



# Potential Impacts of Introduced Fish and Fish Translocations on Australian Amphibians

Graeme Gillespie<sup>1</sup> and Jean-Marc Hero<sup>2</sup>

## ABSTRACT

**This review examines the potential impact of introduced fish on amphibians, with particular emphasis on Australian freshwater systems. Firstly, the ecological relationships between fish predators and their amphibian prey are examined, and how they can be altered when non-native fish are introduced into aquatic systems. The current knowledge and research on the impacts of introduced fish on amphibians both overseas and within Australia is then reviewed. Evidence in the literature strongly suggests that introduction of exotic fish or translocation of native species could have enormous impacts on the amphibian assemblages of Australian freshwater systems.**

**Introduced fish have been implicated in the decline of several anuran species, though few cases have been**

**subject to thorough research. Many Australian amphibian assemblages, including several threatened species, are potentially threatened by a variety of introduced fish species. Future research priorities and guidelines for examining the impact of introduced fish on Australian amphibians are outlined. Key management objectives for conservation agencies are identified.**

## INTRODUCTION

The reported declines of many amphibian populations both in Australia and around the world are now recognised as a very real phenomenon. These declines pose a serious threat to global amphibian diversity, and may result from recent global environmental change associated with human activities. The cause(s) of many species declines, particularly in apparently pristine tropical forests of Central America and Australia, remain obscure (but see Lips 1998). However, in many cases one or other anthropogenic impacts, commonly identified as key threatening processes in the decline or extinction of other vertebrates (Meffe and Carroll 1994;

1. Arthur Rylah Institute, Department of Natural Resources and Environment, PO Box 137, Heidelberg, Victoria 3084 Australia.

2. School of Applied Science, Griffith University Gold Coast, PMB 50 Gold Coast MC, Queensland 4127 Australia.

Leakey and Lewin 1995), are associated with observed declines. These include habitat destruction (Laan and Verboom 1990; Johnson 1992; Wardell-Johnson and Roberts 1991; Gillespie and Hollis 1996; Dubuis 1997; Waldick 1997), pollution (Bishop 1992; Bidwell and Gorrie 1995; Bertram and Berrill 1997), over-exploitation (Jennings and Hayes 1985) and introduction of exotic predators (Orchard 1992; Bradford *et al.* 1993; Lannoo *et al.* 1994). In Australia, anthropogenic impacts on amphibian populations are only now beginning to be appreciated. The relative significance of various potentially threatening processes to the maintenance of many amphibian communities is poorly understood. This is a reflection in part of the inherent difficulties associated with studying amphibian population dynamics, the high diversity of amphibian assemblages present in Australia, and the small number of ecologists and amount of resources available for studying them. Decisions of research and management priorities and allocation of resources must therefore be based upon careful assessments of current knowledge about the importance of all potentially threatening processes, from both within Australia and overseas.

After over-exploitation and habitat destruction, introduced predators have been identified as the main cause of mammal and bird species extinctions in modern times, particularly in Australasia (Meffe and Carroll 1994; Leakey and Lewin 1995). It is likely that introduced predators may also play a significant role in the decline of some amphibian species. The following review examines the potential impact of introduced fish on amphibians, with particular emphasis on Australian freshwater systems. Firstly, we examine the ecological relationships between fish predators and their amphibian prey, and how these may be altered when non-native fish are introduced. We then review current knowledge and research on the impacts of introduced fish on amphibians both overseas and within Australia. Finally, we outline future research priorities and guidelines for examining the impact of introduced fish on Australian amphibians, and identify key management objectives.

## **SIGNIFICANCE OF FISH PREDATORS IN AMPHIBIAN COMMUNITIES**

Predation is considered to be a major factor regulating the distribution of amphibian larvae (e.g. Calef 1973, Heyer *et al.* 1975, Duellman 1978, Scott and Limerick 1983, Smith 1983, Woodward 1983, Wilbur 1984, Hayes and Jennings 1986, Kats *et al.* 1988). Heyer *et al.* (1975) suggested that predation by aquatic predators, primarily fish, was the most important biotic factor influencing the temporal and spatial composition of tadpole communities. The combined direct and indirect effects of fish predators on the local distribution of individual species of tadpole consequently influence local and regional amphibian assemblage structure. Recent studies have demonstrated the importance of fish predators in determining tadpole species-composition (species present) and tadpole species richness (number of species) in temperate (Hecnar and M'Closkey 1997) and tropical systems (Fickling 1995; Hero *et al.* 1988). In this section, we examine the ecological relationships between fish predators and their amphibian prey and how these may be altered when non-native fish are introduced.

Fish may directly impact amphibian species by predation on larvae (Macan 1966; Heyer *et al.* 1975; Sih *et al.* 1988) or eggs (Grubb 1972). Consequently fish predators are capable of eliminating larval amphibian species from some habitats (Tyler 1963, Macan 1974, Petranka 1983). In a comprehensive study by Petranka (1983) the larvae of the salamander *Ambystoma texanum* were found to be restricted to the fish-free, upper portions of breeding streams and this was attributed to predation on larvae by endemic species of fish. Kats *et al.* (1988) identified fish predation as a primary factor influencing marked differences between larval amphibian assemblages in ephemeral and permanent aquatic habitats. Similarly, Fickling (1995) found that *Litoria nannotis* and *L. rheocola* were restricted to streams without predatory fish in the Tully gorge, northern Australia.

## **TADPOLE SURVIVAL STRATEGIES**

Amphibian larvae can physically evade fish predators through spatial or temporal avoidance (Petranka 1983, Bradford 1989, Holomuzki 1995, Hecnar and M'Closkey 1997, Hero *et al.* 1998). Many species of amphibian breed only in temporary water bodies in which fish are absent. Recent studies have shown that females of some species of amphibian choose oviposition sites in waterbodies without fish (Resetarits and Wilbur 1989; Kats and Sih 1992; Bronmark and Edenhamn 1994; Hopey and Petranka 1994; Holomuzki 1995). Alternatively, amphibians can avoid fish predators by reproducing in a waterbody at times when fish predators are absent (e.g. streamside ponds that are isolated from the stream at some times of the year).

The larvae of many amphibian species occur in habitats containing predatory fish, such as permanent lakes and streams. Survival or anti-predator strategies allow these species to coexist with fish predators. These strategies include cryptic colouration (Wasserug 1971), behavioural responses such as use of refugia (Sih *et al.* 1988), schooling (Waldman 1982; Kruse and Stone 1984), protean flight (Taylor 1983), and chemical defences (Liem 1961; Wasserug 1971; Brodie *et al.* 1978; Kruse and Stone 1984; Kats *et al.* 1988; Werner and McPeck 1994). In contrast to species which typically occur in fish-free habitats, larvae of species which coexist with fish predators may possess one or a combination of these survival traits (Kats *et al.* 1988). Many amphibian larvae which coexist with predacious fish are unpalatable or noxious (Liem 1961; Voris and Bacon 1966; Wasserug 1971; Brodie *et al.* 1978; Walters 1975; Kruse and Stone 1984; Kats *et al.* 1988; Hero 1991; Werner and McPeck 1994). Amphibian larvae which do not respond behaviourally to predatory fish are typically toxic or unpalatable to fish (Voris and Bacon 1966; Kruse and Fransis 1977; Kruse and Stone 1984; Kats *et al.* 1988). Antipredator strategies used by tadpole species against invertebrate predators, such as immobility (Azevedo-Ramos *et al.* 1992; Chovanec 1992; Werner and McPeck 1994) are not usually effective against fish predators that use visual cues (Hero 1991; Werner and McPeck 1994). Therefore the distribution of each larval amphibian species is related to the survival strategies it possesses and is strongly influenced by the distribution of predatory fish.

## PREDICTED IMPACTS OF INTRODUCED PREDATORS

Predator-prey relationships are maintained by a constant evolution of both the predator to capture and the prey to avoid capture, commonly described as the “evolutionary arms race” (Dawkins and Krebs 1979). Survival strategies tend to be predator specific and are unlikely to be effective against all predators. For example, female amphibians may not be able to recognise the chemical cues produced by introduced fish species and may inadvertently oviposit in a water body with exotic fish predators, resulting in levels of predation that preclude survival of the species. Palatability of a species of tadpole can differ among different species of fish predator (Hero 1991; Holomuzki 1995). Hence, a species of tadpole may be unpalatable to the native fish predators with which it coexists, but may not be unpalatable to a novel fish predator. Prey species may not identify introduced fish as predators and hence fail to use the appropriate survival strategies (temporal or spatial isolation), or the species of tadpole may not have the necessary antipredator defences that allow them to coexist with introduced fish species. The introduction of an exotic predator is therefore likely to disrupt the arms race in favour of the predator.

Fish predators can also influence tadpole assemblages indirectly by consuming invertebrate tadpole-predators, such as dragonfly naiads and predacious diving beetles (Wilbur and Fauth 1990; Werner and McPeck 1994; Hero *et al.* 1998). Along an environmental gradient Werner and McPeck (1994) found that only *Rana catesbiana* tadpoles were found in waterbodies with fish predators while *R. clamitans* was found primarily in fishless ponds with high densities of invertebrate predators. Furthermore, the presence of fish predators can reduce densities of some species of tadpole, and this may release other species from competition, thus enhancing their survival (Morin 1986; Werner and McPeck 1994). This predator mediated release from competition may result in a shift in species composition from species that are competitively dominant to species that are competitively inferior but have the survival strategies that allow them to coexist with fish.

The general pattern observed in natural systems is that species of tadpole that are vulnerable to predation by invertebrate predators survive in waterbodies with fish (where the density of invertebrate predators is low due to predation by fish), and species of tadpole that are vulnerable to predation by fish survive in waterbodies where predacious fish are absent (Hecnar and M'Closkey 1997; Hero *et al.* 1988). The introduction of predacious fish species will potentially result in the elimination of some tadpole species and a shift in the species composition to those species which have the survival-strategies that allow them to coexist with the introduced predator.

Theory therefore predicts that the introduction of exotic fish to aquatic systems may lead to the elimination of some species of tadpole, resulting in changes in the species composition of natural tadpole assemblages. These changes may be extremely detrimental to the long term survival of some species, undermine amphibian communities and disrupt natural aquatic systems.

## OVERSEAS EVIDENCE FOR IMPACTS OF INTRODUCED FISH ON AMPHIBIANS

The consequences of introducing fish into breeding habitats for amphibians have been well documented overseas. A number of studies in Europe, North and South America have implicated or demonstrated that introductions of predatory fish are responsible for the decline or extinction of some amphibian species.

Brönmark and Edenhamn (1994) suggest that, in Europe, the widespread introduction of various fish species into farm dams and ponds has contributed to the decline of *Hyla arborea*. They found that *H. arborea* in Sweden was predominantly restricted to ponds in which fish had not been introduced. No reproduction was recorded during a three year period in ponds containing either pike (*Esox lucius*), perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), Crucian carp (*Carassius carassius*), rudd (*Scardinius erythrophthalmus*) or tench (*Tinca tinca*). Pike (*Esox lucius*), perch, and Crucian carp have been shown in laboratory studies to readily feed on *H. arborea* tadpoles and metamorphs (Brönmark unpublished, in Brönmark and Edenhamn 1994).

Macan (1966) reported a dramatic decrease in numbers of bufonid and ranid tadpole species following the introduction of brown trout (*Salmo trutta*) into a British tarn. Braña *et al.* (1996) found that amphibian species' numbers and amphibian abundance were significantly lower in lakes of northern Spain containing introduced fish: brown trout, rainbow trout (*Oncorhynchus mykiss*), tench, roach and European minnow (*Phoxinus phoxinus*). They concluded that the presence of these introduced species was responsible for the almost complete disablement of large permanent waterbodies for amphibian reproduction and subsequent decline of amphibian species in the region.

In North America the introduction of salmonids into previously fishless habitats has impacted upon numerous amphibian species. Burger (1950) reported the wide scale elimination of tiger salamander (*Ambystoma tigrinum*) larvae from ponds in Colorado following stocking with trout. Fish introductions, primarily trout, have been suggested as an important factor contributing to the decline of ranid frog species (Hayes and Jennings 1986; Liss and Larson 1991; Hecnar and M'Closky 1996). Several species of introduced salmonids have profoundly affected the distribution of the Mountain Yellow-legged Frog (*Rana mucosa*) within the past century by eliminating the species from nearly all waters where fish have been introduced (Grinnell and Storer 1924; Bradford 1989; Bradford *et al.* 1993). Hayes and Jennings (1986) noted that the abundance of endemic *Rana* species in California was inversely correlated with densities of introduced fish species, primarily trout. Tyler *et al.* (1998) demonstrated that larval salamanders (*Ambystoma macrodactylum*) were found in much higher densities in alpine lakes without fish than in lakes that contained introduced trout populations.

In Canada Liss and Larson (1991) reported the decline of amphibian species in naturally fishless lakes after stocking with trout. Hecnar and M'Closkey (1996) concluded that the presence of introduced predatory fish was responsible for the decline of amphibian species in south-western Ontario. They

found that amphibian species richness was significantly lower in ponds containing introduced predatory fish. However, those amphibian species with either large larval body size or large clutch size were less adversely affected than others, and occurred more frequently with predatory fish.

The introduction or translocation of other species has also been implicated in the decline of some amphibian species in North America. Introduced mosquitofish (*Gambusia spp.*) have been identified as the most likely cause of localised declines of Californian newts (*Taricha torosa*) in southern California (Gamradt and Kats 1996). Petranka (1983) documented decimation of small-mouthed salamander (*Ambystoma texanum*) larvae in local pools in streams following colonisation by Green Sunfish (*Lepomis cyanellus*), and Sexton and Phillips (1986) noted a dramatic reduction in species richness after the introduction of this species. Semlitsch (1983) reported almost complete mortality of *Rana esculenta* tadpoles following the addition of Pike to experimental ponds.

Declines of some amphibians in South America have also been attributed to introduced fish. The introduction of various fish species: salmonids, European carp (*Cyprinus carpio*), *Odonthestes bonariensis* and catfish (*Ictalurus spp.*), is thought to be a principal factor leading to the decline of

amphibians in southern Chile (Formas 1995). Introduced salmonids are also thought to be responsible for the extinction of several *Atelopus* species in Costa Rica (Pough *et al.* 1998).

In most of the above cases, fish introductions have occurred for recreational purposes. Hence, the frequent reports involving trout species, which have been widely introduced in lakes and streams throughout both hemispheres due to their popularity with anglers. It should be emphasized that translocation of native fish species into aquatic systems that have not previously contained the species could have similar impacts on amphibian fauna.

## INTRODUCED FISH IN AUSTRALIA

The list of fish introduced into Australia is extensive (Table 1). At least 24 exotic species have established self-sustaining populations in Australian freshwater systems to date. In addition, several native species have been translocated into aquatic systems in which they did not naturally occur. These include Murray cod (*Maccullochella peelii*), golden perch (*Macquaria ambigua*), Macquarie perch (*M. australasica*), bass (*M. novemaculeata*), barramundi (*Lates calcarifer*), catfish (*Tandanus tandanus*) and rainbow fish (*Melanotaenia spp.*) (Raadik, Arthur Rylah Institute (ARI), Victoria, pers. comm.).

**TABLE 1: List of exotic fish which have established populations in Australian waters.**

Species	Origin	Occurrence in Australia
<b>Salmonidae</b>		
Rainbow Trout	<i>Oncorhynchus mykiss</i>	Nth. America
Chinook Salmon	<i>O. tshawytscha</i>	Nth. America, N.E. Asia
Brook Trout	<i>Salmo fontinalis</i>	Nth. America
Atlantic Salmon	<i>S. salar</i>	Europe, Nth America
Brown Trout	<i>S. trutta</i>	Europe, West Asia
<b>Cyprinidae</b>		
Goldfish	<i>Carassius auratus</i>	East Asia
European Carp	<i>Cyprinus carpio</i>	Europe
Rosy Barb	<i>Puntius conchonius</i> *	Asia
Roach	<i>Rutilus rutilus</i>	Europe
Tench	<i>Tinca tinca</i>	Europe, Central Asia
<b>Percidae</b>		
Redfin Perch	<i>Perca fluviatilis</i>	Europe, Nth. Asia
<b>Poecilidae</b>		
gambusia (Mosquito Fish)	<i>Gambusia holbrooki</i>	Nth. America
One-spot Livebearer	<i>Phalloceros caudimaculatus</i>	Sth. America
Sailfin Molly	<i>Poecilia latipinna</i>	Cent. America
Guppy	<i>P. reticulata</i>	Cent. America, Caribbean
Swordtail	<i>Xiphophorus helleri</i>	Cent. America
Platy	<i>X. maculatus</i>	Cent. America
<b>Cyprinodontidae</b>		
American Flag Fish	<i>Jordanella floridae</i>	Nth. America
<b>Cobitidae</b>		
Oriental Weatherloach	<i>Misgurnus anguillicaudatus</i>	East Asia
<b>Cichlidae</b>		
Blue Acara	<i>Aequidens pulcher</i>	Cent. America
Convict Cichlid	<i>Heros nigrofasciata</i>	Cent. America
Mozambique Mouthbrooder	<i>Oreochromis mossambicus</i>	East Africa
Black Mangrove Cichlid	<i>Tilapia mariae</i>	West Africa
Zilles Cichlid	<i>T. zillii</i> *	Africa

\* Species which established populations that either died out or were successfully removed. (Sources: Allen 1982; Cadwallader and Backhouse 1982; McKay 1984; Allen 1989; Faragher and Harris 1993; Arthington and Blühdorn 1995; Ryan 1995; McDowall 1996).

Introductions have occurred primarily either for recreational fishing purposes, or through releases of species from the aquarium trade. The one exception is the eastern gambusia or mosquito fish (*Gambusia holbrooki*), which was misguidedly introduced to control mosquitoes (Myers 1965).

Salmonids have been widely introduced into streams and lakes for recreational fishing. The brown trout and rainbow trout are the most successful and widespread species. These occur in mainland streams along the Dividing Range from Victoria up to northern NSW, in the Adelaide Hills and in south-western Western Australia (Allen 1982, 1989; McDowall 1996). In south eastern Australia, brown trout are abundant in all upland streams and are only excluded from a few small tributaries where waterfalls have blocked their upstream passage (Cadwallader and Backhouse 1982; Faragher and Harris 1993; McDowall 1996). Rainbow trout have a more patchy distribution but are in high abundance in many small upland water courses (McDowall 1996; Victorian Fish Database, ARI, Victoria). Both species also occur in many lakes and reservoirs in these regions. Stocking of lakes and streams occurs extensively in NSW, and several lakes are stocked in Victoria by Fisheries authorities. These species are also stocked in farm dams. Brook trout have established in Tasmania in lakes of the Tyndall Ranges (McDowall 1996), the Clarence Lagoon on the Central Plateau (Swain, University of Tasmania, pers. comm.), and are currently restricted to one stream on the mainland in Kosciuszko National Park, NSW (Harris, NSW Fisheries, pers. comm.). Chinook salmon are currently restricted to several lakes in south-western Victoria, maintained by stocking (McDowall 1996). Atlantic salmon are stocked in lakes and reservoirs in south-eastern NSW, central Victoria and Tasmania (McDowall 1996). The species has escaped from hatcheries into the Rubicon and Latrobe Rivers in Victoria (McDowall 1996).

Goldfish and European carp were originally introduced as ornamental fish and have spread throughout the Murray-Darling system and other inland and coastal waterways in south-eastern Australia (Cadwallader and Backhouse 1982; Faragher and Harris 1993; McDowall 1996). They also occur in south-western Western Australia (Allen 1982, 1989) and Tasmania (Swain pers. comm.). Tench and roach were introduced in the late 1800's into lakes and rivers in Victoria for fishing and have both spread. Movements of roach have also been recorded up rivers feeding lakes, such as the Howqua and Big Rivers in the catchment of Lake Eildon, Victoria (Victorian Fish Database, ARI, Victoria). Introductions of roach still occur illegally for coarse fishing. Tench have also been stocked for fishing in lakes and reservoirs in southern NSW and Tasmania.

Redfin have been widely introduced throughout the Murray-Darling River system, lakes and farm dams in south-eastern mainland Australia, Tasmania and south-western Western Australia as a popular angling species (Allen 1982, 1989; Rowland 1989; McDowall 1996). This species has also penetrated up major tributaries of some lakes, in some cases considerable distances, such as Eildon and Glenmaggie in Victoria (Victorian Fish database, ARI, Victoria).

*Gambusia* are widespread throughout south-eastern Australia, including the Murray-Darling system, and extend up the east coast as far as Townsville. It also occurs in south-western WA and some water courses near Alice Springs (Allen 1982, 1989; McDowall 1996). The species is exceptionally hardy and is able to tolerate an extremely broad range of environmental conditions (McKay 1984). It is a highly invasive species inhabiting marshes, lakes and dams, slow-flowing streams and associated billabongs and aqueducts. It is most abundant in modified habitats and areas near human settlement (Allen 1989; McDowall 1996).

The remaining species have all originated from the aquarium trade (McKay 1984; Allen 1989; Ryan 1995; McDowall 1996). Only three of these have so far established extensive distributions in the wild. The oriental weatherloach (*Misgurnus anguillicaudatus*) occurs in streams along the east coast of NSW and several south-flowing catchments in Victoria, such as the Yarra and Latrobe Rivers. It also occurs inland in south-eastern Australia, in the Murrumbidgee, Ovens and Murray Rivers (McDowall 1996; Victorian Fish database, ARI, Victoria). The Mozambique mouthbrooder (*Oreochromis mossambicus*) has established populations in the lowland reaches of several coastal rivers in Queensland between Brisbane and Cairns, and has been reported in several rivers in south-western Western Australia (McKay 1984; Allen 1989; McDowall 1996). The guppy (*Poecilia reticulata*) is widespread from Brisbane to north-east Queensland (Ryan 1995). The one-spot livebearer (*Phallocherus caudimaculatus*) has been recorded in ponds and drains around Perth (Allen 1989). The sailfin molly (*Poecilia latipinna*), swordtail (*Xiphophorus helleri*) and platy (*X. maculatus*), are restricted to a few streams around Brisbane (McDowall 1996). The rosy barb (*Puntius conchrochius*) also established itself in one stream in the Brisbane area but has apparently died out (Brumley 1991; McDowall 1996). The American flag fish (*Jordanella floridae*) has been recorded near Cairns (Allen 1989). The convict and black mangrove cichlid (*Tilapia mariae*) are restricted to the Hasellwood Pondage in Morwell Victoria, which contains warm water outflow from the power station. Zilles cichlid (*T. zillii*) was recorded in tributaries of the Swan River estuary in Western Australia. in 1975, but is believed to have been successfully eradicated (Allen 1989). The blue acara (*Aequidens pulcher*) has been recorded in one stream in Brisbane (Ryan 1995).

Many of Australia's inland waters, particularly in south-eastern regions, contain one or more introduced fish species. In some cases these species have completely displaced native fish and substantially modified aquatic ecosystems. In addition to those species already established, there is continual interest from the recreational and commercial fishing industry to establish hatcheries or introduce more species. Several hundred species of exotic ornamental fish have been imported into Australia for the aquarium trade (McKay 1984). The potential for more of these species to become established in natural waters is high, particularly in tropical and subtropical regions (McKay 1984; McDowall 1996).

With the possible exception of the Oriental Weatherloach, all of the introduced species have the potential to prey upon amphibian eggs and larvae, and many species may also prey upon adults. As indicated in the literature reviewed earlier, this has already been demonstrated for most of the more widely introduced species, such as the salmonids, cyprinids, redfin perch and gambusia, on other continents.

## REVIEW OF IMPACTS OF INTRODUCED FISH ON AMPHIBIANS IN AUSTRALIA

Few studies have been conducted to investigate the relationships between introduced fish and amphibians in Australia. To date, the impacts of only three introduced species, brown and rainbow trout, and gambusia, have been investigated. Collectively these studies have assessed impacts on only 16 species of frog to any degree (Table 2). Some information is presented on redfin perch and carp; however, appropriate research is required to further examine the impacts of these species.

### Impact of Fish Predation on Adult Frogs

It is common knowledge among the fishing fraternity that frogs make good bait for trout and redfin perch (Baxter, Victorian Fisheries, pers. comm.; Harris, NSW Fisheries, pers. comm.; Lake, Department of Biological Sciences, Monash University, pers. comm.). This suggests that trout and redfin perch may readily attack frogs in the wild. Collection of frogs for bait may place excessive pressure on some frog populations (Watson *et al.* 1991). The use of frogs for bait is now banned in some States. However, it is likely that fish are able to exert their greatest impact on frog populations by preying upon larval stages.

### Impact of Predation by Trout Species

Species most at risk from predation by trout are those which breed exclusively in streams in south-eastern Australia. There are eight such species, several of which have declined in recent years and are considered endangered or vulnerable (Gillespie and Hines 1999). The spotted tree frog (*Litoria spenceri*) has always been considered rare (Ahern 1982); however, declines were observed in most of the few known populations in the 1970s and 80s (Watson *et al.* 1991), and the species is now listed as endangered (Tyler 1997). Watson *et al.* suggested that introduced trout may be contributing to this decline. Trout are present in all the streams in which the species is known to have occurred (Victorian Fish database, ARI, Victoria). Surveys of the distribution and relative abundance of *L. spenceri* and other upland riverine species have found that *L. spenceri* only occurred in abundance in one reach of stream which was above a waterfall which trout could not negotiate (Gillespie and Hollis 1996; Hunter and Gillespie 1999). Only a few high density upland populations of the leaf-green tree frog (*L. phyllochroa*) have been located, most of which have also been above waterfalls in trout-free streams (Gillespie pers. obs.). In contrast, lesueur's frog (*L. lesueuri*) remains widespread and is abundant along many streams where trout are present (Gillespie and Hollis 1996; Hunter and Gillespie 1999; Gillespie pers. obs.).

Gillespie (1997, unpubl.) examined the relative palatabilities of five riverine frog larvae, *L. booroolongensis*, *L. citropa*, *L. lesueuri*, *L. phyllochroa* and *L. spenceri*, to two sympatric native fish, mountain galaxias (*Galaxias olidus*) and two-spined blackfish (*Gadopsis bispinosis*), and introduced brown trout. All fish readily consumed tadpoles of *Limnodynastes peronii* which occur in lentic habitats without fish; however, only trout ate a significant proportion of tadpoles of any riverine tadpole species. Further in-stream experiments demonstrated that despite the availability of alternative food

sources for trout, and refuge microhabitats for tadpoles, trout were able to impose a significant predation pressure on *L. spenceri* and *L. phyllochroa*. Brown and rainbow trout are now considered to be the primary cause of decline of *L. spenceri* (Robertson *et al.* 1998, unpublished; Robertson and Gillespie, 1998, unpubl.). These findings suggest that upland populations of the other species within the *L. citropa* complex, i.e. *L. subglandulosa* and *L. pearsoniana*, may also be highly vulnerable to predation from trout. Although *L. lesueuri* complex species were less palatable, *L. booroolongensis* has also declined (Gillespie and Hines 1999; NSW NPWS Scientific Committee Determination Advice No. 97/27). Other factors such as habitat degradation may be involved but it remains unclear what impact trout may have on these species. For example, an egg mass of *L. lesueuri* was found in the stomach of a brown trout (Rardik, ARI, Victoria, pers. comm.). This fish was able to take out most of the annual reproductive investment of a single female frog (several hundred eggs) in one sitting. It is expected that predation pressure by trout on these species will be high when alternative food resources are limited.

### Impact of Predation by Gambusia

Gambusia has so far received the most scrutiny regarding its potential impact upon Australian frog populations. The broad distribution and wide range of habitats occupied by gambusia means that it may potentially impact upon many lentic and lotic frog populations across a large area of Australia.

Only one study has examined predation by gambusia upon anuran eggs; Reynolds (1995) found that eggs of *Crinia insignifera* and *C. glauerti* were unpalatable. Preliminary trials also suggested that eggs of *Litoria adelaidensis*, *L. moorei* and *Crinia georgiana* may also be unpalatable (Reynolds 1995). However, several studies have shown experimentally that gambusia are capable of preying on small larvae of a number of Australian anuran species: *Limnodynastes tasmaniensis*, *Litoria lesueuri* and *L. dentata* (Harris 1995); *Crinia insignifera* and *C. glauerti* (Reynolds 1995); *Litoria aurea* and *L. dentata* (Morgan and Buttemer 1996); *Limnodynastes peronii* and *Crinia signifera* (Webb and Joss 1997).

A number of studies have identified negative associations between the presence of gambusia and frog species. Dankers (1977) found that tadpole numbers of several species were drastically reduced in ponds containing gambusia after early December, coinciding with a seasonal increase in fish biomass. McGilp (1994) found a negative correlation between the occurrence of Brown Tree Frog (*Litoria ewingii*) and that of gambusia in waterbodies along the Yarra River in Melbourne.

Blyth (1994) compared survival and recruitment of three species of Western Australian anuran larvae, *Crinia glauerti*, *C. insignifera* and *Heleioporus eyrei*, in the presence or absence of gambusia in experimental field enclosures. Tadpole survival of all three species was significantly lower in the presence of gambusia at the end of the experimental period. However, the design of the enclosures allowed access for oviposition by local frog populations, as evidenced by increases in numbers of experimental animals in some enclosures. Other potential predators of premetamorphic stages also had access, such as invertebrates and birds. Furthermore, each species/fish treatment was not replicated. These factors limit interpretation of the results of this study.

**TABLE 2: List of introduced fish and native frog species-interactions that have been examined in Australia.**

Fish species	Frog species		Source	
Brown Trout ( <i>Salmo trutta</i> )	Booroolong Frog	<i>Litoria booroolongensis</i>	Gillespie (1997), unpublished	
	Blue Mountains Tree Frog	<i>L. citropa</i>	Gillespie (1997), unpublished	
	Lesueur's Frog	<i>L. lesueuri</i>	Gillespie (1997), unpublished	
	Leaf-green Tree Frog	<i>L. phyllochroa</i>	Gillespie (1997), unpublished	
	Spotted Tree Frog	<i>L. spenceri</i>	Gillespie (1997), unpublished	
Rainbow Trout ( <i>Oncorhynchus mykiss</i> )	Striped Marsh Frog	<i>Limnodynastes peroni</i>	Gillespie (1997), unpublished	
	Leaf-green Tree Frog	<i>L. phyllochroa</i>	Gillespie (1997), unpublished	
Eastern gambusia or	Spotted Tree Frog	<i>L. spenceri</i>	Gillespie (1997), unpublished	
Mosquito Fish	Slender Tree Frog	<i>Litoria adelaidensis</i>	Reynolds (1995)	
(Gambusia holbrooki)	Green and Golden Bell Frog	<i>L. aurea</i>	Morgan and Buttemer (1996); Pyke and White (1996)	
	Kerferstein's Tree Frog	<i>L. dentata</i>	Harris (1995); Morgan and Buttemer (1996)	
	Moor's Frog	<i>L. moorei</i>	Reynolds (1995)	
	Lesueur's Frog	<i>L. lesueuri</i>	Harris (1995)	
	Tschudi's Froglet	<i>Crinia georgiana</i>	Reynolds (1995)	
	Glauert's Froglet	<i>C. glauerti</i>	Blyth (1994); Reynolds (1995)	
	Sign-bearing Frog	<i>C. insignifera</i>	Blyth (1994); Reynolds (1995)	
	Common Froglet	<i>C. signifera</i>	Webb and Joss (1997)	
	Moaning Frog	<i>Heleioporus eyrei</i>	Blyth (1994); Reynolds (1995)	
	Striped Marsh Frog	<i>Limnodynastes peroni</i>	Webb and Joss (1997)	
	Spotted Marsh Frog	<i>L. tasmaniensis</i>	Harris (1995)	
	Spotted Marsh Frog	<i>L. tasmaniensis</i>	M. Healey (unpublished data)	
	Goldfish ( <i>Carassius auratus</i> )			

Webb and Joss (1997) examined amphibian species richness and abundance in relation to gambusia density and cover of emergent aquatic vegetation in ten ponds near Sydney. They found a significant negative relationship between fish density and frog abundance but no relationship for species richness. The descriptions provided for each waterbody indicate a high degree of variability in habitat among pond sites. Unfortunately additional factors such as pool size and native vegetation cover, which may strongly affect frog abundance, were not considered in their analyses. Tadpole density is easier to sample systematically than adult frog density in pond habitats (Heyer et al. 1994). Given that tadpoles are one of the life stages on which gambusia potentially preys upon, a measure of their relative abundance, rather than that of adult frogs, will provide a more reliable indicator of the impact of gambusia.

Reynolds (1995) examined the occurrence of six anuran species with gambusia in water bodies near Perth, Western Australia. In contrast to the above studies, he found no relationship between the presence/absence of fish and individual anuran species, with one exception, *Crinia insignifera*, which was found infrequently with gambusia. However, he observed that most of the sites used by *C. insignifera* were ephemeral and unsuitable for gambusia. Species richness was generally lower at sites occupied by gambusia, but many of these sites were also degraded, contributing to their unsuitability as frog breeding habitats.

In addition Reynolds (1995) experimentally examined predation by gambusia on several tadpole species in Western Australia. Trials with tadpoles indicated that gambusia were able to attack and kill tadpoles of *L. adelaidensis*, *C. georgiana* and *H. eyrei*. Controlled palatability experiments showed that survival of *L. moorei* tadpoles was significantly reduced in the

presence of gambusia. However, gambusia showed a strong preference for invertebrate prey (*Daphnia* sp. or mosquito larvae). Both groups were consistently consumed completely before tadpoles in all trials. In a field enclosure experiment, in which tadpoles were also exposed to invertebrate predators, Reynolds (1995) found no significant difference in survival in the presence or absence of gambusia. These results, in conjunction with his field survey data, suggest that the impact of gambusia upon populations of these frog species is influenced by several factors, and under natural conditions may be limited.

Gambusia cannot consume large prey as these small fish are gape-limited predators. Webb and Joss (1997) conducted predation experiments examining the impact upon survival of different size classes of *C. signifera* and *Limnodynastes peroni* tadpoles by hungry and pre-fed gambusia. They found significant differences between predation rates due to tadpole size class and hunger status of fish. Tadpole species which are able to rapidly attain moderate to large size may therefore minimize the impact of predation (Caldwell et al. 1980; Crump 1984).

Several studies have reported damage to the fins of larger tadpoles from gambusia attack (Dankers 1977; Blyth 1994; Harris 1995). This could result in reduced survival of larger tadpoles due to reduced mobility and feeding, inability to escape other predators, or reduced metamorphic fitness. However, some tadpole species have been found to survive tail loss (Harris 1995). Wilbur and Semlitsch (1990) reported tail regeneration by tadpoles of *Rana catesbeiana* even after considerable loss, and suggest that this may be a general mechanism to reduce the impact of predation.

Concerns for the role of gambusia in the decline of amphibian species, particularly members of the *L. aurea* complex, have been expressed by several authors (Mahony 1993; Daly 1995; Morgan and Buttemer 1996; White and Pyke 1996; White and Ehmann 1997). However, evidence linking gambusia to declines of frog populations in the *L. aurea* complex is limited, due in part to conflicting findings and methodological limitations of some studies.

For example, Morgan and Buttemer (1996) conducted controlled predation experiments examining the impact upon survival of tadpoles of *L. aurea* and *L. dentata* by gambusia. The influence of macrophytes on the predatory impact of gambusia was also examined. They found that in the absence of macrophytes gambusia were able to significantly reduce tadpole survival of both species within 24 hours. In the presence of macrophytes, the effect was substantially reduced and no significant impact of gambusia could be detected on *L. aurea* after three days. However, survival of *L. dentata* was still significantly reduced after two days. These findings indicate that presence of gambusia may significantly influence the survival of tadpoles, but that this is likely to be strongly influenced by habitat structure and tadpole behaviour. *Litoria aurea* larvae have also been found in sympatry with native predatory fish (pers. obs.). In the absence of comparative data on the impact of these natural predators upon larval survival, it is difficult to assess the relative ecological significance of gambusia predation.

Pyke and White (1996) surveyed waterbodies in the Sydney region for *L. aurea*, and examined associations between evidence of breeding, occurrence of introduced fish, and habitat. They found that breeding was most strongly associated with ephemeral rather than permanent or 'fluctuating' ponds, followed by the absence of introduced fish, primarily gambusia, and speculated that this fish was a major cause of decline of *L. aurea* (Pyke and White 1996). However, examination of their data reveals that pond permanency and occurrence of gambusia are highly correlated and so the results could also be explained in terms of unmeasured features of pond permanency, or abundance of other predators.

White and Ehmann (1997) suggest that gambusia is also implicated in the decline of *L. flavipunctata*, a closely related species to *L. aurea*. However, Osborne *et al.* (1996) point out that many of the sites from which this species has disappeared do not contain gambusia. Furthermore, both *L. aurea* and *L. raniformis*, an ecologically similar species which hybridises with *L. aurea* (Watson and Littlejohn, 1985), have been recorded in abundance at some sites containing gambusia (van de Mortel and Goldingay 1998; Gillespie pers. obs.; Pyke, Australian Museum, pers. comm.).

The role of gambusia in the decline of *L. aurea* is unclear. Other factors require careful consideration, such as pond duration, habitat quality, presence of other aquatic predators and availability of refugia. Evidence of gambusia having a major impact on the abundance of other Australian amphibians is also unclear. However, many of the studies to date have demonstrated that gambusia are capable of killing a variety of tadpole species and eggs. Considering the wide distribution of gambusia, it probably does have significant impacts on some native amphibian species, particularly in the eastern states where seasonal peak fish abundance coincides with the larval stages of many species

(Reynolds 1995). Further research is required to ascertain the role of gambusia in the decline of amphibian species assemblages with respect to other threatening processes. For instance, as gambusia occur in areas which are mostly disturbed or modified in other ways, the relative impacts of these habitat changes upon amphibian populations need to be differentiated from those wrought by the fish.

### **Impacts of Predation by Redfin Perch and Carp Species**

Research overseas suggests that redfin perch and carp species may be major predators of some tadpole species. No published studies have addressed the impact of carp species or redfin perch upon frogs in Australia. Leslie (1995) has attributed the decline of frogs in some wetlands in the Murray-Darling Basin in part to predation on premetamorphic stages by carp species. Healey *et al.* (1997) observed no evidence of frogs breeding in four billabongs on the Murrumbidgee floodplain and suggested that this may have been explained by the presence of carp species. However, no observations were made at sites where carp were absent and the absence of tadpoles could be explained by a number of alternative abiotic and biotic hypotheses. Laboratory predation experiments have shown that tadpoles of *Limnodynastes tasmaniensis* are palatable to goldfish and redfin perch (Healey, Charles Sturt University, Wogga Wogga, pers. comm.), indicating the potential for these species to consume tadpoles. However, it is unknown whether they prey on tadpoles in the wild when alternative food is available. Carp are able to significantly modify the physical habitat of aquatic systems, by uprooting aquatic vegetation and increasing turbidity (Roberts *et al.* 1995). These changes may have indirect impacts on tadpoles through loss of food resources, cover for protection from other predators, and loss of oviposition sites.

### **Broader Implications of Introduced Fish for Australian Amphibian Species**

The evidence presented here strongly suggests that introduction of exotic fish or translocation of native species could have an enormous impact on the amphibian assemblages of Australian freshwater systems. However, in many cases the impacts have not been investigated. For example, the impact of carp species on Australian amphibian assemblages has not been examined, despite their widespread distribution and frequently-raised concerns about their adverse effects upon freshwater systems.

Introduced fish within mainland Australia are currently generally restricted to the eastern sea board, Murray-Darling system and south-west Western Australia. This distribution also overlaps with regions of high amphibian species richness (see Barker *et al.* 1996). Consequently a large proportion of Australian anurans are potentially affected by one or more introduced fish species.

Species most likely to be affected are those which breed in permanent aquatic habitats, such as streams and wetlands. However, many which breed in more ephemeral habitats, such as billabongs and temporary pools along flood plains of rivers, may also be affected as these habitats are seasonally colonised by introduced fish when water courses swell. Changes to the rural landscape within these regions have

resulted in removal of many natural ephemeral aquatic habitats and the expansion of more permanent habitats by way of stock dams. These are the only breeding habitats in some areas for species which would otherwise breed in ephemeral water bodies. Farm dams are often stocked with introduced and native angling species which are likely to impact these amphibian assemblages. These habitats may have become ecological sinks for some species.

A large proportion of Australia's threatened amphibian species breed in habitats currently occupied by, or within the range of, introduced or translocated fish. Lotic species assemblages are particularly vulnerable. The range of introduced trout species includes part or all of the distributions of ten south-eastern Australian lotic species, five of which have declined (Tyler 1997; NSW NPWS Scientific Committee Determination Advice No. 97/27; Gillespie and Hines 1999). Some populations of these species are probably exposed to redfin perch and gambusia as well.

The three species currently recognised within the *L. aurea* complex have all declined. Gambusia occur throughout much of the range of these species. Redfin perch and carp species occur throughout most of the range of *L. flavipunctata*, *L. raniformis* and in part of the range of *L. aurea*. Gambusia have already been implicated in the decline of this species group; redfin perch and carp species may also be contributing.

Other regions of Australia which contain significant amphibian assemblages, but are currently free of introduced fish, such as the Wet Tropics, may be at risk in the future if further introductions of other exotic fish species occur.

### Potential for Introducing Exotic Pathogens

Recent studies have suggested that an introduced pathogen may be responsible for amphibian declines in Australia and Central America (Blaustein *et al.* 1994; Laurance *et al.* 1996; Lips 1998; Berger *et al.* 1998). The potential for the introduction of disease into Australian freshwater systems via the importation of fish for the aquarium trade has been clearly identified (Mckay 1984; Laurance *et al.* 1996). Laurance *et al.* (1996) has suggested that a pathogen introduced in this way might be responsible for frog declines in north-east Queensland, but at this time there is no evidence to support this (Hero and Gillespie 1997; Alford and Richards 1997). However, disease risk imposed by the continual importation of live freshwater fish into the country cannot be ignored.

### MANAGEMENT SOLUTIONS

The importation of exotic fish for the aquarium trade should only be acceptable following rigid quarantine protocols that eliminate the possibility of introducing pathogens either with the fish or the water they are transported in. The aquarium trade should be advised of the potential impact of introduced pathogens and fish species and a shift towards the use of native fish species for the pet-trade encouraged. Similarly, gambusia should not be introduced into new systems for mosquito control; alternatively native fish species local to the area may be more suitable.

Once fish have been introduced into an aquatic system and established self-sustaining populations, they are extremely difficult to remove. Small, confined water bodies, such as dams,

can be drained to effect 100% removal. However, this option is usually not available. Most introduced fish in Australia occur in streams or larger waterbodies which cannot easily be drained. There have been numerous attempts in the United States of America to eradicate unwanted fish populations from streams and lakes, using a variety of techniques, such as electrofishing, netting and poisoning. The only demonstrated successful approach for complete removal of fish from these systems is with a toxicant. This approach has become a standard management technique throughout the USA (Eschmeyer 1975), mainly as a fishery technique to improve populations of recreational over non-recreational species (Ryan 1977). More recently this has expanded to aquatic conservation to protect threatened fauna from introduced fish species. However, examples of treatments designed to accomplish a complete kill, as required for long-term exclusion, are few and, of these, only few have been successful (Rinne *et al.* 1981; Gresswell 1991; Stefferud *et al.* 1992).

There has been only one successful eradication of salmonids from any Australian waters. This was conducted in several small mountain streams in eastern Victoria as part of the implementation of the barred galaxias Recovery Plan (Raadic 1993). Artificial trout barriers were established across the streams and all fish above the barriers and below remaining native fish populations were killed with rotenone, allowing the native species to recolonise the rehabilitated zones (Raadic, ARI, unpublished data). Expanding this approach to larger water-courses is problematic. It is more difficult to effect a complete eradication due to an exponential increase in stream length and complexity with increased catchment size, barrier construction becomes increasingly more difficult and expensive on larger streams, and the risk of re-introduction also increases. Saddler and Gillespie (1997) assessed the feasibility of excluding trout from streams to protect populations of *L. spenceri*. Of the 13 streams examined, exclusion was considered feasible only on reaches of three streams because of the above constraints. If successful this would afford protection to approximately 7% of the current range of the species.

The environmental and socio-economic costs of eradicating fish must also be measured against the longer-term benefits to conservation. Several problems arise with eradication programs.

1. Native fish species and some invertebrate groups are also affected by rotenone, which disables gill function.
2. Most large waterbodies such as lakes and streams are also used to supply water for human consumption and recreational purposes, including fishing; hence poisoning may risk human health. Furthermore opposition by the recreational fishing community is likely to influence the political decision-making process.
3. For waterbodies which are used for angling, there is a high risk of reintroduction of popular angling species by members of the public. These factors further restrict the range of circumstances in which eradication of introduced fish is feasible.

In the future it may be possible to develop biological agents to control introduced fish populations. However, this would be extremely costly and take many years to develop. Clearly, in many instances removal of introduced fish for maintenance of amphibian populations is not feasible at this time. Management should focus therefore on identifying and acting

on those habitats where the feasibility of removal of introduced fish is high, and restricting the spread of existing exotic species and further introductions of more species.

There is a strong fishing culture in Australia which has a large focus on introduced species. Many introduced species, such as salmonids and redfin perch, continue to be considered desirable alien species by State agencies. However, servicing this culture continues to erode the biotic integrity of Australian freshwater systems. There needs to be a shift in emphasis by State fisheries managers from introduced fish to native species. The ongoing commercial stocking programs for some introduced species in some States, such as salmonids, pose a major threat to several significant amphibian assemblages. Discontinuation of stocking programs, especially in regions where the fish populations are not self-sustaining, will greatly benefit the conservation of some amphibian species. The needs of recreational fishing must be balanced with the benefits derived from maintaining natural fish assemblages. Control of exotic fish stocks may enhance remaining native fish stocks which are also suited to recreational fishing pursuits, while maintaining natural assemblages of native invertebrates and amphibians. It is important to emphasise that native species should not be released into systems in which they did not occur naturally.

## CONCLUSIONS AND FUTURE DIRECTIONS

In summary, fish are a major influence on amphibian assemblage structure. Hence, they play a major role in determining the distribution and abundance of amphibian species. The introduction of exotic fish to aquatic systems has the potential to eliminate amphibian species. Additionally there is potential to introduce disease or pathogens into freshwater systems. These changes may be extremely detrimental to the long-term survival of some species, undermine amphibian communities and disrupt natural aquatic systems. In view of the large number of introduced fish species and extensive distribution of some of these within Australia, many amphibian communities are currently vulnerable to impacts from exotic fish.

Limited research has been carried out in Australia on the impact of introduced fish upon amphibian assemblages. However, there is strong evidence from both overseas and within Australia that those fish species which have been introduced pose a serious threat to a range of anuran species, a number of which have already declined. In particular, trout have been shown to be responsible for the decline of at least one threatened species (*L. spenceri*), and gambusia has been suggested in the decline of others. The impact and management of introduced fish therefore warrants serious consideration in the development and implementation of recovery plans for declining frog species.

Further information is required to assess the impact of introduced fish upon amphibian assemblages throughout the range of habitats and regions in which they have spread. This is essential to gain a proper understanding of the role of introduced fish in frog declines, and identify management objectives. Priority should be given to the following areas of investigation:

*Determine which introduced or translocated fish species are impacting upon frog communities, and which frog species and communities are most at risk.*

Information is required for most fish species which have established self-sustaining populations and a range of exotic and native species which are readily introduced in frog habitats. Information is urgently required on the impacts of redfin perch and carp species, which are widespread and potentially affect numerous frog species, particularly in the Murray Darling system and New England Tablelands region of NSW where several frog species have disappeared. More information is required to ascertain the impact of gambusia in Eastern Australia, particularly on the *L. aurea* complex. The impact of trout upon all upland temperate lotic anuran species in south-eastern Australia also requires further investigation.

Broad-scale surveys are required to determine relationships of occurrence of frog species in relation to the distribution of introduced and native fish, and a range of other biotic and abiotic variables. The ability of fish species to impact frog communities should be tested experimentally. The relative effectiveness of tadpole survival strategies amongst species in the community to native sympatric predators and introduced species should be compared. Predation experiments should include adequate replication and use of known palatable and unpalatable (where available) tadpole species as controls. Fish density, fish size and tadpole sizes that replicate field observations should also be factored into experimental designs. The ability of fish to prey upon eggs should also be examined if possible as this may be a more vulnerable life stage for some species.

*Ascertain the relative importance of the role of introduced fish in frog population declines with relation to other biotic or abiotic factors.*

Relative impact of introduced fish must be examined in conjunction with other factors potentially limiting survival, such as habitat degradation. Other biotic or abiotic factors may either exacerbate or ameliorate the impacts of introduced fish on frog populations. Surveys to determine relationships between occurrence of fish and frogs should incorporate collection and analysis of confounding biotic and abiotic habitat variables (e.g. hydroperiod, water quality, aquatic vegetation, adjacent adult habitat, native predator abundance, etc.). These should be designed where possible with adequate power in sample size (i.e. adequate number of waterbodies) to assess the relative contributions of introduced fish and other factors which significantly influence occurrence of frog species.

For some species which are rare or have limited distributions, surveys of this kind are likely to have inadequate power. The relative impact of introduced fish can be examined in field experiments conducted in stream or pond enclosures which closely mimic conditions experienced in natural breeding bodies, incorporating natural levels of cover, sympatric predators and hydroperiod. One or more variables can be manipulated, in conjunction with predator levels to assess their relative contributions to larval mortality.

The threats imposed by introduced fish to Australian amphibian assemblages require immediate and on-going attention by conservation and fisheries managers. The possibility of eradication of introduced species should be assessed on a case by case basis; however, this is currently expected to have limited feasibility in many instances. There is

a strong need for development of improved effective eradication techniques. However, the immediate priority for managers should be prevention of further translocations and introductions of fish species. For those species under serious threat from introduced fish, all extant populations currently free of introduced predators should be identified and appropriate steps taken to ensure that fish are not introduced.

Current policies and management of introduced fisheries and the aquarium-trade require review and need to take into consideration the potential impact upon amphibian assemblages. Enhancement of native fisheries, rather than those based upon exotic species should be encouraged. Stocking programs for introduced fish should be discontinued in aquatic systems known to support vulnerable amphibian species. Tighter control of the importation and maintenance of ornamental species is required, particularly of those species with potential to establish self-sustaining wild populations and impact upon native biota. The public also need to be educated about adverse effects of releasing or translocating fish on amphibians and other biota.

## ACKNOWLEDGMENTS

We thank the Arthur Rylah Institute, Department of Natural Resources and Environment, Victoria, and Griffith University for financial support. H. Hines, B. Magnusson, R. Loyn, T. Raadik, R. Swain and W. Osborne provided comments on the manuscript.

## REFERENCES

- Alford, R. A. and Richards, S. J. (1997). Lack of evidence for epidemic disease as an agent in the catastrophic decline of Australian rainforest frogs. *Conservation Biology*, 11: 1026-29.
- Ahern, L. D. (1982) Threatened Wildlife in Victoria and Issues Related to its Conservation. Ministry for Conservation, Fisheries and Wildlife Service Paper 27.
- Allen, G. R. (1982) A Field Guide to Inland Fishes of Western Australia. Western Australian Museum, Perth, Australia.
- Allen, G. R. (1989) Freshwater Fishes of Australia. T. F. H. Publications, New Jersey.
- Arthington, A. H. and Blühdorn, D. R. (1995) Improved Management of Exotic Aquatic Fauna: Research and Development for Australian Rivers. Land and Waters Resources Research and Development Corporation.
- Azevedo-Ramos, C., Van Sluys, M., Hero, J.-M. and Magnusson W. E. (1992) Influence of tadpole movement on predation by odonate naiads. *Journal of Herpetology*, 26: 335-38.
- Barker, J., Grigg, G. and Tyler, M. J. (1995). A Field Guide to Australian Frogs. 2nd Edition. Surrey Beattie, Chipping Norton, NSW.
- Berger, L., Spear, R., Daszak, P., Green, D. E., Cunningham, A. A., Goggin, C. L., Hines, H. B., Lips, K. R., Marantelli, G. and Parkes, H. (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rainforests of Australia and Central America. *Proceedings of the National Academy of Sciences*, 95: 9031-9036.
- Bertram, S. and Berrill, M. (1997) Fluctuations in a northern population of gray treefrogs, *Hyla versicolor*. In D. M. Green (ed.) *Amphibians in Decline Canadian Studies of a Global Problem*. Chapture 6, *Herpetological Conservation No. 1*, Canadian Association of Herpetologists, Montréal, pp. 57-63.
- Bidwell, J. R. and Gorrie, J. R. (1995) Acute Toxicity of a Herbicide to Selected Frog Species: Final Report. Western Australian Department of Environmental Protection, Perth.
- Bishop, C. A. (1992) The effects of pesticides on amphibians and implications for determining causes of declines in amphibian populations. In C. A. Bishop and K. E. Pettit (eds.) *Declines in Canadian Amphibian Populations: Designing an National Monitoring Strategy*. Occasional Paper No. 76, Canadian Wildlife Service, Ottawa, pp. 67-70.
- Blaustein, A. R., Hokit, D. G., O'Hara, R. K. and Holt, R. A. (1994) Pathogenic fungus contributes to amphibian losses in the Pacific Northwest. *Biological conservation*, 67: 251-254.
- Blyth, B. (1994) Predation by *Gambusia holbrooki* on Anuran Larvae at the RGC Wetlands Centre, Capel Western Australia. RGC Wetlands Centre Technical Report No. 22, Capel, W.A.
- Bradford, D. F. (1989) Allopatric distribution of native frogs and introduced fishes in the high Sierra Nevada lakes of California: implication of the negative effect of fish introductions. *Copeia*, 1989: 775-8.
- Bradford, D. E., Tabatabai, F. and Graber, D.M. (1993) Isolation of remaining populations of the native frog, *Rana mucosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. *Conservation Biology*, 7: 882-8.
- Braña, F., Frechilla, L. and Orizaola, G. (1996) Effect of introduced fish on amphibian assemblages in mountain lakes of northern Spain. *Herpetological Journal*, 6: 145-148.
- Brodie Jr, E. D., Formanowicz, D. R. and Brodie III, E. D. (1978). The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. *Herpetologica*, 34: 302-306.
- Brönmark, C. and Edenhamn, P. (1994) Does the presence of fish affect the distribution of tree frogs (*Hyla arborea*)? *Conservation Biology*, 8: 841-5.
- Brumley, A. R. (1991) Cyprinids in Australia, In: I. J. Winfield and J. S. Nelson (eds) *Cyprinid Fishes: Systematics, Biology and Exploitation*, Chapman and Hall, London. pp. 265-283.
- Burger, W. L. (1950) Novel aspects of the life history of two *Ambystomas*. *Journal of the Tennessee Academy of Science*, 25: 252-257.
- Cadwallader, P. L. and Backhouse, G. N. (1982) A Guide to the Freshwater Fish of Victoria. Victorian Government Printing Office, Melbourne, Australia.
- Caldwell, J. P., Thorp, J. H., and Jerve, T. O. (1980) Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia*, 46: 285-9.
- Calef, G. W. (1973) Natural mortality of tadpoles in a population of *Rana aurora*. *Ecology*, 54: 741-58.
- Chovanec, A. (1992) The influence of tadpole swimming behaviour on predation by dragonfly nymphs. *Amphibia-Reptilia*, 13: 341-9.

- Crump, M. L. (1984) Ontogenetic changes in vulnerability to predation in tadpoles of *Hyla pseudopumma*. *Herpetologica*, 40: 265-71.
- Daly, G. (1995) Observations on the green and golden bell frog (*Litoria aurea*) (Anura: Hylidae) in southern New South Wales. *Herpetofauna*, 25: 2-9.
- Dankers, N. M. J. A. (1977) The ecology of an anuran community. Ph D. thesis, University of Sydney. Unpublished.
- Dawkins, R. and Krebs, J. R. (1979) Arms races between and within species. *Proceedings of the Royal Society of London*, 205: 489-511.
- Dubuis, L. A. (1997) Effects of logging on terrestrial amphibians of coastal British Columbia. Chapture 20 In D. M. Green (ed) *Amphibians in Decline Canadian Studies of a Global Problem*. *Herpetological Conservation No. 1.*, Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri, pp. 185-90.
- Duellman, W. E. (1978) The biology of an equatorial herpetofauna in Amazonian Ecuador. University Kansas Museum of Natural History Miscellaneous Publication, 65: 1-352.
- Eschmeyer, P. H. (1975) (ed.) *Rehabilitation of Fish Populations with Toxicants: A symposium*. North Central Division Special Publication 4. American Fisheries Society, Bethesda, Maryland, USA.
- Faragher, R. A. and Harris, J. H. (1993) The historical and current status of freshwater fish in New South Wales. *Australian Zoologist*, 29(3-4): 166-76.
- Fickling, S. (1995) The influence of fish predation on the local distribution of frogs and tadpoles in rainforest streams of the Tully River. Unpublished Honours Thesis, James Cook University, Townsville, Australia.
- Formas, J. R. (1995) Amphibians. Chapt. 44, In J. A. Simonetti, M. T. K. Arroyo, A. E. Spotorno and E. Lozada (eds) *Diversidad Biologica de Chile*, pp.314-25.
- Gamradt, S. C. and Kats, L. B. (1996) Effect of introduced crayfish and mosquitofish on Californian newts. *Conservation Biology*, 10: 1155-62.
- Gillespie, G. R. (1997) The Biology of the Spotted Tree Frog (*Litoria spenceri*) and Examination of Factors Responsible for Population Declines. Unpublished Report to the Biodiversity Group, Environment Australia, Canberra. Arthur Rylah Institute, Department of Natural Resources and Environment, Melbourne, Victoria.
- Gillespie, G. R. and Hines, H. B. (1999) Status of temperate riverine frogs in south-eastern Australia. Pp 109-130 in *Declines and Disappearances of Australian Frogs* ed by A. Campbell. Environment Australia: Canberra.
- Gillespie, G. R. and Hollis, G. J. (1996) Distribution and habitat of the spotted tree frog *Litoria spenceri* Dubois (Anura: Hylidae), and an assessment of potential causes of population declines. *Wildlife Research*, 23: 49-75.
- Gresswell, R. E. (1991) Use of antimycin for removal of brook trout from a tributary of Yellowstone Lake. *North American Journal of Fisheries Management*, 11: 83-90.
- Grinnell, J. and Storer, T. I. (1924) *Animal life in the Yosemite*. University of California Press, Berkeley, California.
- Grubb, J. C. (1972) Differential predation by *Gambusia affinis* on the eggs of seven species of anuran amphibians. *The American Midland Naturalist*, 88: 102-108.
- Harris, K. (1995) Is there a negative relationship between gambusia and tadpoles on the Northern Tablelands? B.Sc. Honours thesis, University of New England, Armadale, New South Wales, Unpublished.
- Hayes, M. P. and Jennings, M. R. (1986) Decline of Ranid frog species in Western North America. Are bullfrogs (*Rana catesbeiana*) responsible? *Journal of Herpetology*, 20: 490-509.
- Healey, M., Thompson, D. and Robertson, A. (1997) Amphibian communities associated with billabong habitats on the Murrumbidgee floodplain, Australia. *Australian Journal of Ecology*, 22: 270-78.
- Hecnar, S. J. and M'Closkey, R. T. (1997) The effects of predatory fish on amphibian species richness and distribution. *Biological Conservation*, 79: 123-31.
- Hero, J.-M. (1991) Predation, palatability and the distribution of tadpoles in the central Amazon rainforest. Unpublished PhD thesis, Griffith University, Brisbane, Australia, 234 pp.
- Hero, J.-M., Gascon, C. and Magnusson, W. E. (1998) Direct and indirect effects of predation on tadpole community structure in the Amazon rainforest. *Australian Journal of Ecology*, 23: 474-482.
- Hero, J.-M. and Gillespie, G. R. (1997). Epidemic disease and amphibian declines in Australia. *Conservation Biology*, 11: 1023-25.
- Heyer, W. R., Donnelly, M. A., McDairmid, R. W., Hayek, L.-A. C. and Foster, M. S. (eds.) (1994) *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians*. Smithsonian Institution Press, Washington.
- Heyer, W. R., McDairmid, R. W. and Weigmann, D. L. (1975) Tadpoles, predation and pond habitats in the tropics. *Biotropica*, 7: 100-111.
- Holomuzki, J. R. (1995) Oviposition sites and fish-deterrent mechanisms of two stream anurans. *Copeia*, 1995: 607-613.
- Hopey, M. E. and Petranka, J. W. (1994) Shorter contributions: ichthyology. *Copeia*, 1994(4): 1023-1025.
- Hunter, D. and Gillespie, G. R. (1999) The distribution, abundance and conservation status of riverine frogs in Kosciuszko National Park. *Australian Zoologist*, 31: 198-209.
- Jennings, M. R. and Hayes, M. P. (1985) Pre-1900 overharvest of the Californian red-legged frog (*Rana aurora draytonii*): the inducement for bullfrog (*Rana catesbeiana*) introduction. *Herpetologica*, 41: 94-103.
- Johnson, B. (1992) Habitat loss and declining amphibian populations. In C. A. Bishop and K. E. Pettit (eds) *Declines in Canadian Amphibian Populations: Designing an National Monitoring Strategy*. Occasional Paper No. 76, Canadian Wildlife Service, Ottawa, pp. 71-75.
- Kats, L. B., Petranka, J. W. and Sih, A. (1988) Antipredator defences and the persistence of amphibian larvae with fishes. *Ecology*, 69: 1865-1870.
- Kats, L. B. and Sih, A. (1992) Oviposition site selection and avoidance of fish by streamside salamanders. *Copeia*, 1992: 468-473.

- Kruse, K. C. and Francis, M.G. (1977) A predation deterrent in larvae of the bullfrog, *Rana catesbeiana*. Transactions of the American Fisheries Society, 106: 248-252.
- Kruse, K. C. and Stone, B.M. (1984) Largemouth bass (*Micropterus salmoides*) learn to avoid feeding on toad (*Bufo*) tadpoles. Animal Behaviour, 32: 1035-1039.
- Laan, R. and Verboom, B. (1990) Effects of pool size and isolation on amphibian communities. Biological Conservation, 54: 251-262.
- Lannoo, M. J., Lang, K., Waltz, T. and Phillips, G. S. (1994) An altered amphibian assemblage: Dickinson county, Iowa, 70 years after Frank Blanchard's survey. American Midland Naturalist, 131: 311-319.
- Laurance, W. F., McDonald, K. R. and Speare, R. (1996) Epidemic disease and the catastrophic decline of Australian rain forest frogs. Conservation Biology, 10: 406-413.
- Leakey, R. and Lewin, R. (1995) The Sixth Extinction. Doubleday, New York.
- Leslie, D. J. (1995) Moira Lake: a case study of deterioration of a River Murray natural resource. Unpublished M. Forestry Sc. thesis, University of Melbourne.
- Liem, K. F. (1961) On the taxonomic status and the granular patches of the Javanese frog *Rana chalconota* Schlegel. Herpetologica, 17: 69-71.
- Lips, K. R. (1998) Decline of a tropical montane amphibian fauna. Conservation Biology, 12: 106-116.
- Liss, W. J. and Larson, G. L. (1991) Ecological effects of stocked trout on North Cascades naturally fishless lakes. Park Science, 11: 22-23.
- Macan, T.T. (1966). The influence of predation on the fauna of a moorland fish pond. *Archiv Für Hydrobiologie*, 61: 432-452.
- Macan, T.T. (1974) Freshwater Ecology. Longmans, London.
- Mahony, M. J. (1993) The status of frogs in the Watagon Mountains area, the central coast of New South Wales. In D. Lunney and D. Ayers (eds.) Herpetology in Australia a diverse discipline. Transactions of the Royal Society of New South Wales, Mossman, NSW, pp. 257-264.
- McDowall, R. M. (ed) (1996) Freshwater Fishes of South-eastern Australia. 2nd ed., Reed, Sydney.
- McGilp, E. (1994) Distribution of anuran amphibians in the lower Yarra River valley. Unpublished B. Sc. Honours thesis. University of Melbourne, Parkville, Victoria.
- McKay, R. J. (1984) Introductions of exotic fishes in Australia. In: W. R. Courtenay Jr. and J. R. Stauffer Jr. (eds.) Distributions, Biology and Management of Exotic Fishes. John Hopkins University Press, Baltimore & London pp. 177-199.
- Meffe, G. K. and Carroll, C. R. (1994) Principles of Conservation Biology. Sinauer Associated, Sunderland, M. A.
- Morgan, L. A. and Buttemer, W. A. (1996) Predation by the non-native fish *Gambusia holbrooki* on small *Litoria aurea* and *L. dentata* tadpoles. In G. H. Pyke and W. S. Osborne (eds) The Green and Golden Bell Frog (*Litoria aurea*): Biology and Conservation. Royal Zoological Society of NSW, pp. 143-49.
- Morin, P. J. (1986) Interactions between intraspecific competition and predation in an amphibian predator-prey system. Ecology, 67: 713-20.
- Myers, G. S. (1965) *Gambusia*, the fish destroyer. Tropical Fish Hobbyist, 13: 31-32.
- Orchard, S. A. (1992) Amphibian population declines in British Columbia. In C. A. Bishop and K. E. Pettit (eds) Declines in Canadian Amphibian Populations: Designing an National Monitoring Strategy. Occasional Paper No. 76, Canadian Wildlife Service, Ottawa, pp. 10-13.
- Osborne W. S., Littlejohn, M. J. and Thomson, S. A. (1996) Former distribution of the *Litoria aurea* complex from the southern tablelands of New South Wales and the Australian Capital Territory. In G. H. Pyke and W. S. Osborne (eds) The Green and Golden Bell Frog (*Litoria aurea*): Biology and Conservation. Royal Zoological Society of NSW, pp. 190-98.
- Petranka, J. W. (1983) Fish predation: a factor affecting the spatial distribution of a stream-breeding salamander. Copeia, 1983: 624-28.
- Pough F. H., Andrews, R. M., Cadle, J. E., Crump, M. L., Savitzky, A. H. and Wells, K. D. (1998) Herpetology. Prentice-Hall, New Jersey.
- Pyke, G. H. and White, A. W. (1996) Habitat requirements of the green and golden bell frog *Litoria aurea* (Anura: Hylidae) In G. H. Pyke and W. S. Osborne (eds) The Green and Golden Bell Frog (*Litoria aurea*): Biology and Conservation. Royal Zoological Society of NSW, pp.224-32.
- Raadik, T.A. (1993) A Research Recovery Plan for the Barred Galaxias, *Galaxias fuscus* Mack 1936, in South-eastern Australia. Unpublished report to the Australian National Parks and Wildlife Service; Department of Conservation and Natural Resources, Victoria.
- Resetarits, W. J. Jr and Wilbur, H. M. (1989) Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. Ecology, 70: 220-28.
- Reynolds, S. J. (1995) The impact of introduced mosquitofish (*Gambusia holbrooki*) on the mortality on premetamorphic anurans. Unpublished B. Sc. Honours thesis, University of Western Australia, Perth, Western Australia.
- Rinne, J. N., Minkley, W. L., and Hanson, J. N. (1981) Chemical treatment of Ord Creek, Apache County, Arizona, to re-establish Arizona Trout. Journal of Arizona-Navada Academy of Science, 16: 74-78.
- Roberts, J., Chick, A., Oswald, L. and Thompson, P. (1995) Effect of carp, *Cyprinus carpio* L., an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. Marine and Freshwater Research, 46: 1171-80.
- Robertson, P. and Gillespie, G. R. (1998 unpublished report) Draft Spotted Tree Frog Recovery Plan. Prepared for the Biodiversity Group, Environment Australia, by Department of Natural Resources and Environment, Melbourne, Victoria.
- Robertson, P., Lowe, K. and Gillespie, G. R. (1998 unpublished report) Flora and Fauna Guarantee Action Statement for the Spotted Tree Frog, *Litoria spenceri*. Flora and Fauna Branch, Department of Natural Resources and Environment, Melbourne, Victoria.
- Rowland, S. J. (1989) Aspects of the history and fishery of the murray cod *Maccullochella peelii* (Mitchell) (Percichthyidae) Proceedings of the Linnean Society of New South Wales, 111 (3): 201-13.

- Ryan, J. H. (1977) Non-game fish control at Frenchman Reservoir, Plumas County, California. Department of Fisheries and Game, Inland Fisheries Administration Report 78-1, Sacramento, California, USA.
- Ryan, M. (Ed.). (1995) Wildlife of Greater Brisbane. Queensland Museum, Brisbane
- Saddler, S. R. and Gillespie, G. R. (1997) Feasibility Study of Trout Eradication for Spotted Tree Frog Conservation. Unpublished Report for New South Wales National Parks and Wildlife Service, Jindabyne, Arthur Rylah Institute, Department of Natural Resources and Environment, Victoria.
- Scott, N. J. and Limerick, S. (1983) Reptiles and amphibians. In D. H. Janzen (ed.) Costa Rican Natural History. University of Chicago Press, Chicago, pp. 351-416.
- Semlitsch, R. D. (1983) Effects of different predators on the survival and development of tadpoles from the hybridogenetic *Rana esculenta* complex. *Oikos*, 67: 40-46.
- Sexton, O. J. and Phillips, C. (1986) A quantitative study of fish-amphibian interactions in three ponds. *Transactions of the Missouri Academy of Sciences*, 20: 25-35.
- Sih, A., J. Petranka, W. and Kats, L. B. (1988) The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. *American Naturalist*, 132: 463-83.
- Smith, D. C. (1983) Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale. *Ecology*, 64: 501-10.
- Strefferud, J. A., Propst, D. L. and Burton, G. L. (1992) Use of antimycin to remove rainbow trout from White Creek, New Mexico. In Hendrickson, D. A. (ed.). Proceedings of the Desert Fishes Council. Volumes 22 and 23, 1990 and 1991, Annual Symposia and Index for Volumes 16 through 23. Desert Fishes Council, Bishop, California, USA, pp. 55-66.
- Taylor, J. (1983) Orientation and flight behaviour of a neotenic salamander (*Ambystoma gracile*) in Oregon. *The American Midland Naturalist*, 109: 40-49.
- Tyler, M. J. (1963) A taxonomic study of amphibians and reptiles of the central highlands of New Guinea. *Transactions of the Royal Society of South Australia*, 86: 105-30.
- Tyler, M. J. (1997) Action Plan for Australian Frogs. Wildlife Australia Endangered Species Program, Canberra.
- Tyler, T., Liss, W. J., Ganio, L. M., Larson, G. L., Hoffman, R., Deimling, E. and Lomnick, G. (1998) Interaction between introduced trout and larval salamanders (*Ambystoma macrodactylum*) in high-elevation lakes. *Conservation Biology*, 12: 94-105.
- van de Mortel, T. and Goldingay, R. (1998). Population assessment of the endangered green and golden bell frog *Litoria aurea* at Port Kembla, New South Wales. *Australian Zoologist*, 30: 398-404.
- Voris, H. K. and Bacon, J. P. (1966) Differential predation on tadpoles. *Copeia*, 1966: 594-98.
- Waldick, R. (1997) Effects of forestry practices on amphibian populations in eastern North America. Chapter 21 In D. M. Green (ed) Amphibians in Decline Canadian Studies of a Global Problem. *Herpetological Conservation No. 1*. Society for the Study of Amphibians and Reptiles, Saint Louis, Missouri. pp. 191-205.
- Waldman, B. (1982) Sibling association among schooling toad tadpoles: field evidence and implications. *Animal Behaviour*, 30: 700-713.
- Walters, B. (1975) Studies of interspecific predation within an amphibian community. *Journal of Herpetology*, 9: 267-79.
- Wardell-Johnson, G. and Roberts, J. D. (1991) The survival status of the *Geocrinia rosea* (Anura: Myobatrachidae) complex in riparian corridors: biogeographical implications. In D. A. Saunders, and R. J. Hobbs (eds) *Nature Conservation 2: The Role of Corridors*, Surrey Beatty & Sons, Chipping Norton, NSW, pp. 167-75.
- Wasserug, R. (1971) On the comparative palatability of some dry-season tadpoles from Costa Rica. *American Midland Naturalist*, 86: 101-9.
- Watson, G. F. and Littlejohn, M. J. (1985) Patterns of distribution, speciation and vicariance biogeography of southeastern Australian amphibians. In G. Grigg, R. Shine and H. Ehmann (eds) *Biology of Australasian Frogs and Reptiles*. Royal Zoological Society of New South Wales, Sydney, pp. 91-7.
- Watson, G. F., Littlejohn, M. J., Hero, J.-M. and Robertson, P. (1991) Conservation Status, Ecology and Management of the Spotted Tree Frog (*Litoria spenceri*) Arthur Rylah Institute for Environmental Research Technical Report Series No. 116. Department of Conservation and Environment, Melbourne.
- Webb, C. and Joss, J. (1997) Does predation by the fish *Gambusia holbrooki* (Atheriniformes: Poeciliidae) contribute to declining frog populations? *Australian Zoologist*, 30(3): 316-24.
- Werner, E. E. and McPeck, M. A. (1994) Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology*, 75: 1368-82.
- White, A. and Ehmann, H. (1997) Southern Highlands Bell Frog. In H. Ehmann (ed) *Threatened Frogs of New South Wales*. Frog and Tadpole Study Group of New South Wales, Sydney, pp. 171-76.
- White, A. W. and Pyke, G. H. (1996) Distribution and conservation status of the green and golden bell frog *Litoria aurea* in New South Wales. In G. H. Pyke and W. S. Osborne (eds) *The Green and Golden Bell Frog (Litoria aurea): Biology and Conservation*. Royal Zoological Society of NSW, pp. 177-189.
- Wilbur, H. M. (1984) Complex life cycles and community organisation in amphibians. In P. W. Price, C. N. Slobodchikoff and W. S. Gaud (eds.) *A New Ecology: Novel Approaches to Interactive Systems*. John Wiley, New York. pp. 195-224.
- Wilbur, H. M. and Fauth, J. E. (1990) Experimental aquatic food webs: interactions between two predators and two prey. *American Naturalist*, 135: 176-204.
- Wilbur, H. M. and Semlitsch, R. D. (1990) Ecological consequences of tail injury in *Rana* tadpoles. *Copeia*, 1990: 18-24.
- Woodward, B. D. (1983) Predator-prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. *Ecology*, 64: 1549-55.