion by, for example, Frank (1998), Simberloff and Stiling (1998), Thomas and Willis (1998), Cory and Myers (2000) and chapters in Follett and Duan (2000).

Most biological control endeavours have been undertaken against insect pests or weeds and have involved release of an insect species (predator, parasite or herbivore) known to prey upon, parasitize or feed on the pest or weed species. Most of the pests or weeds are species that have been introduced to an area from elsewhere: most biocontrol agents are introduced from the native range of the pest/weed, where they are considered to be co-evolved 'natural enemies'. This is 'classical biological control' (Barbosa and Braxton, 1993; Lockwood, 1993; Ehler, 2000). In the past, adequate testing was rarely done. Usually now, at least in officially sanctioned programmes, screening is undertaken to show that non-target species in the release region are not at risk, or to demonstrate that the putative biocontrol agent lacks specificity, in which case it should not be released. However, how specificity is defined may vary (Cory and Myers, 2000), and even now, testing rarely takes into account the full suite of potential complex ecological effects of introduction of a biocontrol agent (Strong, 1997; OTA, 1995; Ewel et al., 1999). Some effects may be completely unanticipated. In addition, post-release monitoring of such complex effects is almost never carried out.

Compared with the extensive use of insects for biological control, snails have been used in relatively few biocontrol efforts. Most snail species, both herbivorous and predatory species. appear rather generalist. This fact, combined with the fact that most biocontrol introductions using snails have been and continue to be undertaken by people with entomological or agricultural but not malacological experience, as noted for example by Mead (1956) and van der Schalie (1969), has meant that adequate understanding of snail biology has not been incorporated into the biocontrol efforts, adequate screening has not taken place, and predatory snails have been released without due regard, or with explicit disregard (Pemberton, 1956), for their potential impacts on native faunas. This casual approach persists even though its inadequacies have been apparent from the early days of the use of snails as biocontrol agents (Mead, 1955, 1956). Similar problems have also been recognized with insect and other biocontrol agents (Howarth, 1983, 1991; Simberloff and Stiling, 1996a, b).

Furthermore, not only must a putative biocontrol agent be shown prior to release to be specific to the pest/weed it is intended to control, but it must also be shown that it is indeed capable of reducing populations of the pest/weed. Just because

†Contribution number 2000.008 of Bishop Museum's Pacific Biological Survey. #Fax: +1 (808) 847 8252; e-mail: rhcowie@bishopmuseum.org it can be shown to feed on the pest/weed does not mean that it will control its populations. Other factors (both deterministic and stochastic) may limit pest/weed populations, such that the biocontrol agent simply removes a proportion of the population that would not have survived anyway. The huge body of predator/prey literature demonstrates the complexity of these interactions (e.g. references in Sih *et al.*, 1998), and shows that it is extremely difficult to prove that predation limits prey populations— often it may not. And the theory underpinning this aspect of biological control is complex (Murdoch and Briggs, 1996). In few cases of putative biological control using snails has it been demonstrated prior to release that the snail biocontrol agent indeed has the potential to control the pest populations.

In the terrestrial realm, predatory snails have been used as putative biocontrol agents against a number of other snail species, notably *Achatina fulica* Bowdich (Achatinidae) (the giant African snail) and various species of Helicidae, especially *Helix aspersa* Müller (the brown garden snail). In aquatic habitats, a number of predominantly herbivorous snail species have been used as competitors of aquatic snails carrying human schistosomes, and against aquatic weeds. In this paper I review the use of snails as biocontrol agents, asking whether any implementation of such a programme has achieved the levels of control anticipated or hoped for; I review the detrimental effects on native biotas that have resulted from their implementation; and I make recommendations regarding the future of biocontrol using snails.

2. Control of the giant African snail, Achatina fulica

Achatina fulica has been widely introduced throughout the tropics and subtropics. After introduction, its populations generally increase dramatically, perhaps following a variable lag time, as seen in many other introductions of non-native species (Crooks and Soulé, 1996; Ewel et al., 1999). They frequently reach such enormous numbers, at least locally, that they become not only agricultural and garden pests but also a major public nuisance, causing road hazards and making it difficult to avoid them while walking (Mead, 1961). A. fulica has been considered the most important snail pest in the tropics and subtropics and perhaps the world (Civeyrel and Simberloff, 1996). However, its agricultural impacts may have been exaggerated, the nuisance factor perhaps being more important (Mead, 1961, 1979). A. fulica is also a vector of Angiostrongylus cantonensis (Chen) (Nematoda; Protostrongylidae), the roundworm responsible for eosinophilic meningoencephalitis in humans (Alicata, 1969) and the spread of the disease has been correlated with the spread of A. fulica (Alicata, 1991). However, many other introduced snails in the tropics are vectors of this parasite and the spread of the disease has not definitively been related to the spread of A. fulica (Civeyrel and Simberloff, 1996). For more detail on all these issues see Mead (1961, 1979) and Civeyrel and Simberloff (1996).

2.1. Snails introduced to control Achatina fulica

Serious efforts to control Achatina fulica using biocontrol agents began in Hawaii. A. fulica was introduced to Hawaii in

1936, first reported by Pemberton (1938, and see Cowie, 1997). By the 1950s its populations had become so dense locally that the Hawaii Department of Agriculture (then the Board of Agriculture and Forestry) began to look at the possibility of biological control using predatory snails. The history of these efforts is presented in detail by Mead (1961) and summarized here. The first predator to be considered was the East African species Gonaxis kibweziensis (Smith) (Streptaxidae). Prior to its introduction to Hawaii, testing on the remote uninhabited island of Aquijan in the northern Mariana Islands of the western Pacific demonstrated that the introduced predator would survive and would prev on A. fulica but did not demonstrate that it could control populations of A. fulica. The question of its preying on native snails was not addressed. While additional research was being undertaken on Aguijan, under intense pressure from the people of Hawaii to 'do something' about A. fulica, the Board of Agriculture, without waiting for the results of the research programme, in 1952 released G. kibweziensis into the Hawaiian Islands.

With no clear effect of *Gonaxis kibweziensis* on the populations of *Achatina fulica* in Hawaii, then thought to be because the small size of *G. kibweziensis* permitted it to prey on only small juvenile *A. fulica*, the Board of Agriculture introduced in 1957 another, larger, East African species, *Gonaxis quadrilateralis* (Preston) (Streptaxidae).

Meanwhile, in 1955, the voracious predatory snail *Euglandina rosea* (Férussac) (Spiraxidae), known commonly as the cannibal snail or rosy wolf snail and native to the south-eastern USA, was released in Hawaii. It rapidly multiplied and spread and is now readily found on most of the main Hawaiian Islands (Cowie, 1997). This species is not a 'natural' enemy of *A. fulica*, as it does not occur in the native range of *A. fulica*.

These three predatory species are now established in the Hawaiian Islands. However, an additional 12 species of predatory snails were released in Hawaii during the 1950s and 1960s in the attempt to control *A. fulica*, although as far as is possible to determine none of these became established (Davis and Butler, 1964; Krauss, 1964; Mead, 1979; Cowie, 1998a).

Subsequently, and often on the recommendations of authorities in Hawaii, Euglandina rosea in particular, but also the Gonaxis species, have been introduced to many regions where Achatina fulica has become a problem, mostly islands of the Pacific and Indian Oceans but also the Caribbean, and southern and eastern Asia (Griffiths et al., 1993; Civeyrel and Simberloff, 1996). In some instances these introductions have been official but in others they have been unofficial or even illegal; some were accidental. Furthermore, a number of these introductions, for instance to Tahiti (Coote et al., 1999) and American Samoa (Cowie, 1998b) have been done against the express objections of experienced experts and despite the well publicized negative impacts of the predatory snails on native snail faunas in areas to which they have been previously introduced (see below). A number of other nonnative predatory species have been recorded on Pacific islands (e.g. Cowie, 1998c; in press a). They may have been introduced deliberately, though unofficially. Adequate testing of specificity and ability to control A. fulica, prior to introduction, was never carried out (Civeyrel and Simberloff, 1996).

2.2. Has Achatina fulica been controlled?

There is no convincing scientific evidence that introduced predatory snails have effected control of populations of *Achatina fulica* (Christensen, 1984). In many places, *A. fulica* populations, having expanded dramatically to an extent that prompted the biocontrol efforts, have declined to more or less tolerable levels (Mead, 1979; Cowie, 1992). This decline has been attributed to the biocontrol programmes by their supporters (e.g. Davis and Butler, 1964) and sometimes by an ill-informed and receptive public. Much of the 'evidence' that these predators can control populations of *A. fulica* is based on a poor understanding of ecological principles. That the predators will *prey* on *A. fulica* is not evidence that they can *control* its populations; other factors (e.g. food) may be limiting, even to the extent that heavy predation has no effect on population densities of the extremely fecund and rapidly reproducing *A. fulica*.

The studies of Davis and Butler (1964) and Nishida and Napompeth (1975), supporting Gonaxis spp. and Euglandina rosea as effective biocontrol agents against Achatina fulica in Hawaii, are seriously inadequate. Davis and Butler (1964) recorded size/age structure of A. fulica populations at a number of localities over intervals of a number of years. They argued that Euglandina rosea and Gonaxis quadrilateralis had modified the age structure of the A. fulica populations by predation on juveniles and that as a result there was no recruitment into the adult A. fulica populations, which therefore declined. Nishida and Napompeth (1975) studied only single collections of dead shells of A. fulica from each of two localities, one with E. rosea and one with Gonaxis spp. Absence of small juvenile A. fulica in these two collections was attributed to predation by the biocontrol agents, solely on the basis of the presence of the latter at the sample sites. In neither study was convincing causative evidence presented. If heavy predation on juveniles were taking place, one would expect the exact opposite: large numbers of dead juvenile shells (though the smallest juveniles would probably be swallowed whole, at least by E. rosea, and leave no trace-see below). Adequate series of control observations (populations with no predatory snails present) were not included: Davis and Butler (1964) reported only one control population of A. fulica; Nishida and Napompeth (1975) had no control populations. Absence of small juveniles can readily be explained by other factors, in particular seasonality of reproduction. Nishida and Napompeth (1975) made their single collections of A. fulica at a time of year when an earlier study (Kekauoha, 1966) had already shown that because of reproductive seasonality juveniles would not be expected. The deduction that the absence of juveniles was a result of predation, and then the conclusion that the predators had effectively controlled A. fulica populations, were not justified. In neither case can the introduced predators be credited with any proven effect; these and other proponents of introduction of predatory snails simply assumed the success of the 'biocontrol' efforts wherever A. fulica decreased, without ever proving a cause-and-effect relationship.

A number of studies have shown that (1) *Euglandina rosea* preys preferentially on species other than *Achatina fulica*, and (2) when it does prey on *A. fulica* it preys preferentially on small individuals. Adults of *A. fulica* may reach 15 cm or more in shell height, whereas those of *E. rosea* rarely exceed 5 cm. In the

wild in Mauritius (Griffiths et al., 1993), E. rosea did not prey on A. fulica even though it was present in the study area, preferring smaller (predominantly native) species. Experimental studies have also shown that E. rosea prefers smaller species and, within species, smaller individuals; and that smaller prey are preferentially swallowed whole, probably to gain calcium (Simmonds and Hughes, 1963; Cook, 1985a, 1989a, b). Small individuals of Achatina fulica are preferred over large ones (Davis and Butler, 1964). E. rosea finds its prey by locating and following their slime trails (Cook, 1985b). All these studies point to E. rosea being unlikely to prey heavily on A. fulica, much less control its populations. Fewer such studies have been undertaken on Gonaxis spp., though Davis and Butler (1964) stated that Gonaxis kibweziensis and G. quadrilateralis attack predominantly the eggs and juveniles of A. fulica and not larger individuals.

The most telling evidence that predatory snails are not responsible for the declines in *Achatina fulica* comes from French Polynesia. *A. fulica* populations declined on the island of Huahine just as they did on neighbouring Moorea and Tahiti, although *Euglandina rosea* had not at that time been introduced to Huahine; and *A. fulica* declined prior to the spread of *E. rosea* into certain valleys on Moorea (Pointier and Blanc, 1982, 1984; Tillier and Clarke, 1983; Clarke *et al.*, 1984; Civeyrel and Simberloff, 1996). In the Mariana Islands, similar scenarios in which *A. fulica* declined in areas free of predatory snails at the same time as it did in areas with predatory snails were hinted at by Kondo (1952) on Rota and by Mead (1956) on Aguijan.

It is now generally recognized that the *A. fulica* populations declined for other reasons. These reasons are unknown but have been widely speculated on (e.g. Mead, 1961, 1979; Clarke *et al.*, 1984; Pointier and Blanc, 1984; Cowie, 1992). Diseases, from which the initial introductions escaped, but which ultimately caught up with the expanding populations, have been most frequently invoked (Mead, 1979; Pointier and Blanc, 1982; Tillier and Clarke, 1983). Genetic effects akin to inbreeding depression may also play a part (cf. Sailer, 1978; Simberloff, 1986). *A. fulica* is a vector of the rat lung-worm, *Angiostrongylus cantonensis* (Alicata, 1969); but whether these parasites influence *A. fulica* population dynamics, directly or indirectly (Civeyrel and Simberloff, 1996), is not known. A combination of disease and a depauperate genetic makeup has also been suggested (Civeyrel and Simberloff, 1996).

2.3. Impacts of the predatory snails on native biotas

Introduction of predatory snails, especially *Euglandina rosea*, in attempts to control *Achatina fulica* has been widely seen as disastrous (Civeyrel and Simberloff, 1996). Not only is there no convincing evidence that the control programmes have been successful (above), but there is ample evidence that the predatory snails have had major impacts on native snail species, perhaps to the extent of causing the extinction of a large number of endemic species (Hadfield, 1986; Murray *et al.*, 1988; Cowie, 1992). The most widely publicized impacts have been on the slow-reproducing endemic tree snails of the islands of the Pacific (Partulidae and Achatinellinae). Statements that *E. rosea* is entirely ground-dwelling (e.g. Craig, 1973) are not true; it is well known to climb trees (e.g. van der Schalie, 1969; Voss, 1976; Hadfield *et al.*, 1993; R.H. Cowie, unpublished observa-

tions; M.G. Hadfield, personal communication). Even proponents of its use (e.g. Davis and Butler, 1964) report that it feeds on tree snails in its native Florida. Not only the well-known Pacific island tree snails but also other land snail species, both arboreal and ground-dwelling species, have also probably declined as a result of predation by *E. rosea*, e.g. endemic species of Pacific island Helicarionidae (Tillier and Clarke, 1983). These native snails are generally confined to relatively undisturbed habitat and are not themselves considered pests of any kind.

Davis and Butler (1964), early proponents of the biological control programmes in Hawaii, recognized that these predatory species would feed on native snails but appeared not to consider this important. There is now convincing evidence that Euglandina rosea in particular has had a major impact on endemic Hawaiian achatinelline tree snails (Hadfield and Kay, 1981; Hadfield and Mountain, 1981; Hadfield, 1986; Hadfield and Miller, 1989; Hadfield et al., 1993; Stone, 1999) and probably on other species of Hawaiian land snails, including species in the extremely speciose endemic Hawaiian family Amastridae (Griffiths et al., 1993). Approximately 750 species of endemic land snails have been described from Hawaii (Cowie, 1996). Solem (1990) estimated that only 25-35% remained; in fact the figure may be as low as 10% (R.H. Cowie, unpublished). In Hawaii, Achatina fulica tends to occur only in modified lowland areas, but E. rosea has expanded its distribution far beyond these areas and into higher elevation native forest (van der Schalie, 1969). Predation by introduced snails is not the only reason (e.g. habitat destruction, predation by rats, shell collecting) for the catastrophic decline of native Hawaiian snails (Hadfield, 1986) but may well be the factor that has led to the ultimate extinction of a large part of this unique fauna.

Elsewhere in the Pacific, partulid tree snails (Partulidae) have been the focus of much intensive ecological and evolutionary research (Crampton, 1916, 1925, 1932; Johnson et al., 1993) and have prompted considerable publicity (e.g. Gould, 1991). They are found on most of the high volcanic archipelagos of the tropical and subtropical Pacific, with the notable exception of the Hawaiian Islands (Cowie, 1992). Cowie and Cook (in press) termed them the 'flagships of terrestrial invertebrate conservation in the Pacific'. Euglandina rosea was the precipitous cause of the extinction in the wild of the Partula spp. of Moorea, the process taking only 10 years from its introduction (Tillier and Clarke, 1983; Clarke et al., 1984; Murray et al., 1988). Often, it has been difficult to prove a causal link between introduction of predatory snails and decline of native species (Griffiths et al., 1993). Just as the evidence for the success of the control programmes has been criticized for being circumstantial or correlative (above), so also is much of the evidence for the impacts of the predators on native faunas. However, while the evidence for the success of the predators in controlling Achatina fulica remains highly questionable, the weight of evidence for their negative impacts has become compelling. Furthermore, as the events that took place on Moorea demonstrate, there is indeed convincing evidence of a causative link between introduction of a predator and extinction of native species: as the wave of Euglandina rosea spread across the island, partulids could only be found in areas as yet not invaded (Clarke et al., 1984). Also, at the same time,

partulids survived in large numbers on Huahine, to which *E. rosea* had not been introduced (Murray *et al.*, 1988). Similarly, the partulids of Tahiti vanished from areas invaded by *E. rosea* (Clarke *et al.*, 1984) and are now under serious threat, with some species possibly extinct (Tillier and Clarke, 1983; Coote *et al.*, 1999). A similar situation obtains on Guam (Hopper and Smith, 1992). The partulids of American Samoa are also under threat, though surviving in low numbers (Cowie and Cook, in press).

Many of these endemic island tree snail species probably evolved in the absence or near absence of predators, allowing a life history of slow growth, extremely slow reproduction, and ovoviviparity (Cowie, 1992). They seem especially vulnerable to heightened levels of predation resulting from human introductions, probably because their slow rate of reproduction means that it will take a long time for a population to recover from a single predation episode that destroys a significant portion of the population, or for a population to withstand a consistent, lower, but nevertheless artificial level of predation (e.g. Hadfield and Mountain, 1981; Hadfield, 1986; Hadfield *et al.*, 1993). Other species with more rapid reproduction and higher fecundity may be able to withstand predation, but this has not been demonstrated.

In the Ogasawara (Bonin) Islands of Japan (Takeuchi et al., 1991) and in New Caledonia (Gargominy et al., 1996), at the time of these reports, Euglandina rosea had not become widespread but concerns were expressed for the native malacofaunas should it do so. In Mauritius and Rodrigues, it has been suggested that E. rosea is reducing populations of native snails that are already declining because of habitat destruction (Griffiths et al., 1993). Elsewhere, where E. rosea has been introduced (Griffiths et al., 1993; Civeyrel and Simberloff, 1996), its impacts on native snail faunas have not been reported but may yet be important. It has been suggested that E. rosea tends not to invade native forest but is generally restricted to disturbed habitats (Griffiths et al., 1993). However, in many areas this is not true, for instance in Hawaii (Hadfield, 1986), the Society Islands (Murray et al., 1988) and American Samoa (Cowie and Cook, in press), where in all cases E. rosea has invaded native forest and native snails have become extinct or are under serious threat, as discussed above. E. rosea will even go under water to attack freshwater snails (Kinzie, 1992).

Gonaxis kibweziensis is now the second most widely introduced of these predatory species (Cowie, in press a). It rarely seems to become as abundant as E. rosea, and has not been so heavily implicated in causing extinctions of native species. It appears to be entirely ground-dwelling. Native ground-dwelling species, though a large proportion of the terrestrial snail faunas of most places, including Pacific islands, have not received the attention the tree snails have, so it is unknown whether G. kibweziensis has had any impact on them. Gonaxis quadrilateralis, larger than G. kibweziensis, is probably the third most widely introduced of the predatory species. As for G. kibweziensis, little is known about its impacts, but it may have had impacts on ground-dwelling native snails. Other factors (e.g. predation by rats, ants, etc.) may have already had major effects on native ground-dwelling species such that the effects of Gonaxis spp. have been rather obscured. Impacts of other introduced predatory snail species are unknown.

3. Control of helicid and other snails and slugs

Many European snail species in the family Helicidae have been deliberately introduced and released to many parts of the world for development and harvest as 'escargot' (Cowie and Robinson, submitted). These helicids and many others, as well as species in the related families Hygromiidae and Cochlicellidae, are also frequently distributed inadvertently, for instance in or on shipping containers (Robinson, 1999). Most of these species are western European and especially Mediterranean in origin. Robinson (1999) listed 20 helicid species, 50 hygromiid species and two cochlicellid species intercepted by US quarantine officials in the period 1993-98. Notable among these are the helicids Helix aspersa (the common brown snail, brown garden snail, 'petit gris' in the French edible escargot world), Cepaea nemoralis (Müller), Theba pisana (Müller), Otala lactea (Müller), and Eobania vermiculata (Müller), the hygromiids Cernuella virgata (DaCosta) and Candidula intersecta (Poiret), and the cochlicellids Cochlicella acuta (Müller) and Cochlicella barbara [= Prietocella barbara] (Linnaeus). Theba pisana and Cernuella virgata have sometimes been referred to as 'white snails' and the cochlicellids as 'conical snails' (Baker, 1986; Roth et al., 1987; Hopkins and Baker, 1993) and in Australia these four species are serious pasture and cereal pests (Baker, 1986; Hopkins and Baker, 1993; Coupland and Baker, 1994, 1995; Coupland, 1995). Theba pisana and Helix aspersa have also been considered pests in South Africa (Joubert and Walters, 1951).

A number of these helicid species, notably *Theba pisana* and *Helix aspersa*, introduced to California, became major pests, especially in citrus groves (Gammon, 1943). *Theba pisana* was thought to have been eradicated, after many years of intensive effort that did not include biological control (Gammon, 1943; Armitage, 1949), but subsequently reappeared (Roth *et al.*, 1987). *Helix aspersa* is widespread, not only in California but in many parts of the USA (Hanna, 1966; Dundee, 1974).

3.1. Snails introduced to control helicids (and other snails and slugs)

In order to control Helix aspersa in particular, the predatory snails Euglandina rosea and Gonaxis kibweziensis were introduced to California, against the protests of molluscan experts (e.g. Mead, 1955); they did not become established (Hanna, 1966; Fisher and Orth, 1985). Subsequently, in the 1970s, the facultative carnivorous snail Rumina decollata (Linnaeus) (Subulinidae) (the 'decollate snail'), first recorded in California in 1966 and probably introduced accidentally with horticultural plants (Fisher, 1966), was suggested as a potential control agent for Helix aspersa (Fisher, 1974). It has now been widely dispersed for this purpose (Sakovich, 1996). Rumina decollata occurs naturally around the Mediterranean. It was first recorded in the USA in 1813, in South Carolina, and has since been reported from most states across the southern part of the country from Virginia, South Carolina, Georgia and Florida to Arizona and California (Hanna, 1966; Dundee, 1974; Fisher et al., 1980). In some localities it became sufficiently abundant to be considered a plant pest (Fisher and Orth, 1985). Most of these early introductions of R. decollata were probably

accidental, not deliberate introductions for biological control. Rather little is known of its general biology (e.g. Selander *et al.*, 1974; Fisher and Orth, 1985 and references therein; Dundee, 1986).

A number of commercial suppliers of *Rumina decollata* advertise on the web, and the University of California Statewide Integrated Pest Management Project (Integrated Pest Management Education and Publications Group, 1991) promotes the use of *R. decollata* for controlling *Helix aspersa* in citrus groves, both in its manual and on the web. *R. decollata* is no doubt being dispersed relatively indiscriminately not only in California but elsewhere, by the general public, by citrus growers and by official agencies. These people and agencies can readily obtain this supposedly environmentally friendly and effective, but relatively unregulated, biocontrol agent for use against snails in their gardens/yards, citrus groves, public landscaped areas, freeway verges, and so on.

In Bermuda, Euglandina rosea, Gonaxis kibweziensis, and an additional African species, Natalina cafra (Férussac) (Rhytididae), were introduced for control of the helicid Otala lactea, the subulinid Rumina decollata (in this context R. decollata was considered a plant pest), and slugs (Bennett and Hughes, 1959; Simmonds and Hughes, 1963; Gould, 1969). Euglandina rosea is now widespread and Gonaxis kibweziensis has spread from the release area (Bieler and Slapcinsky, submitted). Rumina decollata has also been reported in other parts of the world, e.g. South America (Miquel et al., 1995), China (Beckmann, 1989) and Japan (Hosaka, 1996), but whether it was deliberately or inadvertently introduced to these localities is not known.

In Australia, predatory snails have not and will not be considered for control of white snails because of the predators' non-specific feeding preferences and therefore concern for the native fauna (G.H. Baker, personal communication).

3.2. Has control been successful?

Fisher and Orth (1985) reported that in experimental sites in California to which Rumina decollata was introduced, Helix aspersa populations declined. These sites included citrus groves, domestic gardens/yards, and landscaped areas adjacent to roads/freeways. However, these authors did not demonstrate direct causality. Other factors (e.g. rodent predation on snails) were important at some sites; not all sites showed declines in H. aspersa populations; changes in relative numbers of R. decollata and H. aspersa in samples were interpreted as control, whereas they may have been in some cases simply a result of the build up of R. decollata populations following introduction; and some results were highly qualitative and subjective. Nevertheless, these authors enthusiastically supported the use of R. decollata as a control agent. Control was reported as being effective in 4-10 years from introduction of R. decollata, although the supporting evidence was only correlative and often inconsistent. Sakovich (1996) reported that properties on which R. decollata had become well established harboured few or no H. aspersa, again correlative evidence only. In southern Portugal, where both R. decollata and *H. aspersa* are native and abundant, the latter is frequently seen above ground on walls, tree trunks, etc., whereas the former is found exclusively on the ground (D.G. Robinson, personal communication); differences in microhabitat preferences may therefore influence any interaction between the two species. Fisher and Orth (1985) also cited a number of instances of *R. decollata* preying on various other introduced European snail species.

Introduction of *Euglandina rosea* to Bermuda was said by Simmonds and Hughes (1963) to have been 'spectacularly successful' in controlling *Otala lactea*, although its effect on *Rumina decollata* and slugs was 'negligible'. Gould (1969) repeated this belief regarding *O. lactea*. However, the evidence for control was entirely correlative, so factors other than predation by *E. rosea* may have caused the decline of *O. lactea*. Later, Gould (1991) contradicted his earlier statement, stating that *E. rosea* had not 'even dented *Otala*'. Based on survey work over 30 years after the introductions, Bieler and Slapcinsky (submitted) considered the control of *O. lactea* and *R. decollata* to have failed.

3.3. Impacts on native species

Fisher and Orth (1985) argued that introduction of Rumina decollata to disturbed habitats in California (freeway verges, domestic gardens, citrus groves) presents no threat to native Californian snails, some of which are officially listed by the US Fish and Wildlife Service as endangered species. However, the only published tests of the specificity (or lack thereof) of R. decollata that have been undertaken (Fisher and Orth, 1985) demonstrated that it would indeed feed on a number of native species (and this has been confirmed; B. Roth, unpublished observations). Nevertheless, Fisher and Orth (1985) argued that it would not be able to invade the native habitats to which the native snails were essentially confined, though this was little more than speculation with no substantive support. In fact R. decollata has been found in the same localities as a number of listed species, some of which indeed do occur in highly disturbed habitat (B. Roth, unpublished observations). Competition with native snails (perhaps for food but more likely for shelter sites), as well as predation on them, may also be an issue (B. Roth personal communication).

Fisher and Orth (1985) further argued that Rumina decollata would remain restricted to irrigated or otherwise moist areas in southern California, while native species occur in drier areas. In fact native species often occur in locally moist habitats within these drier areas, localities in which R. decollata could probably thrive if it were introduced. The native Mediterranean habitat of R. decollata in any case experiences similarly dry summers to those in southern California. Fisher and Orth (1985) also suggested that R. decollata would not be able to become established in moist habitats in northern California because of the limited calcium carbonate (limestone) resources of the substrates, which make this region a poor one for snails. However, northern California indeed does have a significant native snail fauna and in any case it has not been demonstrated that R. decollata is dependent on limestone substrates. Also, they argued that the presence of native predatory snails in northern California would make establishment of R. decollata there difficult, but this was sheer conjecture.

It has not, therefore, been adequately demonstrated that native species would not be affected by *Rumina decollata*. Indeed, because of the potential impact on endangered mollusc species, importation, transportation or use of *R. decollata* is

now prohibited in California except in certain counties (essentially those in which it already occurs). Unfortunately, no studies have been undertaken specifically addressing such potential impacts.

In addition, Fisher and Orth (1985) implied that *Rumina decollata* had no impact on the vegetation of the areas to which it was introduced, although they did acknowledge that in domestic gardens the large numbers of *R. decollata* might be considered a nuisance and that some damage might occur. Furthermore, they argued that because *R. decollata* was already well established in California, its further promotion for biological control purposes was acceptable.

Elsewhere in the USA there have been no studies of the likely impact of *Rumina decollata* on native species, nor of its likely effectiveness in controlling pest species of snails, yet it is readily available and probably continues to be dispersed to many localities in the southern USA, with unknown consequences.

In Bermuda, Simmonds and Hughes (1963) entirely ignored the impacts of the introduced predators on native species, except to say that in captivity one of the predators, *Euglandina rosea*, would feed on 'various local species'. It seems quite possible that populations of native species in the wild were affected by *E. rosea*. And indeed by 1973, Gould (1991) was unable to find the formerly abundant native species in the endemic genus *Poecilozonites*, considering *E. rosea* to have caused their drastic decline. It is also possible that *Rumina decollata* was a factor in this decline. Bieler and Slapcinsky (submitted) also suggested that the decline, almost to extinction, of *Poecilozonites* spp. since the 1960s might have been caused by the introduced predatory snails.

4. Control of snail vectors of schistosomes

Schistosomiasis in humans (also known as bilharzia or bilharziasis) is caused by the adult stage of trematode flatworms in the genus Schistosoma (Platyhelminthes; Trematoda; Digenea; Schistosomatidae) (Rollinson and Simpson, 1987). Three species, Schistosoma mansoni Sambon, S. haematobium (Bilharz) and S. japonicum Katsurada, are the most important and widespread in humans, though other species (e.g. S. mekongi Voge, Bruckner and Bruce) infect humans locally. Other species attack other mammals and birds. Schistosome eggs pass from the human body in faeces (S. mansoni, S. japonicum) or urine (S. haematobium), producing free-swimming miracidia that penetrate aquatic snails. The miracidia develop into cercariae within the snail intermediate host. The cercariae are then released into the water and on contact with human skin are able to penetrate it. enter the blood stream, and develop into adult worms. Schistosoma is an Old World genus but S. mansoni has been introduced to the Neotropics, probably during the slavetrade era (Pointier, 1999). The snail vectors of S. mansoni are in the genus Biomphalaria (Basommatophora: Planorbidae) and those of S. haematobium are in the genus Bulinus (also Planorbidae) (Brown, 1978; Kristensen and Brown, 1999), while those of S. japonicum, which is a species complex (Woodruff et al., 1999), are in the genus Oncomelania (Caenogastropoda: Pomatiopsidae) (Rollinson and Southgate, 1987).

4.1. Snails introduced to control schistosome vectors

Various freshwater snails have been introduced in attempts to control these snail vectors of schistosomes, by out-competing them and/or preying on them (especially on eggs and juveniles). These introductions have been predominantly Ampullariidae (Pomacea glauca (Linnaeus), and especially Marisa cornuarietis (Linnaeus)) and Thiaridae (Melanoides tuberculata (Müller), and to a lesser extent Tarebia granifera [= Thiara granifera] (Lamarck)), although other groups such as Lymnaeidae (Michelson and DuBois, 1974) and Planorbidae (Frandsen and Madsen, 1979) have been investigated. Pomacea glauca is native to northern South America (Alderson, 1925); its occurrence on some Caribbean islands may be natural but may also have resulted from artificial introduction, and it has certainly been artificially distributed in the Caribbean to bodies of water in which it did not occur naturally. Marisa cornuarietis is also native to northern South America (Neck, 1984; Horne et al., 1992) but its presence on islands of the Caribbean is through introduction. The geographic origin of Melanoides tuberculata is Old World; that of Tarebia granifera is unknown (Cowie, 1997) but possibly South East Asia (Prentice, 1983; Pointier, 1999). These two thiarid species are now among the most widely distributed freshwater snails in the world (which contributes to the difficulty in determining their geographic origins), probably largely as a result of human activities (Cowie and Robinson, submitted).

The major efforts involving these snails as biocontrol agents began in the Caribbean in the 1950s with the introduction of Marisa cornuarietis to Puerto Rico, where, as well as feeding on vegetation, it also fed, perhaps incidentally, on the eggs, young and adults of Biomphalaria glabrata (Say) (Robins, 1971; Peebles et al., 1972; Jobin et al., 1977; Perera and Walls, 1996; Pointier, 1999). Elsewhere in the Caribbean, M. cornuarietis was introduced to St Kitts (Prentice, 1983), Guadeloupe (Pointier et al., 1991b), the Dominican Republic (Perera and Walls, 1996), and Cuba (Gutiérrez et al., 1997). It has also been introduced, recommended for introduction, or considered for introduction for schistosome control in Egypt (Demian and Kamel, 1973; Berthold, 1991), Tanzania (Nguma et al., 1982) and Sudan (Haridi and Jobin, 1985; Haridi et al., 1985). Another ampullariid, Pomacea canaliculata (Lamarck), has been tested in Thailand (Kruatrachue and Upatham, 1993).

During the 1980s in the Caribbean, the focus moved towards the thiarids *Melanoides tuberculata* and *Tarebia granifera*, notably involving introductions on the islands of St Lucia (Prentice, 1983), Guadeloupe (Pointier, 1989; Pointier *et al.*, 1993), Martinique (Pointier *et al.*, 1989; Pointier and Guyard, 1992) and Cuba (Perera *et al.*, 1993).

Most of these biocontrol programmes are what has been termed 'neoclassical' biological control (Lockwood, 1993; Simberloff and Stiling, 1996a, b; Ehler, 2000); that is, control of a native species (the snail vectors) by importing a non-native species with which the native species has not co-evolved, a subset of the 'new associations' (Hokkanen and Pimentel, 1989) technique of biological control.

4.2. Has control been achieved?

In the Grand Etang of Guadeloupe (West Indies), decline of Biomphalaria glabrata and the water lettuce (Pistia stratiotes Linnaeus [Araceae]) that it inhabited, from 1976 to 1985, was correlated with the accidental introduction and spread of *Pomacea glauca* in the lake (Pointier *et al.*, 1988). Subsequent (1987) deliberate introduction of *Marisa cornuarietis*, which feeds heavily on water lettuce and colonized the lake rapidly, apparently led to the elimination of both water lettuce and *B. glabrata* (Pointier *et al.*, 1991b; Pointier, 1999). In Puerto Rico, a decline in *B. glabrata* was correlated with the introduction of *M. cornuarietis* (Robins, 1971; Peebles *et al.*, 1972; Jobin *et al.*, 1977). Similar results were found for control of various snail species by *M. cornuarietis* in the Dominican Republic (Perera and Walls, 1996), Egypt (Demian and Kamel, 1973; Berthold, 1991) and Tanzania (Nguma *et al.*, 1982).

In Martinique, between 1983 and 1986, Melanoides tuberculata was introduced to 22 water-cress beds inhabited by Biomphalaria glabrata and B. straminea (Dunker) (Pointier et al., 1989). In all beds, a strong decline in the Biomphalaria spp. was noted about 2 years after the introduction. By 1990 the Biomphalaria spp. in eight beds had disappeared and only very few individuals remained in 12 others (two beds had dried up) (Pointier and Guyard, 1992). The disappearance of the Biomphalaria spp. was attributed to competition with Melanoides tuberculata. Experimental introduction of M. tuberculata to a small pond in Guadeloupe in 1981 was correlated with 83–98% reductions in numbers of B. glabrata (Pointier, 1989), but later studies in a range of habitats in Guadeloupe gave variable results (Pointier et al., 1993). In Cuba (Perera et al., 1993), introductions of Melanoides tuberculata and Tarebia granifera were correlated with declines of Biomphalaria havanensis (Pfeiffer) and B. peregrina (d'Orbigny) but not of B. helophila (d'Orbigny), and population densities of the target snails fluctuated widely.

In Venezuela, both *Melanoides tuberculata* and *Tarebia granifera*, probably introduced accidentally in the past, are spreading naturally. Competition with them has been suggested as the reason for the concomitant decline of *Biomphalaria glabrata* (Pointier *et al.*, 1991a, 1994). Similarly, *T. granifera* has been suggested as the cause of the absence of *B. glabrata* from some localities in Puerto Rico, Dominica and Grenada (Prentice, 1983; Michelson, 1992). *T. granifera*, at least, may in some localities have somewhat different microhabitat preferences from *B. glabrata* (Jobin *et al.*, 1977), though it is usually considered tolerant of a wide range of microhabitats (Prentice, 1983; Gutiérrez *et al.*, 1997).

Many of these introductions thus appear to be correlated with declines in the Biomphalaria species, and have therefore been considered as successful biological control efforts. Few field studies (e.g. Demian and Kamel, 1973; Prentice, 1983; Perera et al., 1993) have incorporated control experiments or observations, which would then more convincingly allow support for a causal relationship between introduction of the biocontrol snails and decline of the schistosome snails. In laboratory studies, changes in relative abundances of target and control snails can be complex (Kruatrachue and Upatham, 1993). The precise mechanism of control, if control it really is, is in most cases not clear. Competition and predation (at least for instances involving Marisa cornuarietis) have been suggested. If the vegetation on which the schistosome snails depend is completely destroyed by the biocontrol agent then this is a clear case of exploitation competition (Begon et al., 1986). This may be the case in some of the instances in which ampullariids have been used. However, when thiarids have been used, although competition has been suggested as the cause of the decline of the schistosome snails, the mechanism is not as obvious, as the thiarids feed primarily on diatoms, algae and detritus but do not attack growing vegetation (Prentice, 1983; Pointier et al., 1989; Pointier and Guyard, 1992). However, the schistosome snails are probably also not macrophytophagous, and if diatoms, algae and detritus are limiting, then exploitation competition might operate. That the mechanism of control is not understood means that we cannot be certain that the biocontrol agents, and not some other factor, are the cause of the decline of the target snails, as noted by Loker et al. (1993). The variable results of Pointier et al. (1993) were interpreted as reflecting the snails' 'variable response to diverse environmental factors' and prompted these authors to state that the 'success or failure of biological control programmes . . . will depend . . . on a sound knowledge of, and capacity to predict . . . the main parameters governing the ecology of the transmission sites'. We do not yet have such understanding. To add to the complexity, some experimental studies have even demonstrated an increase in growth of the target species and an increase in parasite production in the presence of the putative competitor snails (Bayne and Loker, 1987; Moné, 1991).

As yet, neither the thiarids nor the ampullariids have been deliberately introduced widely around the world for biocontrol purposes, although both *Melanoides tuberculata* and *Tarebia granifera* are already extremely widespread, having been accidentally distributed via other pathways (Pointier, 1999; Cowie and Robinson, submitted).

4.3. Impacts on native ecosystems

The *Biomphalaria and Bulinus* species that are the schistosome vectors are generally part of the native biotas of the areas in which they occur, but are considered pests from a human health perspective. In the Old World the schistosome parasites are also native, though they are introduced in the New World. Thus, complex issues of biodiversity conservation versus human health are raised by this system because successful control explicitly involves destruction of native biota (Kristensen and Brown, 1999).

For the very reasons that ampullariids may be able to control schistosome snails, that is, their extremely voracious, relatively generalist, macrophytophagous feeding habits, they also have the potential to damage native and desirable aquatic plants and the fauna associated with them (Neck, 1984; Horne et al., 1992). Nguma et al. (1982), while stating that introduction of Marisa cornuarietis to a reservoir in Tanzania for control of schistosome snails had caused no adverse environmental impacts, also stated that certain aquatic plants (Cyperus spp.) had been eliminated from the reservoir by the snails. They also argued that the snails would not be a threat to cultivated rice, as did Haridi and Jobin (1985) in Sudan, although another ampullariid, Pomacea canaliculata, has become an extremely serious rice pest in South East Asia and elsewhere (Cowie, in press b). Kruatrachue and Upatham (1993) showed that P. canaliculata successfully controlled target snail species in experimental field tests in Thailand but acknowledged that this species could act as a vector for other human parasites and that its potential as an agricultural pest 'should be taken into serious consideration before using this snail species as a biological control agent'. In schistosome control programmes, as well as the schistosome vector snails that are the targets of control, other animals in the community, including other native snails, may also be destroyed; and some of these snails are of conservation concern (Kristensen and Brown, 1999). Loker *et al.* (1993) recommended that no further introductions of *M. cornuarietis* into sub-Saharan Africa should be contemplated because of the potential negative impacts of non-native ampullariids. Kristensen and Brown (1999) recommended more generally that no alien molluscs should be introduced to Africa because of their unpredictable effects on native faunas.

As mentioned above, thiarids feed primarily on diatoms, algae and detritus but not on growing macrophytes. Thus, any negative impacts are likely to be more subtle, but may involve other organisms dependent on these resources. Invasion by *Thiara granifera* is correlated with the disappearance of endemic native freshwater snail species in Cuba (Pointier, 1999), but whether *T. granifera* was the cause of these declines is not certain.

5. Control of aquatic weeds

The most serious invasive aquatic weeds world-wide are probably water hyacinth (*Eichhornia crassipes* Martius (Solms-Laubach) [Pontederiaceae]) and water fern (*Salvinia molesta* Mitchell [Salviniaceae]), with water lettuce (*Pistia stratiotes*) also a major problem (Waterhouse and Norris, 1987; Harley *et al.*, 1996; Julien *et al.*, 1996; Lach, in press).

5.1. Snails introduced to control aquatic weeds

Ampullariid snails such as Marisa cornuarietis are voracious, relatively generalist feeders on aquatic plants; this is partly the reason for their reported success in controlling other snail species (above), because they reduce the available food supply and/or microhabitat (Perera and Walls, 1996). They have therefore been used or suggested for control of aquatic weeds (e.g. references in Horne et al., 1992). In Florida and Puerto Rico, Marisa cornuarietis has been deliberately introduced in attempts to control aquatic plant nuisances, notably water hyacinth and hydrilla (Hydrilla verticillata (Linnaeus) Royle [Hydrocharitaceae]) (Robins, 1971; Simberloff and Stiling, 1996b). Pomacea glauca has been used in the Caribbean (Guadeloupe) for control of water lettuce (Perera and Walls, 1996). Pila globosa (Swainson) (Ampullariidae) has been tested as a control agent for Salvinia molesta in India (Thomas, 1975). In addition, Pomacea canaliculata has been suggested as a possible agent for general aquatic weed control in its native Argentina (Cazzaniga, 1981) and in Japan, where it is introduced (Okuma et al., 1994; Wada, 1997).

5.2. Can snails control aquatic weeds?

In laboratory studies of *Pomacea canaliculata*, Lach *et al.* (submitted) demonstrated food preferences and differential growth rates when the snails were fed on different plants. In particular, they reported that water hyacinth was not preferred and that when it was the only available plant no feeding on it

was evident and juvenile snails grew very little. However, in these experiments P. canaliculata would feed and grow on water lettuce, but whether it could reduce water lettuce populations in the wild is not known. In Guadeloupe, however, introduction of *Pomacea glauca* to a pond heavily infested with water lettuce led to almost complete destruction of the weed (Perera and Walls, 1996). Also in Guadebupe, introduction of both Pomacea glauca and Marisa cornuarietis to the Grand Etang to control schistosome snails (see above) was correlated with a decline in aquatic vegetation including water lettuce (Pointier et al., 1988, 1991b; Pointier, 1999). However, without control experiments it is not possible to rigorously demonstrate that the snails were indeed the cause of the decline of the weeds, although their generally voracious feeding habits certainly suggest this. In Hawaii, for instance, the local extent of water hyacinth can fluctuate widely (R.H. Cowie, personal observations).

The success or not of introduced *Marisa cornuarietis* in Puerto Rico and Florida in controlling hydrilla and water hyacinth has not been reported (Simberloff and Stiling, 1996b). However, since *Pomacea canaliculata*, also an ampullariid, will not feed on water hyacinth (Lach *et al.*, submitted), this suggests that not all aquatic weeds could be controlled by these species.

5.3. Impacts on native ecosystems

The voracious, relatively generalist, macrophytophagous feeding habits of ampullariids seem to have been seen as an advantage from a weed control perspective. Little testing of food preferences has been undertaken prior to release of snails for aquatic weed control, although there is some evidence of distinct preferences, in laboratory studies of Pomacea canaliculata in its native (Cazzaniga, 1981; Cazzaniga and Estebenet, 1984; Estebenet, 1995) and introduced (Lach et al., submitted) ranges. Some ampullariids have the capacity for extremely rapid growth and reproduction (Cowie, in press b) and thence rapid population growth when introduced to a new and suitable environment. Marisa cornuarietis, however, though 'an efficient consumer of some types of aquatic weed', was reported as having a slow intrinsic rate of increase (Nguma et al., 1982). In general, the basic biology of many of these ampullariids remains inadequately documented and undoubtedly there are differences among the numerous species.

Marisa cornuarietis, released unofficially in Florida for aquatic weed control, has been reported to feed indiscriminately on many native plants and thereby also damage populations of aquatic animals dependent on those plants (Simberloff and Stilling, 1996b). Otherwise, there is little documentation of the actual or potential non-target impacts of ampullariids introduced for aquatic weed control. However, accidental introduction of M. cornuarietis, for instance in Texas, has led to dramatic destruction of aquatic vegetation with potential impacts on endangered animal species in the habitat (Horne et al., 1992). Despite some evidence of food preferences and demographic differences, and despite the rather little published evidence of non-target impacts, ampullariids, whether introduced for schistosome snail control (above) or for control of aquatic weeds, must be considered as potentially having serious environmental impacts.

6. Discussion

Some of the biocontrol efforts discussed above probably can be considered successful from the perspective of controlling the target organisms. For many, however, success has not been demonstrated. Many have also had major impacts on non-target organisms, in some cases leading to the extinction of native species, and others have the clear potential for such impacts. Table 1 summarizes this information.

6.1. Predatory snails for control of the giant African snail

The weight of evidence is strongly against the introduction of predatory snails for control of the giant African snail, *Achatina fulica*. Predatory snails have not been shown to control *A. fulica* populations, but have devastated native snail faunas, causing the extinction of a number of species.

Most governments and other authorities appear to be aware of the potential threat posed to native faunas by these predatory snails, especially Euglandina rosea. However, under pressure from voters to 'do something' about Achatina fulica, they often at least consider the introduction of E. rosea (and other snail predators like the flatworm Platydemus manokwari de Beauchamp [Platyhelminthes; Rhynchodemidae]-e.g. Hopper and Smith, 1992; Civeyrel and Simberloff, 1996). In the early days of the use of predatory snails against A. fulica, the impacts on native species were recognized but explicitly considered unimportant (Pemberton, 1956). Many island people are not aware of their unique native faunas, or do not understand their precarious existence, but have heard that Euglandina rosea can solve the Achatina fulica problem. The pressure to introduce E. rosea may then become intense, or people may resort to introducing it unofficially. The official introduction of E. rosea to Tutuila (American Samoa) in 1980 was against the express written protests of widely respected land snail experts and others. The World Conservation Union (IUCN) has formally condemned the deliberate introduction of E. rosea and other carnivorous snails (Anon., 1989).

The use of predatory snails in attempts to control Achatina fulica for human health reasons, because it is a vector of Angiostrongylus cantonensis, is not justified. Euglandina rosea is also a vector of this parasite (Wallace and Rosen, 1969), and although Gonaxis spp. and other predatory snails have not been identified as hosts of A. cantonensis, its lack of host specificity suggests that they too may be vectors.

Until the causes of the observed declines of Achatina fulica are determined, it is extremely unvise to continue any biocontrol attempts against it on the off-chance that they may work. The burden of proof must be on the proponents of biocontrol: they must show that their agents, and not some other cause, are responsible for the declines. However, with the continuing spread of Achatina fulica, the threat posed by the likely continued introduction of *E. rosea* is serious.

More recently, there is a lesser tendency to consider introduction of *Gonaxis kibweziensis* and *G. quadrilateralis* (or any other predatory snails) than introduction of *Euglandina rosea* in control efforts against *Achatina fulica*. Nevertheless, whether officially or unofficially, there remains the possibility that the *Gonaxis* spp. will be introduced more widely. They therefore still pose a potential, though less understood threat. Their

Snail control agent	Targets ^a	Location	Successful control?	Adverse effects (k nown and potential)	Key references ^b
Euglandina rosea	Achatina fulica	Pacific islands, Indian Ocean islands, Caribbean, southern and eastern Asia ^c	2	Decline (possibly extinction) of native snails	Mead (1979), Hadfield (1986), Murray <i>et al.</i> (1988), Cowie (1992), Hadfield <i>et al.</i> (1993), Griffiths <i>et al.</i> (1993), Civeyrel and Simberloff (1996)
	Helix aspersa	USA (California)	Ŷ	None; predator not established	Hanna (1966), Mead (1979), Fisher and Orth (1985)
	Otala lactea	Berrruda	92	Probable decline of native snails	Sirmonds and Hughes (1963), Gould (1991), Bieler and Slap- cinsky (submitted)
	Rumina decollata	Berrruda	02	Probable decline of native snails	Sirmonds and Hughes (1963), Gould (1991), Bieler and Slap- cinsky (submitted)
	Slugs	Berruda	2	Probable decline of native snails	Simmonds and Hughes (1963), "a Gould (1991), Bieler and Slap- T cinsky (submitted)
Gonaxis kibweziensis	Achatina fulica	Pacific islands, Indian Ocean islands, southern and eastern Asia ^c	2	Possible impact on native snails	Mead (1979), Civeyrel and Simbertoff (1996), Cowie (in press a)
	Helix aspersa	USA (California)	٩ ٧	None; predator not established	Hanna (1966), Mead (1979), Fisher and Orth (1985)
	Otala lactea	Berrruda	Q	Possible impact on native snails	Simmonds and Hughes (1963), Gould (1991), Bieler and Slap- cinsky (submitted)
	Rumina decollata	Berrruda	Q	Possible impact on native snails	Simmonds and Hughes (1963), Gould (1991), Bieler and Slap- cinsky (submitted)
	Slugs	Berrruda	2	Possible impact on native snails	Sirrmonds and Hughes (1963), Gould (1991), Bieler and Slap- cinsky (submitted)
Gonaxis quadrilateralis	Achatina fulica	Pacific islands ^c	9	Possible impact on native snails	Mead (1979), Civeyrel and Sim- berloff(1996), Cowie (in press a)

Table 1. Snail species used as putative biocontrol agents, whether they have achieved control of the targetis), and their adverse ecological effects

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7, 1998a) 7_1998a)	7, 1998a)	7, 1998a)	7, 1998a)	7, 1998a)	7, 1998a)	and Hughe	and Hughe	and Hughe	Orth (198	al. (1988)	al. (1988)						
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None; predator not established None: predator not established	None; predator not established	Probably none; predator probably not established	Probably none; predator probably not established	Probably none; predator probably not established	None; predator not established	None; predator not established	Ę	Ę	Ę	Possible impact on native snails	Possible impact on native ecosystems	Possible impact on native ecosystems					
None; p	None; p	None; p	None; p	None; p	None; p	None; p	Probab	Probab	Probab	None; p	None; p	Unknown	Unknown	Unknown	Possibl	Possibl	Possibl
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Hawaii Hawaii	Hawaii	Hawaii	Hawaii	Hawaii	Hawaii	Bermuda	Bermuda	Bermuda	USA (C	Caribbean	Caribbean						
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Achatina fulica Achatina fulica	Achatina fulica	Achatina fulica	Achatina fulica	Achatina fulica	Achatina fulica	Subulina octona	Achatina fulica	Achatina fulica	Achatina fulica	Achatina fulica	Achatina fulica	Otala lactea	Rumina decollata	(0	Helix aspersa	Biomphalaria glabrata (s)	Pistia stratiotes (w)
Acha Acha	Acha	Acha	Acha	Acha	Acha	Subu	Acha	Acha	Acha	Acha	Acha	Otala	Rum	Slugs	Helix	Biom	Pistia
ea		nis	riformis	i.			rgi	valikalense	Ġ	tundata					ata	ca	
Oleacina oleacea Oleacina sn	Salasiella sp.	Edentulina affinis	E. obesa bulimiformis	Gonaxis vulcani	Gulella bicolor		Gulella wahlbergi	Ptychotrema walikalense	P tychotrema sp.	Streptaxis contundata	Natalina cafra				Rumina decollata	Pomacea glauca	
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Can snails ever be effective and safe biocontrol agents?

(continued)

Table 1 (concluded)					
Snail control agent	Targets ^a	Location	Successful control?	Adverse effects (known and potential)	Key references ^b
Marisa cornuarietis	Biomphalaria glabrata (s)	Caribbean	Yes	Probable impact on native ecosystems	Jobin <i>et al.</i> (1977), Pointier <i>et al.</i> (1991b), Perera and Walls (1996), Pointier (1999)
	Biomphalaria pfeifferi (s)	Tanzania	Yes	Probable impact on native ecosystems	Nguma <i>et al.</i> (1982)
	Bulinus tropicus (s)	Tanzania	Yes	Probable impact on native ecosystems	Nguma <i>et al.</i> (1982)
	Bulinus truncatus (s)	Egypt	Yes	Probable impact on native ecosystems	Demian and Kamel (1973), Bert- hold (1991)
	Hychilla verticillata (w)	USA (Florida), Caribbean	Yes	Severe damage to native plants and animals	Simberloff and Stiling (1996b)
	Eichhornia crassipes (w)	USA (Florida), Caribbean	Yes	Severe damage to native plants and animals	Simberloff and Stiling (1996b)
Melanoides tuberculata	Biomphalaria glabrata (s)	Caribbean	Variable results	Possible competition with native snail species	Pointier and Guyard (1992), Pointier <i>et al.</i> (1993)
	Biomphalaria straminea (s)	Caribbean	Yes	Possible competition with native snail species	Pointier and Guyard (1992)
	Biomphalaria havanensis (s)	Caribbean	Possibly	Possible competition with native snail species	Perera <i>et al.</i> (1993)
	Biomphalaria peregrina (s)	Caribbean	Possibly	Possible competition with native snail species	Perera <i>et al.</i> (1993)
	Biomphalaria helophia (s)	Caribbean	No	Possible competition with native snail species	Perera <i>et al.</i> (1993)
Tarebia granifera	Biomphalaria havanensis (s)	Caribbean	Possibly	Possible competition with native snail species	Perera <i>et al.</i> (1993)
	Biomphalaria peregrina (s)	Caribbean	Possibly	Possible competition with native snail species	Perera <i>et al.</i> (1993)
	Biomphalaria helophila (s)	Caribbean	N	Possible competition with native snail species	Perera <i>et al.</i> (1993)
^a Targets are terrestrial snails	"Targets are terrestrial snails unless followed bv 's' to indicate freshwater snails that are schistosome vectors or 'w' to indicate aguatic weeds.	freshwater snails that are schis	stosome vectors or 'W to	indicate acuatic weeds.	

^{ar}Targets are terrestrial snails unless followed by 's' to indicate freshwater snails that are schistosome vectors or 'W' to indicate aquatic weeds. ^bAdditional references, often numerous, are cited in the text; those listed here are the key references permitting entry into the literature.

"Wore details of specific locations, with references, are tabulated by Griffiths et al. (1993) (for Euglandina rosea only) and by Civeyrel and Simberloff (1996).

smaller size may mean that they can be transported inadvertently more easily than *E. rosea*. Every effort should be made to prevent the spread of all these predatory land snails.

Control of Achatina fulica is extremely difficult. Biological control using predatory snails does not work. Biological control using the predatory flatworm *Platydemus manokwari* may be successful but also places native snail faunas in grave danger (Hopper and Smith, 1992). A species-specific, non-molluscan biocontrol agent may exist, but as yet has not been discovered. Laborious hand-collecting of snails and expensive and environmentally questionable use of molluscicides may achieve some control. Promotion of the development of A. fulica as a human food resource as a means of control should not be countenanced as it will lead to further spread of the pest (Cowie, in press a). Prevention of introduction is obviously crucial. However, if A. fulica is introduced, eradication is possible if undertaken promptly (Colman, 1977, 1978; Mead, 1979; Anon., 1996). If the new introduction is not eradicated and the population expands, the only recourse may unfortunately be to simply wait for the inevitable subsequent decline, though this may take many years and may still not be sufficient to ameliorate pressure for control.

6.2. Rumina decollata for control of helicid land snails

There has been no rigorous scientific study demonstrating that Rumina decollata is able to control populations of Helix aspersa, or that it will not have an impact on populations of native (including endangered) snail species, the report by Fisher and Orth (1985) notwithstanding. As far as is known, it has not, as yet, had a serious impact on native species, but to assume that it will not in the future is potentially dangerous. Its continued promotion by official agencies as well as by the commercial suppliers of biocontrol agents to the general public has no adequate basis in science. Even with legal restrictions on its use (as in California), its ready availability through mail order, especially now over the internet, means that it will continue to be spread indiscriminately (sometimes illegally) by an ill-informed and receptive public. In general, and in this instance specifically. mail ordering of biological control agents should be much more tightly regulated (Simberloff and Stiling, 1996a). Even though R. decollata is already established widely in the USA this cannot justify its further deliberate spread.

At least in citrus groves in California, the major economic focus of control of helicids by Rumina decollata, a number of management techniques, including the use of molluscicide baits, have been recommended and considered successful (Integrated Pest Management Education and Publications Group, 1991). Molluscicides are widely available for use in domestic gardens/yards, though they also pose significant environmental problems and are expensive if used on a large scale, for instance against 'white snails' in Australia (Hopkins and Baker, 1993). Alternative biocontrol agents have been sought for helicids and other snail pests in Australia, including nematodes (Coupland, 1995) and predatory or parasitic flies (Coupland and Baker, 1994, 1995), with at least one of the fly species (Sarcophaga penicillata Villeneuve (Sarcophagidae)) perhaps being sufficiently host-specific to warrant further investigation (Carter and Baker, 1997; G.H. Baker, personal communication).

6.3. Ampullariids for control of aquatic weeds and snail vectors of schistosomes

As noted above, the ampullariid *Pomacea canaliculata*, although usually considered a voracious generalist, does indeed exhibit food preferences and in particular will not feed on water hyacinth (*Eichhornia crassipes*). It, and probably other ampullariids such as *Marisa cornuarietis*, should therefore not be considered as biocontrol agents against water hyacinth, certainly not without adequate prior testing.

Major ongoing international research programmes have developed integrated management strategies for aquatic weeds that include biological control involving host-specific insects (Harley et al., 1996; Julien et al., 1996; Lach, in press). Because of their voracious and relatively generalist feeding habits, ampullariids, especially the popular Marisa cornuarietis, should not become part of these weed control strategies, nor indeed be considered for control of schistosome snails. Their potential impacts on native biotas may be profound and far-reaching. Similarly, major international efforts to control schistosomiasis have been undertaken, in part involving snail control but also including a range of other management practices (e.g. Gaddal, 1985; Mott, 1987), including chemotherapy (i.e. treatment with drugs), environmental management and habitat modification, better management of sanitation and water supply; and public education should be expanded in order to inform people of the mechanism of transmission of the disease and how best to avoid contracting and spreading it. Although promoted as potential biocontrol agents against the snails, predatory flies also do not appear to be host-specific (Maharaj et al., 1992); and use of molluscicides is expensive, of limited efficacy, and also affects non-target native snail species (Herbert, 1998; Kristensen and Brown, 1999).

6.4. Thiarids for control of snail vectors of schistosomes

The two thiarid species used to date in biocontrol efforts against Biomphalaria glabrata in the Caribbean, Melanoides tuberculata and Tarebia granifera, are extremely widespread throughout the tropics and subtropics (Pace, 1973). Their distributions are probably expanding as they are inadvertently dispersed further by humans (Cowie and Robinson, submitted). The likelihood is that they will become ubiquitous in regions of suitable climate and occupy all suitable bodies of water. Arguing that it is only a matter of time before this happens, Prentice (1983) justified the introduction of Tarebia granifera to water bodies harbouring Biomphalaria glabrata in St Lucia. In general, although introduced deliberately to the specific biocontrol localities in the Caribbean, these thiarids were probably already present at other localities on these islands prior to the initiation of the biocontrol programmes, perhaps introduced via the aquatic plants trade (Pointier, 1989, 1999; Pointier et al., 1993). However, the fact that the further spread of these alien species seems inevitable, should not be invoked, against concerns regarding impacts on native ecosystems, to justify their deliberate introduction. Under that logic, all invasive species would simply be permitted to spread without any effort being made to halt that spread. In addition, these thiarids may be vectors of other human and animal parasites such as lung flukes (e.g. Prentice, 1983; Woodruff and Upatham, 1992;

Pointier, 1999), although this has been questioned by Michelson (1992) regarding *Tarebia granifera* as a vector of lung flukes. Again, alternatives should be sought in a range of management practices as mentioned above.

7. Conclusion

Biological control has often been considered as 'environmentally friendly' because it does not involve extensive use of pesticides that might be harmful to, for instance, human health. However, even the most harmful pesticides can be removed from the environment, although perhaps at huge cost. In principle, they are not permanent. Biocontrol agents, however, may be even more environmentally 'unfriendly' because of their impacts on non-target species and ecosystems, and because in almost all cases once they have been introduced they can never be removed. They become permanent components of the ecosystems into which they are introduced.

Snails, because of their usually rather generalist feeding preferences, will rarely be appropriate for use as biocontrol agents, notwithstanding recent, though diminishing, support for polyphagous biocontrol agents (cited by Miller and Aplet, 1993). In the past, ill-conceived biocontrol efforts using snails have had catastrophic effects on native biodiversity. Yet similar efforts are frequently still considered and even undertaken. The purpose of this paper has been to bring these issues regarding snails to the attention of a wider audience of pest management practitioners. While many of my examples (especially regarding control of *Achatina fulica*) come from islands, I do not believe that continental regions are immune from the non-target effects of snails used as biocontrol agents (cf. Simberloff, 1995).

I do not condemn all biological control efforts. Strong arguments can be made in certain instances that the potential but unknown damage that a biocontrol agent might have could not be worse than the damage being caused by the extremely invasive and damaging pest it is intended to control; and there are certainly examples of successful and safe biological control (OTA, 1995; Simberloff and Stiling, 1996b). Nevertheless, even in extreme situations like this, it remains axiomatic that adequate specificity testing be undertaken prior to release and that a thorough assessment of the suite of ecological consequences of release be undertaken. That this is extremely difficult to do (Miller and Aplet, 1993), I acknowledge, but the fact that it is so difficult endorses the potential complexity of the impacts of biocontrol agents.

There should therefore be better regulation of the future movement of snail species that appear to be effective biocontrol agents, taking due regard of their potential negative impacts (this might include *Marisa cornuarietis* and *Melanoides tuberculata*). Further import of species that are ineffective as biocontrol agents or that cause environmental harm should be discouraged or prohibited (e.g. *Euglandina rosea*). As a step in the right direction, various countries that have not previously regulated biocontrol introductions are becoming increasingly aware that regulation of this kind is necessary and are beginning to develop such regulation, or at least beginning to follow, for instance, the Food and Agriculture Organization of the United Nations (FAO) Code of Conduct on biological control introductions. Research remains necessary in some cases. For instance, *Rumina decollata* may be a pest under some circumstances, may have

negative environmental impacts under others, yet may sometimes be an effective biocontrol agent: what determines this? Thiarids may be effective in controlling schistosome snails, but what is the mechanism of control and how can it be predicted? Does reduction of populations of schistosome snails in fact reduce levels of human infection? Research investigating the causative linkages, as opposed to simply documenting correlations, between biocontrol agents and their putative effects, both positive and negative, is crucial. And in general, as has frequently been stated, pre-release testing of efficacy and potential impacts and post-release monitoring of efficacy and actual impacts should be required and the results adequately reported.

I concur with the views of Miller and Aplet (1993) and Simberloff and Stiling (1996b) that, because of their unpredictability and especially their irreversibility, all biological control efforts must be viewed as inherently risky, and that no project should be considered environmentally innocuous without substantial effort having been made to demonstrate that this is so.

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References

- ALDERSON, E.G., 1925. *Studies in* Ampullaria (Cambridge: Heffer), xx + 102 pp., 19 pll.
- ALICATA, J. E., 1969. Parasites of Man and animals in Hawaii (Basel: S. Karger), 190 pp.
- ALICATA, J. E., 1991. The discovery of Angiostrongylus cantonensis as a cause of human eosinophilic meningitis. *Parasitology Today*, 7, 151 – 153.
- ANON., 1989. IUCN commission blasts *Euglandina* introductions. *Hawaiian* Shell News, **37**(4), 11.
- ANON., 1996. Spread of giant African snail of great concern to the Pacific. Newsletter of the South Pacific Commission Agriculture Programme, 5(1), 3.
- ARMITAGE, H. M., 1949. Bureau of entomology. Thirtieth annual report. California Department of Agriculture Bulletin, 38, 157 – 216.
- BAKER, G. H., 1986. The biology and control of white snails (Mollusca: Helicidae), introduced pests in Australia. Commonwealth Scientific and Industrial Research Organization, Australia, Division of Entomology Technical Paper, 25, 1–31.
- BARBOSA, P. and BRAXTON, S., 1993. A proposed definition of biological control and its relationship to related control approaches. In R.D. Lumsden and J.L. Vaughn (eds) *Pest Management: Biologically Based Technolgies* (Washington, DC: American Chemical Society), pp. 21–27.
- BAYNE, C. J. and LOKER, E. S., 1987. Survival within the snail host. In D. Rollinson and A.J.G. Simpson (eds) *The biology of schistosomes. From genes to latrines* (London: Academic Press), pp. 321–346.
- BECKMANN, K.-H., 1989. Rumina decollata (L. 1758) in China. (Gastropoda: Pulmonata: Subulinidae). Schriften zur Malakozoologie aus dem Haus der Natur–Cismar, 2, 62.
- BEGON, M., HARPER, J. L. and TOWNSEND, C. R., 1986. Ecology (Oxford: Blackwell Scientific Publications), xii + 876 pp.

- BENNETT, F. D. and HUGHES, I. W., 1959. Biological control of insect pests in Bermuda. Bulletin of Entomological Research, 50, 423 – 436.
- BERTHOLD, T., 1991. Vergleichende anatomie, phylogenie und historische biogeographie der Ampullariidae (Mollusca, Gastropoda). Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF), 29, 1–256.
- BIELER, R. and SLAPCINSKY, J., A case study for the development of an island fauna: recent terrestrial mollusks of Bermuda. *Nemouria, Occasional Papers of the Delaware Museum of Natural History* (submitted).
- BROWN, D. S., 1978. Pulmonate molluscs as intermediate hosts for digenetic trematodes. In V. Fretter and J. Peake (eds) *Pulmonates. Volume 2A. Systematics, evolution and ecology* (London: Academic Press), pp. 287– 333.
- CARTER, P. J. and BAKER, G. H., 1997. Parasitic flies to reduce snail contamination. *Farming Ahead*, 69, 59.
- CAZZANIGA, N. J., 1981. Evaluación preliminar de un gasterópodo para el control de melezas acuáticas su sumergidas. In II Reunión sombre Malezas Subacuáticas en Canales de Desagüe de CORFO [Corporación de Fomento del Valle Bonaerense del Río Colorado] (La Plata: Comisión de Investigaciones Científicas de la Provincia de Buenos Aires), pp. 131– 165.
- CAZZANIGA, N. J. and ESTEBENET, A. L., 1984. Revisión y notas sombre los hábitos alimentarios de los Ampullariidae (Gastropoda). *Historia Natural*, 4, 213–224.
- CHRISTENSEN, C. C., 1984. Are Euglandina and Gonaxis effective agents for biological control of the giant African snail in Hawaii? American Malacological Bulletin, 2, 98–99.
- CIVEYREL, L. and SIMBERLOFF, D., 1996. A tale of two snails: is the cure worse than the disease? *Biodiversity and Conservation*, **5**, 1231 1252.
- CLARKE, B., MURRAY, J. and JOHNSON, M. S., 1984. The extinction of endemic species by a program of biological control. *Pacific Science*, 38, 97–104.
- COLMAN, P. H., 1977. An introduction of Achatina fulica to Australia. Malacological Review, 10, 77 – 78.
- COLMAN, P. H., 1978. An invading giant. Wildlife in Australia, 15, 46-47.
- COOK, A., 1985a. The organisation of feeding in the carnivorous snail *Euglandina rosea. Malacologia*, **26**, 183 – 189.
- COOK, A., 1985b. Functional aspects of trail following by the carnivorous snail *Euglandina rosea. Malacologia*, **26**, 173 – 181.
- COOK, A., 1989a. Factors affecting prey choice and feeding technique in the carnivorous snail *Euglandina rosea*. Journal of Molluscan Studies, 55, 469–477.
- COOK, A., 1989b. The basis of food choice by the carnivorous snail, *Euglandina* rosea. British Crop Protection Council Monographs, 41, 367 – 372.
- COOTE, T., LOEVE, E., MEYER, J.-Y. and CLARKE, D., 1999. Extant populations of endemic partulids on Tahiti, French Polynesia. *Oryx*, **33**, 215–222.
- CORY, J. S. and MYERS, J. H., 2000. Direct and indirect ecological effects of biological control. *Trends in Ecology and Evolution*, **15**, 137 – 139.
- COUPLAND, J. B., 1995. Susceptibility of helicid snails to isolates of the nematode Phasmarhabditis hermaphrodita from southern France. Journal of Invertebrate Pathology, 66, 207 – 208.
- COUPLAND, J. B. and BAKER, G. H., 1994. Host distribution, larviposition behaviour and generation time of Sarcophaga penicillata (Diptera: Sarcophagidae), a parasitoid of conical snails. Bulletin of Entomological Research, 84, 185 – 189.
- COUPLAND, J. B. and BAKER, G. H., 1995. The potential of several speices of terrestrial Sciomyzidae as biological control agents of pest helicid snails in Australia. *Crop Protection*, 14, 573–576.
- COWIE, R. H., 1992. Evolution and extinction of Partulidae, endemic Pacific island land snails. *Philosophical Transactions of the Royal Society of London* B, 335, 167 – 191.
- COWIE, R. H., 1996. Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution*, 49(6)[1995], 1191 – 1202.
- COWIE, R. H., 1997. Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. *Bishop Museum Occasional Papers*, 50, 1–66.
- COWIE, R. H., 1998a. Patterns of introduction of non-indigenous non-marine snails and slugs in the Hawaiian Islands. *Biodiversity and Conservation*, 7, 349–368.

- COWIE, R. H., 1998b. Predatory snails in Hawaii and the Pacific: biocontrol run amuck. World Conservation, quarterly bulletin of IUCN- The World Conservation Union, 4/97 – 1/98, 18.
- COWIE, R. H., 1998c. Catalog of the nonmarine snails and slugs of the Samoan Islands. *Bishop Museum Bulletins in Zoology*, **3**, i – viii, 1 – 122.
- COWIE, R. H., Non-indigenous land and freshwater molluscs in the islands of the Pacific: conservation impacts and threats. In G. Sherley (ed) *Invasive* species in the Pacific: a Technical Review and Regional Strategy (Apia: South Pacific Regional Environment Programme) (in press a).
- COWIE, R. H., Apple snails as agricultural pests: their biology, impacts and management. In G.M. Barker (ed) *Molluscs as Crop Pests* (Wallingford: CAB International) (in press b).
- COWIE, R. H. and COOK, R. P., Extinction or survival: partulid tree snails in American Samoa. *Biodiversity and Conservation* (in press).
- COWIE, R. H. and HOWARTH, F. G., 1998. Biological control: disputing the indisputable. Trends in Ecology and Evolution, 13, 110.
- COWIE, R. H. and ROBINSON, D. G., Pathways of introduction of nonindigenous land and freshwater snails and slugs In G. Ruiz and J.T. Carlton (eds) (submitted).
- CRAIG, A. K., 1973. A new record for *Liguus*: the Boynton Beach colony. *The Nautilus*, **87**, 83–85.
- CRAMPTON, H. E., 1916. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Tahiti. *Carnegie Institution of Washington Publication*, 228, 313 pp., 34 pll.
- CRAMPTON, H. E., 1925. Studies on the variation, distribution, and evolution of the genus *Partula*. The species of the Mariana Islands, Guam and Saipan. *Carnegie Institution of Washington Publication*, 228A, vii + 116 pp., 14 pll.
- CRAMPTON, H. E., 1932. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Moorea. *Carnegie Institution of Washington Publication*, 410, vi + 335 pp., 24 pll.
- CROOKS, J. and SOULÉ, M. E., 1996. Lag times in population explosions of invasive species: causes and implications. In O.T. Sandlund, P.J. Schei and A. Viken (eds) *Proceedings of the Norway/UN conference on alien species. Trondheim*, 1–5 July 1996 (Trondheim: Directorate for Nature Management and Norwegian Institute for Nature Research), pp. 39–46.
- DAVIS, C. J. and BUTLER, G. D., 1964. Introduced enemies of the giant African snail, Achatina fulica Bowdich, in Hawaii. Proceedings, Hawaiian Entomological Society, 18, 377 – 389.
- DEMIAN, E. S. and KAMEL, E. G., 1973. Effect of Marisa cornuarietis on Bulinus truncatus populations under semi-field conditions in Egypt. Malacologia, 14, 439.
- DUNDEE, D. S., 1974. Catalog of introduced molluscs of eastern North America (north of Mexico). *Sterkiana*, 55, 1 – 37.
- DUNDEE, D. S., 1986. Notes on the habits and anatomy of the introduced snails, *Rumina* and *Lamellaxis* (Subulinidae). *The Nautilus*, 100, 32–37.
- EHLER, L. E., 2000. Critical issues related to nontarget effects in classical biological control of insects. In P.A. Follett and J.J. Duan (eds) *Nontarget effects of biological control* (Norwell, Massachusetts: Kluwer Academic Publishers), pp. 3 – 13.
- EL GADDAL, A. A., 1985. The Blue Nile Health Project: a comprehensive approach to the prevention and control of water-associated diseases in irrigated schemes of the Sudan. *Journal of Tropical Medicine and Hygiene*, 88, 47–56.
- ESTEBENET, A. L., 1995. Food and feeding in *Pomacea canaliculata* (Gastropoda: Ampullariidae). *The Veliger*, **38**, 277 – 283.
- EWEL, J. J., O'DOWD, D. J., BERGELSON, J., DAEHLER, C. C., D'ANTONIO,
 C. M., GÓMEZ, L. D., GORDON, D. R., HOBBS, R. J., HOLT, A.,
 HOPPER, K. R., HUGHES, C. E., LAHART, M., LEAKEY, R. R. B., LEE,
 W. G., LOOPE, L. L., LORENCE, D. H., LOUDA, S. M., LUGO, A. E.,
 MCEVOY, P. B., RICHARDSON, D. M. and VITOUSEK, P. M, 1999.
 Deliberate introductions of species: research needs. *BioScience*, 49, 619–630.
- FISHER, T. W., 1966. *Rumina decollata* (Linnaeus, 1758) (Achatinidae) discovered in southern California. *The Veliger*, **9**, 16.
- FISHER, T. W., 1974. Miscellaneous observations on Rumina decollata (Linnaeus, 1758) (Achatinidae) and a request. The Veliger, 16, 334 – 335.
- FISHER, T. E. and ORTH, R. E., 1985. Biological control of snails. Occasional Papers, Department of Entomology, University of California , Riverside, 1, i-viii, 1–111.

- FISHER, T. W., ORTH, R. E. and SWANSON, S. C., 1980. Snail against snail. *California Agriculture*, November–December, 18–20.
- FOLLETT, P. A. and DUAN, J. J., 2000. Nontarget effects of biological control (Norwell, Massachusetts: Kluwer Academic Publishers), xiii + 316 pp.
- FRANDSEN, F. and MADSEN, H., 1979. A review of *Helisoma duryi* in biological control. Acta Tropica, 36, 67-84.
- FRANK, J. H., 1998. How risky is biological control? Comment. *Ecology*, 79, 1829 1834.
- GAMMON, E. T., 1943. Helicid snails in California. Bulletin of the State of California Department of Agriculture, **32**, 173 187.
- GARGOMINY, O., BOUCHET, P., PASCAL, M., JAFFRÉ, T. and TORNEUR, J.-C., 1996. Conséquences des introductions d'espèces animales et végétales sur la biodiversité en Nouvelle-Calédonie. *Revue d'Écologie* (*Terre et Vie*), **51**, 375–402.
- GOULD, S.J., 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail P. (Poecilozonites) in Bermuda. Bulletin of the Museum of Comparative Zoology, 138, 407 – 532.
- GOULD, S. J., 1991. Unenchanted evening. Natural History, 9/91, 4-14.
- GRIFFITHS, O., COOK, A. and WELLS, S. M, 1993. The diet of the carnivorous snail *Euglandina rosea* in Mauritius and its implications for threatened island gastropod faunas. *Journal of Zoology*, 229, 79–89.
- GUTIÉRREZ, A., PERERA, G., YONG, M. and FERNANDEZ, J. A., 1997. Relationships of the prosobranch snails *Pomacea paludosa, Tarebia granifera* and *Melanoides tuberculata* with the abiotic environment and freshwater snail diversity in the central region of Cuba. *Malacological Review*, 30, 39 – 44.
- HADFIELD, M G., 1986. Extinction in Hawaiian achatinelline snails. Malacologia, 27, 67–81.
- HADFIELD, M. G. and KAY, E. A., 1981. The multiple villainies of Euglandina rosea (or its human proponents). Hawaiian Shell News, 29(4), 5 – 6.
- HADFIELD, M. G. and MLLER, S. E., 1989. Demographic studies on Hawaii's endangered tree snails: *Partulina proxima. Pacific Science*, 43, 1 – 16.
- HADFIELD, M. G. and MOUNTAIN, B. S., 1981. A field study of a vanishing species, Achatinella mustelina (Gastropoda, Pulmonata), in the Waianae Mountains of Oahu. Pacific Science, 34, 345 – 358.
- HADFIELD, M. G., MILLER, S. E. and CARWILE, A. H., 1993. The decimation of endemic Hawai'ian [sic] tree snails by alien predators. *American Zoologist*, 33, 610–622.
- HANNA, G. D., 1966. Introduced mollusks of western North America. Occasional Papers of the California Academy of Sciences, 48, 1–108, pll. 1–4.
- HARIDI, A. A. M. and JOBIN, W. R., 1985. Estimated risks and benefits from introducing *Marisa cornuarietis* into the Sudan. *Journal of Tropical Medicine and Hygiene*, 88, 145–151.
- HARIDI, A. A. M, EL SAFI, S. H. and JOBIN, W. R., 1985. Survival, growth and reproduction of the imported ampullarid [sic] snail Marisa cornuarietis in central Sudan. Journal of Tropical Medicine and Hygiene, 88, 135 – 144.
- HARLEY, K. L. S., JULIEN, M. H. and WRIGHT, A. D., 1996. Water hyacinth: a tropical worldwide problem and methods for its control. In H. Brown, G.W. Cussans, M.D. Devine, S.O. Duke, C. Fernandez-Quintanilla, A. Helweg, R.E. Labrada, M. Landes, P. Kudsk and J.C. Streibig (eds) *Proceedings of the Second International Weed Control Congress, Copenhagen, 25–28 June 1996, volume II* (Slagelse, Denmark: Department of Weed Control and Pesticide Ecology), pp. 639–644.
- HERBERT, D. G., 1998. Molluscan conservation in South Africa: diversity, issues and priorities. *Journal of Conchology Special Publication*, 2, 61 – 76.
- HOKKANEN, H. M. T. and PIMENTEL, D., 1989. New associations in biological control: theory and practice. *The Canadian Entomologist*, **121**, 829–840.
- HOPKINS, D. C. and BAKER, G. H., 1993. Biological control of white and conical snails. In S.A. Corey, D.J. Dall and W.M. Milne (eds) *Pest control and sustainable agriculture* (Melbourne: CSIRO Information Services), pp. 246 – 249.
- HOPPER, D. R. and SMITH, B. D., 1992. Status of tree snails (Gastropoda: Partulidae) on Guam, with a resurvey of sites studied by H.E. Crampton in 1920. Pacific Science, 46, 77 – 85.
- HORNE, F. R., ARSUFFI, T. L. and NECK, R. W., 1992. Recent introduction and potential botanical impact of the giant rams-horn snail, *Marisa* cornuarietis (Pilidae), in the Comal Springs ecosystem of central Texas. *The Southwestern Naturalist*, 37, 194–196.

- HOSAKA, K.-I., 1996. Notes on the intrusion of three non-marine gastropods into Ube City, Yamaguchi Prefecture, western Japan, found in 1996. The Yuriyagai, Journal of the Malacozoological Association of Yamaguchi, 4, 191 – 194.
- HOWARTH, F. G., 1983. Biological control: panacea or Pandora's box? Proceedings of the Hawaiian Entomological Society, 24, 239 – 244.
- HOWARTH, F. G., 1991. Environmental impacts of classical biological control. Annual Review of Entomology, 36, 485 – 509.
- INTEGRATED PEST MANAGEMENT EDUCATION AND PUBLICATIONS GROUP, 1991. Integrated Pest Management for Citrus, 2nd edition (Oakland: University of California, Statewide Integrated Pest Management Project, Division of Agriculture and Natural Resources), 144 pp.
- JOBIN, W. R., BROWN, R. A., VÉLEZ, S. P. and FERGUSON, F. F., 1977. Biological control of *Biomphalaria glabrata* in major reservoirs of Puerto-Rico. *American Journal of Tropical Medicine and Hygiene*, 26, 1018– 1024.
- JOHNSON, M. S., MURRAY, J. and CLARKE, B., 1993. The ecological genetics and adaptive radiation of *Partula* on Moorea. Oxford Surveys in Evolutionary Biology, 9, 167 – 238.
- JOUBERT, C. J. and WALTERS, S. S., 1951. The control of snails and slugs. Farming in South Africa, 26, 379 – 380.
- JULIEN, M. H., HARLEY, K. L. S., WRIGHT, A. D., CILLIERS, C. J., HILL, M. P., CENTER, T. D., CORDO, H. A. and COFRANCESCO, A. F., 1996. International co-operation and linkages in the management of water hyacinth with emphasis on biological control. In V.C. Moran and J.H. Hoffmann (eds) Proceedings of the IX International Symposium on Biological Control of Weeds, 19–26 January 1996, Stellenbosch, South Africa (Capetown: University of Capetown), pp. 273–282.
- KEKAUOHA, W., 1966. Life history and population studies of Achatina fulica. The Nautilus, 80, 3-10, 39-46.
- KINZIE, R. A., III, 1992. Predation by the introduced carnivorous snail Euglandina rosea (Ferussac) on endemic aquatic lymnaeid snails in Hawaii. Biological Conservation, 60, 149 – 155.
- KONDO, Y., 1952. Report on carnivorous snail experiment on Agiguan Island; primary and secondary Achatina-free areas on Rota; and gigantism among Achatina on Guam. Unpublished report to the Pacific Science Board of the National Research Council (Honolulu: Bishop Museum).
- KRAUSS, N. L. H, 1964. Investigations on biological control of giant African (Achatina fulica) and other land snails. The Nautilus, 78, 21–27.
- KRISTENSEN, T. K. and BROWN, D. S., 1999. Control of intermediate host snails for parasitic diseases—a threat to biodiversity in African freshwaters? *Malacologia*, 41, 379–391.
- KRUATRACHUE, M and UPATHAM, E. S., 1993. Biological control of schistosomiasis-mediating snails in Thailand: simulated field experiments. *Journal of Medical and Applied Malacology*, 5, 117 – 128.
- LACH, L., Losses from aquatic weeds. In D. Pimentel (ed) *Encyclopedia of Pest Management* (New York: Marcel Dekker) (in press).
- LACH, L., BRITTON, D. K., RUNDELL, R. J. and COWIE, R. H., Food preference and reproductive plasticity in an invasive freshwater snail. *Biological Invasions* (submitted).
- LOCKWOOD, J. A., 1993. Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environmental Entomology*, 22, 503 – 518.
- LOKER, E. S., HOFKIN, B. V., MKOJI, G. M., MUNGAI, B., KIHARA, J. and KOECH, D. K., 1993. Distributions of freshwater snails in southern Kenya with implications for the biological control of schistosomiasis and other snail-mediated parasites. *Journal of Medical and Applied Malacology*, 5, 1–20.
- MAHARAJ, R., APPLETON, C. C. and MILLER, R. M., 1992. Snail predation by larvae of Sepedon scapularis Adams (Diptera: Sciomyzidae), a potential biocontrol agent of snail intermediate hosts of schistosomiasis in South Africa. Medical and Veterinary Entomology, 6, 183 – 187.
- MEAD, A. R., 1955. The proposed introduction of predatory snails into California. *The Nautilus*, 69, 37 40.
- MEAD, A. R., 1956. Predators need defending. The Nautilus, 70, 65-69.
- MEAD, A. R., 1961. The Giant African Snail: a problem in Economic Malacology (Chicago: University of Chicago Press), xvii + 257 pp., 6 pll.
- MEAD, A. R., 1979. Pulmonates volume 2B. Economic malacology with particular reference to Achatina fulica (London: Academic Press), x + 150 pp.

- MESSING, R. H., 2000. The impacts of nontarget concerns on the practice of biological control. In P.A. Follett and J.J. Duan (eds) *Nontarget effects of biological control* (Norwell, Massachusetts: Kluwer Academic Publishers), pp. 45–55.
- MICHELSON, E. H., 1992. Thiara granifera: a victim of authoritarianism. Malacological Review, 25, 67 – 71.
- MCHELSON, E. H. and DUBOIS, L., 1974. Lymnaea emarginata, a possible agent for the control of the schistosome-snail host, *Biomphalaria glabrata*. *The Nautilus*, 89, 101–108.
- MILLER, M. and APLET, G., 1993. Biological control: a little knowledge is a dangerous thing. *Rutgers Law Review*, 45, 285 – 334.
- MQUEL, S. E., PARENT, H. and SCARABINO, F., 1995. Achatinoidea introducidos en la Argentina y el Uruguay (Mollusca: Gastropoda: Stylommatophorida [sic]). *Neotrópica*, 41, 105–106.
- MONÉ, H., 1991. Influence of non-target molluscs on the growth of Biomphalaria glabrata infected with Schistosoma mansoni: correlation between growth and cercarial production. Journal of Molluscan Studies, 57, 1–10.
- MOTT, K. E., 1987. Schistosomiasis control. In D. Rollinson and A.J.G. Simpson (eds) *The biology of schistosomes. From genes to latrines* (London: Academic Press), pp. 431–450.
- MURDOCH, W. W. and BRIGGS, C. J., 1996. Theory for biological control: recent developments. *Ecology*, 77, 2001 – 2013.
- MURRAY, J., MURRAY, E., JOHNSON, M. S. and CLARKE, B., 1988. The extinction of *Partula* on Moorea. *Pacific Science*, 42, 150–153.
- NECK, R. W., 1984. Occurrence of the striped ram's horn snail, Marisa cornuarietis, in central Texas (Ampullariidae). The Nautilus, 98, 119–120.
- NGUMA, J. F. M., MCCULLOUGH, F. S. and MASHA, E., 1982. Elimination of Biomphalaria pfeifferi, Bulinus tropicus and Lymnaea natalensisby the ampullarid [sic] snail, Marisa cornuarietis, in a man-made dam in northern Tanzania. Acta Tropica, 39, 85 – 90.
- NISHIDA, T. and NAPOMPETH, B., 1975. Effect of age-specific predation on age distribution and survival of the giant African snail, *Achatina fulica*. *Proceedings, Hawaiian Entomological Society*, 22, 119–123.
- OKUMA, M., TANAKA, K. and SUDO, S., 1994. Weed control method using apple snail (*Pomacea canaliculata*) in paddy fields. Weed Research, Japan, 39, 114 – 119.
- PACE, G. L., 1973. The freshwater snails of Taiwan (Formosa). *Malacological Review Supplement*, 1, 1–118.
- PEEBLES, C. R., OLIVER-GONZÁLEZ, J. and FERGUSON, F. F., 1972. Apparent adverse effect of *Marisa cornuarietis* upon *Lymnaea columella* and *Biomphalaria glabrata* in an ornamental pond in Puerto Rico. *Proceedings, Hawaiian Entomological Society*, 21, 247 – 256.
- PEMBERTON, C. E., 1938. The giant African snail Achatina fulica (Fér.) discovered in Hawaii. The Hawaiian Planters' Record, 42, 135 – 140.
- PEMBERTON, C. E., 1956. Defense of a predator. The Nautilus, 69, 142-144.
- PERERA, G. and WALLS, J. G., 1996. Apple Snails in the Aquarium (Neptune City, New Jersey: TFH Publications, Inc.), 121 pp.
- PERERA, G., YONG, M and FERRER, J., 1993. Biological control of snail intermediate hosts by competitor thiarid snails in Cuba. *Journal of Medical* and Applied Malacology, 5, 97 – 101.
- POINTIER, J. P., 1989. Comparison between two biological control trials of Biomphalaria glabrata in a pond in Guadeloupe, French West Indies. Journal of Medical and Applied Malacology, 1, 83–95.
- POINTIER, J. P., 1999. Invading freshwater gastropods: some conflicting aspects for public health. *Malacologia*, **41**, 403 411.
- POINTIER, J. P. and BLANC, C., 1982. *Achatina fulica* dans les îles de la Société. Unpublished report, Museum National d'Histoire Naturelle, École Pratique des Hautes Études, Antenne de Tahiti.
- POINTIER, J. P. and BLANC, C., 1984. Achatina fulica en Polynésie française. Unpublished report, Museum National d'Histoire Naturelle, École Pratique des Hautes Études, Antenne de Tahiti.
- POINTIER, J. P. and GUYARD, A., 1992. Biological control of the snail intermediate hosts of *Schistosoma mansoni* in Martinique, French West Indies. *Tropical Medicine and Parasitology*, 43, 98–101.
- POINTIER, J. P., THÉRON, A. and IMBERT-ESTABLET, D., 1988. Decline of a sylvatic focus of *Schistosoma mansoni* in Guadeloupe (French West Indies) following competitive displacement of the snail host *Biomphalaria* glabrata by Ampullaria glauca. Oecologia, 75, 38–43.

- POINTIER, J. P., GUYARD, A. and MOSSER, A., 1989. Biological control of Biomphalaria glabrata and B. straminea by the competitor snail Thiara tuberculatain a transmission site of schistosomiasis in Martinique, French West Indies. Annals of Tropical Medicine and Parasitology, 83, 263 – 269.
- POINTIER, J. P., BALZAN, C., CHROSCIECHOWSKI, P. and INCANI, R. N., 1991a. Limiting factors in biological control of the snail vectors of schistosomiasis in Venezuela. *Journal of Medical and Applied Malacology*, 3, 53 – 67.
- POINTIER, J. P., THÉRON, A., IMBERT-ESTABLET, D. and BOREL, G., 1991b. Eradication of a sylvatic focus of *Schistosoma mansoni* using biological control by competitor snails. *Biological Control*, 1, 244 – 247.
- POINTIER, J. P., THÉRON, A. and BOREL, G., 1993. Ecology of the introduced snail *Melanoides tuberculata* (Gastropoda: Thiaridae) in relation to *Biomphalaria glabrata*in the marshy forest zone of Guadeloupe, French West Indies. *Journal of Molluscan Studies*, 59, 421 – 428.
- POINTIER, J. P., INCANI, R. N., BALZAN, C., CHROSCIECHOWSKI, P. and PRYPCHAN, S., 1994. Invasion of the rivers of the littoral central region of Venezuela by Thiara granifera and Melanoides tuberculata (Mollusca: Prosobranchia: Thiaridae) and the absence of Biomphalaria glabrata, snail host of Schistosoma mansoni. The Nautilus, 107, 124–128.
- PRENTICE, M. A., 1983. Displacement of Biomphalaria glabrata by the snail Thiara granifera in field habitats in St. Lucia, West Indies. Annals of Tropical Medicine and Parasitology, 77, 51 – 59.
- ROBINS, C. H., 1971. Ecology of the introduced snail, *Marisa cornuarietis* (Ampullariidae) in Dade County, Florida. *The Biologist*, **53**, 136 – 152.
- ROBINSON, D. G., 1999. Alien invasions: the effects of the global economy on non-marine gastropod introductions into the United States. *Malacologia*, 41, 413–438.
- ROLLINSON, D. and SIMPSON, A. J. G. (eds), 1987. The biology of schistosomes. From genes to latrines (London: Academic Press), xii + 472 pp.
- ROLLINSON, D. and SOUTHGATE, V. R., 1987. The genus Schistosoma a taxonomic appraisal. In D. Rollinson and A.J.G. Simpson (eds) The biology of schistosomes. From genes to latrines (London: Academic Press), pp. 1–49.
- ROTH, B., HERTZ, C. M. and CERUTTI, R., 1987. White snails (Helicidae) in San Diego County, California. *The Festivus*, **19**, 84–88.
- SAILER, R. I., 1978. Our immigrant insect faunas. Bulletin of the Entomological Society of America, 24, 3–11.
- SAKOVICH, N. J., 1996. An integrated pest management (IPM) approach to the control of the brown garden snail, (*Helix aspersa*) in California citrus orchards. British Crop Protection Council Symposium Proceedings, 66, 283–287.
- SELANDER, R. K, KAUFMAN, D. W. and RALIN, R. S., 1974. Self-fertilization in the terrestrial snail *Rumina decollata*. *The Veliger*, **16**, 265–270.
- SIH, A., ENGLUND, G. and WOOSTER, D., 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, **13**, 350–355.

SIMBERLOFF, D., 1986. Introduced insects: a biogeographic and systematic perspective. In H.A. Mooney and J.A. Drake (eds) *Ecology of Biological Invasions of North America and Hawaii* (New York: Springer), pp. 3–26.

- SIMBERLOFF, D., 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science*, 49, 87 – 97.
- SIMBERLOFF, D. and STILING, P., 1996a. How risky is biological control? Ecology, 77, 1965 – 1974.
- SIMBERLOFF, D. and STILING, P., 1996b. Risks of species introduced for biological control. *Biological Conservation*, 78, 185 – 192.
- SIMBERLOFF, D. and STILING, P., 1998. How risky is biological control? Reply. Ecology, 79, 1834 – 1836.

SIMMONDS, F. J. and HUGHES, I. W., 1963. Biological control of snails exerted by Euglandina rosea (Ferussac) in Bermuda. Entomophaga 8, 219 – 222.

SOLEM, A., 1990. How many Hawaiian land snail species are left? and what we can do for them. *Bishop Museum Occasional Papers*, **30**, 27 – 40.

- STONE, R., 1999. Keeping paradise safe for the natives. Science, 285, 1837.
- STRONG, D. R., 1997. Fear no weevil? Science, 277, 1058 1059.
- TAKEUCHI, K., KOYANO, S. and NUMAZAWA, K., 1991. Occurrence of the giant African snail in the Ogasawara (Bonin) Islands, Japan. *Micronesica Supplement*, 3, 109 – 116.
- THOMAS, K. J., 1975. Biological control of Salvinia by the snail *Pila globosa* Swainson. *Biological Journal of the Linnean Society*, 7, 243 – 247.

- THOMAS, M. B. and WILLIS, A. J., 1998. Biocontrol-risky but necessary? Trends in Ecology and Evolution, 13, 325 - 329.
- TILLIER, S. and CLARKE, B. C., 1983. Lutte biologique et destruction du patromoine génétique: le cas des mollusques gastéropodes pulmonés dans les territoires français du Pacifique. Génétique, Sélection, Évolution, 15, 559 – 566.
- US CONGRESS, OFFICE OF TECHNOLOGY ASSESSMENT [OTA], 1995. Biologically Based Technologies for Pest Control (Washington, DC: US Government Printing Office), x + 204 pp.
- VAN DER SCHALIE, H., 1969. Man meddles with nature— Hawaiian style. The Biologist, 51, 136 – 146.
- VOSS, R. S., 1976. Observations on the ecology of the Florida tree snail, Liguus fasciatus (Müller). The Nautilus, 90, 65–69.
- WADA, T., 1997. Introduction of the apple snail Pomacea canaliculata and its impact on rice agriculture. In Proceedings. International Workshop on Biological Invasions of Ecosystems by Pests and Beneficial Organisms (Tsukuba: National Institute of Agro-Environmental Sciences, Ministry of Agriculture, Forestry and Fisheries), pp. 170 – 180.

- WALLACE, G. D. and ROSEN, L., 1969. Studies on eosinophilic meningitis V. Molluscan hosts of Angiostrongylus cantonensis on Pacific Islands. American Journal of Tropical Medicine and Hygiene, 18, 206 – 216.
- WATERHOUSE, D. F. and NORRIS, K. R., 1987. Biological Control. Pacific Prospects (Melbourne: Inkata Press), viii + 454 pp.
- WOODRUFF, D. S. and UPATHAM, E. S., 1992. Snail-transmitted diseases of medical and veterinary importance in Thailand and the Mekong Valley. *Journal of Medical and Applied Malacology*, 4, 1–12.
- WOODRUFF, D. S., CARPENTER, M. P., UPATHAM, E. S. and VIYANANT, V., 1999. Molecular phylogeography of Oncomelania lindoensis (Gastropoda: Pomatiopsidae), the intermediate host of Schistosoma japonicum in Sulawesi. Journal of Molluscan Studies, 65, 21 – 31.