A review of the impact of eastern gambusia on native fishes of the Murray–Darling Basin

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Prepared by: Jed Macdonald and Zeb Tonkin

Arthur Rylah Institute for Environmental Research
123 Brown Street Heidelberg
Victoria 3084 Australia

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SUMMARY

Invasion by alien species is recognised as one of the primary threats to global biodiversity. Rapid growth in international trade is accelerating the rate of invasion worldwide and freshwater ecosystems and their native fish communities are particularly vulnerable. Alien fishes are implicated in the displacement and local extinction of many native fish species across the world. They can alter ecosystem function, impact genetic integrity and transmit parasites and disease, potentially resulting in high ecological, economic and social damage.

In Australia’s Murray-Darling Basin (MDB), alien fish species are identified as one of the key threats to the native fish fauna [MDB 2004]. The Murray-Darling Basin Authority’s (MDBA) Native Fish Strategy promotes the principles of integrated pest management to mitigate such threats, and has recently funded a three-year study entitled ‘Native fish recovery following the removal of alien fish species’ (Project MD1043) that aims to explore the relative economic costs of alien species control actions in relation to the ecological benefits to native fish communities. The Arthur Rylah Institute for Environmental Research was commissioned to undertake this project, which will use eastern gambusia (Gambusia holbrooki) as a model alien fish species, and provide a template to evaluate the relative costs of controlling other potentially harmful alien species across the MDB.

This literature review is the first output from this project. Its primary purpose is to review all known and potential impacts of eastern gambusia on native fishes in the MDB; to identify native fish species most at risk of detrimental impacts; and to document the mechanisms underpinning these impacts. Ultimately, the review aims to provide a comprehensive resource that will guide the direction of the project and inform future management strategies for eastern gambusia in the MDB. Information for the review was sourced through searches of the Web of Science, Scopus and Aquatic Sciences and Fisheries Abstract databases, the FishBase database, and from knowledge of experts in government and non-government organisations throughout Australia. These searches resulted in the compilation of several hundred published scientific articles and unpublished documents pertaining to the process of invasion by alien fishes, the biology, ecology, distribution and ecological impacts of Gambusia species around the world, in Australia and in the MDB, and options for, and effects of mitigating such impacts. These topics form the basis of this document.

The collation of biological information on wetland fishes in the MDB reveal that 16 of the 37 native freshwater species exhibit major niche overlaps (habitat and/or dietary) with eastern gambusia, and thus are at greatest risk. Specifically, the review highlights a number of key families, in particular the Ambassids (glassfish), Nannopercids (pygmy perchies), Melanotaenids (rainbowfishes), Atherinids (hardyheads), Eleotrids (gudgeons), and Retropinnids (smelt), which together make up the majority of the MDB’s wetland fish communities. Field-based studies and/or controlled aquaria experiments also indicate that eastern gambusia are likely to have contributed to the decline in distribution and/or abundance of olive perchlet, southern pygmy perch, Murray-Darling rainbowfish and purple-spotted gudgeon, which belong to these families. Conversely, other species identified to have major niche overlaps such as Australian smelt or carp gudgeon species remain relatively widespread throughout the MDB, most likely a result of high flexibility in their trophic niche, which buffers these species from such impacts. Such species are still likely to suffer localised impacts, particularly in areas of limiting resources such as habitat availability. In addition to the direct impacts eastern gambusia are likely to have on the MDB’s smaller species (occupying at least in-part, slow or still water habitats), we cannot disregard indirect impacts on larger riverine species, particularly if eastern gambusia create energetic blocks within aquatic food webs as suggested by Wilson (2006).
While the threats eastern gambusia pose to freshwater ecosystem function outside their native range are widely recognised, there is little information available on mitigating such impacts. This is due to the difficulties of removing small species in cryptic habitats using conventional control techniques and a lack of knowledge about the ecosystem-level effects of the species in invaded systems. Integrating information collected during Project MD1043 and two concurrent studies, one aimed at clarifying eastern gambusia’s dynamic food-web effects relative to the abiotic disturbance factors common to wetlands, and the other aimed at quantifying the nature and extent of aggressive interactions between eastern gambusia and native freshwater fishes in aquaria-based experiments, will provide a strong platform for determining the level of ‘impact’ eastern gambusia may exert on native fish communities in the MDB. Most importantly, this will aid in the development of a truly integrated approach to management of this alien fish species in the MDB.
Invasion by alien species is recognised as one of the primary threats to global biodiversity (Clavero and Garcia-Berthou 2005; Leprieur et al. 2008). Growth in international trade and concurrent increases in transport capacity have accelerated the rate of introduction of alien species worldwide, with freshwater ecosystems, and their native fish communities, being particularly susceptible (Vitousek et al. 1997; Sala et al. 2000; Kolar and Lodge 2002; Rahel 2002; Marchetti et al. 2004; Clavero and Garcia-Berthou 2006; Gozlan 2008). Alien fishes are implicated in the displacement, reductions in abundance, distributional range and condition, local extirpation and extinction of many native fish species worldwide (see Moyle and Light 1996; Kaufman 1992; Amundsen et al. 1999; Irons et al. 2007). They can alter ecosystem function, impact genetic integrity (Weigel et al. 2002) and transmit parasites and disease (Gozlan et al. 2005), potentially resulting in high ecological, economic and social damage (Pimentel et al. 2000, 2005, see Rowe et al. 2008).

In the last 30 years, the number of freshwater fish species translocated outside their natural range has more than doubled (see Williamson 1996), with the increase in freshwater aquaculture production identified as a major driving factor (De Silva 2006; Gozlan 2008). In an analysis of the Food and Agriculture Organisation database and FishBase, Gozlan (2008) reported that 624 species of fish have now been introduced worldwide. Fifty-one per cent of these introductions were for aquaculture production, 21% for the ornamental market and 12% for angling or sport fishing purposes, with the remainder introduced for biological control, or to fill an ecological niche. A total of 132 species were imported or exported for aquaculture practices for which data were available on the existence and nature of ecological impacts (defined in that case as negative). Of these, 103 species were introduced outside their native range, and 52% of these were reported as having no ecological impact on the native ecosystem. Further, Gozlan (2008) estimated the risk of ecological impact post-introduction of a freshwater fish species is less than 10% for 84% of introduced fishes. This estimate is quite similar to that provided by Simberloff (2007) or the ‘tens rule’ of Williamson (1996), which predicted that 10% of introductions will become established, with 10% of these in turn having an ecological impact on the recipient ecosystem (but see Gherardi 2007).

As these data suggest, despite the clear threats to recipient ecosystems posed by the invasion of alien fishes, some introductions may impart neutral, and even positive ecological, economic and social outcomes (see Copp et al. 2005; Pimentel et al. 2005; Sagoff 2005, 2007; Gozlan 2008). Moreover, how biologists, politicians and the general public judge the ‘impact’ of an alien fish species on a recipient ecosystem may differ substantially both within and between countries, and depend greatly on their perception of the relative costs and benefits (environmental, economical, social) associated with a particular alien species. Often, perceptions of a species’ worth are based on value judgments rather than scientific data (see Rosenzweig 2001).

One of the most dramatic trade-offs between economic benefits and ecological costs, and a good example of how the public perception of impacts may differ, involves introductions of common carp (Cyprinus carpio L.). Native to eastern Europe and central Asia, carp have been introduced and become successfully established in many parts of Asia, Europe, Africa, the Americas and Oceania primarily for the ornamental and aquaculture purposes (Li and Moyle 1993). In south-eastern Australia, the accidental release of the ‘Boolara strain’ of carp in the 1960s triggered a rapid population expansion (Hume et al. 1983), and recent estimates indicate that carp may now comprise over 90% of the fish biomass in many systems (Harris and Gehrke 1997). The potential ecological impacts imposed by carp include the capacity to increase turbidity and phytoplankton loads (Fletcher et al. 1985; Breukelaar et al. 1994; Roberts et al. 1995; King et al. 1997), destroy aquatic vegetation.
(Roberts et al. 1995), and alter benthic and surficial processes (Robertson et al. 1997). Although quantitative evidence of impacts on native fishes in Australia is still lacking, carp have been implicated in the decline of several species through competition for food and space (see Cadwallader 1978). The social perception of carp in Australia is generally negative, and substantial economic costs are incurred each year to fund research projects and implement carp management strategies (estimated at $4 million annually - see Bomford and Hart 2002; McLeod 2004). This value does not include the predicted economic losses due to the environmental damage caused by carp, which may total $11.8 million per year (McLeod 2004). Despite these costs, the commercial harvest of carp in Australia forms the basis of a profitable industry, with annual processing targets of over 1000 tonnes of carp per year (Keith Bell personal communication). Much of the product is exported to Europe and the Middle East for human consumption, but local demand is also high with markets for food, fertiliser production, pet food and bait for the crayfish fisheries. Several companies have greatly benefited from the prevalence of carp in Australian inland waters, and through their products may provide economic benefits to suppliers and end-users.

The perception of common carp impact in the United Kingdom is very different. Carp were introduced into the UK in the 13th or 14th Century as a food fish (Hoffmann 1996) and are now highly prized as a recreational and commercial angling species (Linfield 1980; Balon 1995). So lucrative is this fishery, that it has lead to a change in focus of aquaculture production in Europe. Formerly, the market demanded fish mainly for consumption. More recently, a significant quantity of the carp produced has been stocked into natural waters and privately owned reservoirs in the UK and mainland Europe solely for angling purposes (see Arlinghaus and Mehner 2003). Although actual figures were unavailable at the time of writing, revenue generated from private fisheries is substantial (John Littlewood personal communication), and the social benefits of carp to the angling community appear to be high. There are currently two magazines published monthly in the UK devoted entirely to carp fishing (Carpworld and Crafty Carper), and the Environment Agency (the National body charged with protecting and improving the environment in England and Wales) actively supports carp angling and does not list the species as ‘non-native’ or ‘alien’ on their website (see http://www.environment-agency.gov.uk/?lang=_e). There may be potential for carp to impart some level of negative impact to sympatric native fish species and recipient ecosystems in the UK. However, it appears that in the UK at least, 700 years post-invasion is time enough to consider an alien species almost ‘native’, especially if it is associated with significant economic and social benefits.

What constitutes an ‘alien’ species is still debated, with several definitions and terms used interchangeably in the recent literature (Williamson and Fitter 1996; Richardson et al. 2000; IUCN 2001; Clunie et al. 2002; Copp et al. 2005). The lack of consistency in definitions, particularly among government departments and management agencies, is identified as a major impediment to the development of effective strategies to prevent introductions and the establishment of alien species, and to mitigate their impacts (Copp et al. 2005). In their paper discussing the concept of ‘non-nativeness’ Copp et al. (2005) provide a very useful summary of terms. Based on several sources (i.e. IUCN 1987; Manchester and Bullock 2000), they group alien, non-native, non-indigenous and exotic into one definition: ‘a species, sub-species, race or variety (including gametes, propagules or part of an organism that might survive and subsequently reproduce; that does not occur naturally in a geographical area, i.e. it did not previously occur there or its dispersal into the area was mediated or facilitated directly or indirectly by humans, whether deliberately or unintentionally’. This definition does not cover the word ‘invasive’ for which Copp et al. (2005) provide a further definition: ‘These are native or alien species that spread, with or without the aid of humans, in natural or semi-natural habitats, producing a significant change in composition, structure, or ecosystem processes, or cause severe economic losses to human activities.’ For the purposes of this review, we define ‘alien species’ according to the IUCN definition in their 2001 Global Strategy on Invasive Alien Species: ‘a species, subspecies or lower taxon introduced outside its normal past or present distribution; includes any part, gametes, seeds, eggs or propagules of such species that might survive and subsequently reproduce (IUCN 2001). Furthermore, based on the same document, we define an invasive alien species as ‘an alien species whose establishment and spread threaten ecosystems, habitats or species with economic or environmental harm’ (IUCN 2001).
In their synthesis of global patterns of freshwater fish invasion, Leprieur et al. (2008) identified Australian freshwater systems as one of six major invasion hotspots where alien fish species represent more than a quarter of the total number of species present. Australian freshwater systems currently harbour 34 known alien fish species (Lintermans 2004), 11 of which are established in the Murray-Darling Basin (MDB) (Lintermans 2007). Four of these 11 (brown trout Salmo trutta, common carp Cyprinus carpio, rainbow trout Oncorhynchus mykiss and Gambusia species Gambusia holbrooki/affinis) are classified in the top eight ‘worst’ invasive fish taxa as detailed by the International Union for the Conservation of Nature (Lowe et al. 2000; see also Koehn and Mackenzie 2004; Fausch 2007).

The ecological consequences of invasion by these alien fishes have been a major focus of research in Australian freshwater systems (e.g. Roberts et al. 1995; Arthington and McKenzie 1997; King et al. 1997; Howe et al. 1997; Koehn et al. 2000; Jackson et al. 2004). Yet until quite recently, the potential economic and societal costs and benefits of such invasions have been mostly overlooked (but see Bomford and Hart 2002; McLeod 2004; Agtrans Research 2005; Wilson 2006; West et al. 2007). In a recent comprehensive review, Rowe et al. (2008) used a triple-bottom line approach to assess the environmental, economic and social impacts of six species of alien fish present in Australian freshwaters, including eastern gambusia (Gambusia holbrooki).

This document focuses on the impacts of eastern gambusia on native fishes in the MDB. First, we provide some background into the invasion process and the scope of impacts both globally and in Australia, illustrated with some case studies from the literature. Next, we review the history, taxonomy, biology and ecology of eastern gambusia, before discussing the relative impacts of Gambusia species around the world, in Australia and in the MDB. Potential control options and methods to mitigate the ecological impacts of the species will be reviewed, and lastly we will discuss the potential effects of control and eradication of gambusia on ecosystem processes and sympatric native fishes.
2. THE INVASION PROCESS AND THE SCOPE OF IMPACTS

2.1 The invasion process

The process of invasion by an alien species can be defined as a collection of events and processes leading to, and associated with, the establishment and impacts of the alien species on recipient communities and ecosystems (Copp et al. 2005). Several authors have attempted to summarise the process into distinct stages, in order to better understand the mechanisms underpinning invasion success or failure (see Moyle and Light 1996; Richardson et al. 2000; Kolar and Lodge 2001; Sakai et al. 2001). In a recent study to determine the best predictors of invasion success by alien fishes in Californian freshwaters, Moyle and Marchetti (2006) divided the invasion process into five major phases: i) transport to a new region; ii) inoculation; iii) establishment; iv) spread; v) integration, and discussed the relative importance of each phase as a barrier to successful invasion (see Moyle and Marchetti 2006 for definitions of each phase). Invasion success is generally conferred on species that become established, spread or proliferate in a novel region (see Colautti et al. 2006a). However, to reach the final stage of ‘integration’ into the existing ecosystem, invading alien species must survive through all preceding phases, combating substantial demographic (e.g. issues associated with small population sizes) and environmental (e.g. lack of suitable spawning habitats) stressors, while also exhibiting biological traits that promote success at all stages of invasion (e.g. high physiological tolerance). It is not surprising then, that the vast majority of invasions fail (Williamson and Fitter 1996; Jeschke and Strayer 2005).

2.2 What promotes invasion success?

Invasion success is greatly influenced by the ability of the introduced species to utilise available resources and exploit vacant and occupied ecological niches in a novel environment. Different traits of both the invader and the recipient environment may become important during the different invasion phases; for example, a characteristic that enhances a specific phase may compromise success in the next one (Kolar and Lodge 2001, 2002; Jeschke and Strayer 2006). Moyle and Marchetti (2006) identified several key factors that increase the probability of success for a given alien fish species: a history of successful establishment outside the species’ native range; biological traits that favour survival in unpredictable environments including r-selected tendencies, parental care and long lifespan (see also Marchetti et al. 2004). In addition, the existence of habitat types in the recipient ecosystem that are similar to the native habitat of the alien species; the presence of novel, favourable environments (e.g. created through human-induced disturbance); high fish species richness, including other alien fishes; release from predators, competitors, disease and parasites; and frequent invasion attempts involving high densities of invaders, are all factors that may promote successful establishment (Moyle and Marchetti 2006).

Despite the strong influence of ecological processes in facilitating successful invasions, particularly in the latter stages of the invasion process (see Colautti and McIsaac 2004; Moyle and Marchetti 2006; Gjelland et al. 2007), Leprieur et al. (2008) reported that natural processes are often overridden by human-related activities, especially economic activity, in driving successful fish invasions throughout the world’s river systems. These authors produced a global map of fish invasions incorporating datasets on fish occurrence, environmental variables and human-related activities across 1,055 river basins covering over 80% of the earth’s surface. Their analysis lends support to a ‘human activity’ hypothesis (Taylor and Irwin 2004), which argues that human-induced activities promote the successful invasion of alien fishes through disturbing natural landscapes and/or increasing propagule pressure (i.e. a measure of the number of individuals introduced and the frequency of their introduction – Williamson and Fitter 1996). This hypothesis is supported by several other studies (Colautti and MacIsaac 2004; Copp et al. 2007). For example, Copp et al. (2007) identified propagule pressure (i.e. the intensity) and diversity of live fish imports for ornamental purposes and sport fishing as principal factors governing the introduction, establishment and geographical occurrence of alien
The Invasion Process and the Scope of Impacts

freshwater fishes in England. Olden et al. (2008) found clear evidence for the homogenization of the Australian freshwater fish fauna in response to increased risk of invasion through human disturbance (i.e. physical infrastructure and land use changes). Furthermore, Leprieur et al. (2008) show that the level of human activity (expressed as gross domestic product, population density, % urban area) in a given river basin strongly predicts its invisibility, with more developed countries harbouring greater numbers of alien fish species. It follows then, that with the population of many developing countries in southern Asia, western and central Africa, predicted to rise dramatically in the next 40 years (United Nations 2007), river basins in these countries and may be particularly susceptible to future invasions by alien fishes. Given the high levels of endemism in the freshwater fish fauna of these countries, the potential threats of invasion to global biodiversity are obvious.

As discussed in the previous chapter, the consequences of successful invasion may be manifested in environmental, economic and/or social costs and benefits. The nature and relative magnitude of these impacts are difficult to predict and may alter at each phase of invasion. However, knowledge of the invading species’ biological traits, environmental tolerances, and impacts in regions where it is already established can greatly improve precision in predicting both invasion success and the subsequent impacts of invasion on the receiving system (Moyle and Marchetti 2006). Perhaps the best way to grasp the scope of impacts is to examine the consequences of some well-publicised fish invasions.

2.3 The scope of impact

2.3.1 Ecological impacts

If we examine ecological effects alone, the mechanisms of impact of alien fishes on native fishes and recipient ecosystems are many, including direct and indirect alteration of food web structure (Bøhn and Amundsen 1998); niche overlap that may drive competitive exclusion of native fishes from critical food (Bøhn and Amundsen 2001) and habitat resources (Gjelland et al. 2007; Bøhn et al. 2008); habitat modification [Roberts et al. 1995] direct predation [Adams 1991, Witte et al. 1992], pathogen transmission [Gozlan et al. 2005] or genetic effects such as hybridisation between alien and native species (Boyer et al. 2008), or among alien species (Hume et al. 1983). These factors may act alone or simultaneously on multiple trophic levels within an ecosystem (Mack et al. 2000). Thus the net impact of the invader on the recipient ecosystem is not simple to predict (Moyle and Light 1996; Williamson 1999) and may alter throughout the different phases of invasion (Kolar and Lodge 2001; Sakai et al. 2001; Moyle and Marchetti 2006; Garcia-Berthou 2007).

A good illustration of the ecosystem-wide effects at various stages of a fish invasion is shown in the body of research in Norway examining the displacement of the native whitefish (Coregonus lavaretus) by vendace (Coregonus albula) in the sub-arctic Pasmik watercourse over a 14 year period (1991-2004) (Amundsen et al. 1999; 2003; Bøhn and Amundsen 1998; 2001; Bøhn et al. 2004, 2008). Vendace were first detected in the Pasmik in 1989 (Amundsen et al. 1999), and between 1991 and 2004 the population underwent a classic boom and bust cycle, resulting in a 90% reduction in the densely-raked (dr) morph of the whitefish population over the study period, decreased growth of dr whitefish during the vendace boom, and marked alteration to the structure and dynamics of the zooplankton community. The dr whitefish naturally occupies the same ecological niche (the pelagic zone) as the vendace. It dominated this zone prior to the vendace invasion but was quickly displaced to the profundal and littoral zones as the vendace population expanded. In summarising the empirical data on the invasion, Bøhn et al. (2008) lend support to the ‘Competitive Exclusion Principle’ and state that the primary cause of the whitefish decline was asymmetrical competition with the invading vendace, and the competitive exclusion of whitefish from their preferred pelagic habitat. These authors also suggest that indirect interactions arising from the niche shift of dr whitefish to the littoral zone (i.e. increased competition with the other sympatric whitefish morph – the sparsely-rakered whitefish, and increased predation by pike) may have also contributed to the whitefish decline.

Ecological change driven by fish invasions is often intrinsically linked with impacts on humans. Perhaps one of the most well publicised examples of the potential for ecological, economic and social impacts following an alien species invasion involves the apparent extinction of c. 200 species of haplochromine cichlids following the explosion of the Nile perch (Lates niloticus L.) population in Lake
Victoria in the mid-1980s, 30 years after its introduction [Kaufman 1992; Witte et al. 1992; Goldschmidt et al. 1993; Balirwa et al. 2003]. The Nile perch was introduced to support the local economy and subsequently sustained an extensive and viable commercial fishery, generating hundreds of millions of dollars revenue at its peak [Pitcher and Bundy 1994]. The profit from Nile Perch exports to bordering Uganda, Kenya and Tanzania continues to be an important economic driver for the region; however, the distribution of wealth is unbalanced and the environmental costs are substantial. Although losses of haplochromines may also have been partially mediated by human-induced changes to the watershed [see Balirwa et al. 2003], the removal of approximately 65% of the endemic planktivorous cichlids drastically altered the food web dynamics of the lake, and drove major changes in the species targeted by the lake’s commercial fishers [Witte et al. 1992; Balirwa et al. 2003]. A resurgence of indigenous species is recently evident, due at least in part to overfishing of Nile perch in the system [Witte et al. 2000], resulting in changes to the targeted catch of local fishers.

2.3.2 Economic impacts

The estimation of economic costs and benefits associated with invasive alien species is critical to sound environmental management and policy development yet relatively few studies have quantitatively evaluated the impact of invasive alien species on local and national economies (but see Pimentel et al. 2006b). This is particularly true in Australia, where robust economic assessments of species invasions are rare, and for freshwater fish invasions to our knowledge total one, for carp [McLeod 2004; Rowe et al. 2008]. The only other available cost estimates for alien fishes in Australia relate to eastern gambusia control. The 2003 NSW threat abatement plan estimated that research and control costs for gambusia would equate to $220,000 over five years, and the new MDBA project ‘Native fish recovery following the removal of alien species’, for which this review is produced, is funded for approximately $450,000 over three years. Globally, the estimated total economic cost of alien invasive species reaches into the trillions of US dollars [Pimentel et al. 2001]. This is most likely an underestimate, as most economic evaluations consider only direct costs associated with control programs, research funding or loss of marketable goods or services. This is primarily due to the difficulty associated with calculating indirect market and non-market costs and expenses to other parties not obviously affected by the invasion (i.e. externality costs, see Colautti et al. 2006b).

The introduction of the Zebra mussel (Dreissena polymorpha) into the Laurentian Great Lakes in the USA illustrates the potential complexity associated with accurately measuring the economic impacts of an invasion. Zebra mussels are believed to have been transported to the Great Lakes through ballast water releases, and were first detected in Lake St Clair in 1988. The mussels rapidly spread eastwards through Lakes Erie and Ontario [Riessen et al. 1993] and are now present in many major waterways in the US and Canada. Some of the first economic losses were to the electrical power industry when water treatment facilities became infested with mussels [Colautti et al. 2006b]. This had substantial impacts on water delivery to hydroelectric, industrial and municipal users, necessitating the implementation of large-scale and costly control measures (i.e. market impacts, see Maclsaac 1996). Large densities of mussels colonised rock surfaces, macrophytes, native molluscs, canal and dock walls, and caused serious damage to boats and outboard motors (i.e. non-market impacts). Concurrently, the mussels ability to reduce water turbidity increased macrophyte production in some systems. The proliferation of macrophytes in turn increased production of geosmin, a compound that affects the taste of potable water [see Maclsaac 2002 cited in Colautti et al. 2006b]. Affected municipalities demanded improved water quality, and this cost the City of Windsor in Ontario between $400,000–$450,000 Canadian per year for activated charcoal treatment [Colautti et al. 2006b].

Clear economic benefits can also result from the invasion and establishment of alien fish species. In the US, recreational fishing that targets alien fishes contributes many billions of dollars per year to the US economy [Bjergo et al. 1995 cited in Pimentel et al. 2005]. However, the net annual economic loss due to negative ecological impacts of alien fishes on native fishes and aquatic biota is estimated at $5.4 billion annually (see Pimentel et al. 2005). In southern Australia, recreational angling for introduced brown and rainbow trout provides substantial benefits to local and state economies [Unkles 1997; Jackson et al. 2004], as well as many social benefits to anglers and communities. Over 25,000 trout fishing licenses are sold in Tasmania annually, and the fishery injects approximately $40 million into the State’s economy each year through tourism alone [IFS 2008].
2.3.3 Social impacts

The effects of alien species on societal values is perhaps the most difficult to quantify, and thus has received the least attention of the ‘triple bottom line’ impacts. Measures of social impact are often qualitative, based on community, individual or cultural perception. However, in some cases the perception of a particular alien species may be linked with economic costs or benefits to tourism, commercial or recreational activities [Agtrans Research 2005], measures that sometimes may be more quantifiable [Rowe et al. 2008].

Recognising the need for more robust information, Rowe et al. [2008] recently developed a Social Impact Assessment (SIA) framework for six alien fish species in Australia, including eastern gambusia, to identify the type and magnitude of impacts these species may have on society, and the public perception of such impacts. A review of the existing literature was undertaken, the results of which informed the development of a stakeholder consultation process involving representatives from scientific, environmental and fishing-related backgrounds across Victoria, South Australia and New South Wales. The literature review revealed that alien species in Australia may impact on social values through a decline in local economies, for example, through a reduction in tourism, agricultural productivity, electricity production, employment opportunities and loss of amenity values. Yet some species may also contribute positively to local businesses and communities through recreational angling pursuits and profitable commercial harvest. Furthermore, the review found that to date, there has been very limited assessment of socio-economic impacts on Indigenous communities and their cultural values. Based on this information, Rowe et al. [2008] defined six key socio-economic and cultural attributes that may be affected by the six alien fish species: 1) way of life, 2) culture and community, 3) the environment, 4) health and well being, 5) personal property rights and 6) fears and aspirations. Rowe et al. [2008] collated anecdotal data on each of these through the stakeholder consultation process. They concurrently developed a risk classification framework for each attribute to determine the likelihood of each alien species impacting upon it. Results of the SIA suggest that apart from anglers and those involved with native fish species conservation, community awareness of the value or impacts of alien fish species in Australian freshwater systems is low. All stakeholders considered eastern gambusia a ‘nuisance’ species with no ecological, economic or social value. Redfin perch were highly prized by recreational anglers in Victoria, but were also recognised as harbouring Epizootic Haemotopietic Necrosis Virus (EHNV), which may be transferred to other recreational target species. These two species, in addition to tench (Tinca tinca) and roach (Rutilus rutilus) were regarded as capable of preying upon and competing with native fishes, which may reduce recreational fishing opportunities and cause ecological harm—both undesirable social outcomes.

Rowe et al. [2008] stress that the SIA outlined above is of a preliminary nature, and recommend further refinement and testing of the framework in specific locations and for specific species. This assessment highlights the importance of building social impacts into any examination of ‘impact’ of alien invasive species, and how often the line between social, ecological and economic impact is blurred.

In relation to eastern gambusia, the social perception of the species is generally negative in Australia, yet the current impact of the species on social values appears to be relatively low [Wilson 2006; Rowe et al. 2008]. At present, the ecological impact eastern gambusia have on native fishes, frogs and ecosystem processes, and the economic costs incurred through funding research into effective management and control options appear to comprise the scope of the species’ impact. In the case of eastern gambusia control, the benefits of controlling or eradicating populations do not have a quantifiable monetary value, thus they cannot be directly contrasted with the costs of control (i.e. research, sampling time and effort). Under these conditions, bioeconomic modelling can be used to identify strategies that maximise the level of improvement to the native fish community of various control options given a fixed budget (budget maximisation), or minimise the cost of achieving a defined significant improvement in a native fish community (cost minimisation) [see Choquenot et al. 2004; Koehn and MacKenzie 2004]. Such modelling techniques (including a robust estimation of the economic costs associated with physical control of eastern gambusia) will form a major component of Project No. MD1043. Accordingly, we will not deal with economic impacts further in this review. We discuss the ecological impacts associated with the species in Chapter 4.
There is an extensive array of literature available on eastern and western gambusia (Gambusia affinis) due to their widespread distribution, high abundance, ease of capture and maintenance and mixed attitudes towards them (Pyke 2005). McKay et al. (2001; and subsequent NSW NPWS report 2003), Pyke (2005, 2008), Maynard et al. (2008), and Rowe et al. (2008) have recently presented extensive reviews on eastern gambusia including taxonomy, biology and ecology of the species. These reviews complement the numerous publications regarding this species (e.g. McKay 1984; Meffe and Snelson 1989; McDowall 1996; Lintermans 2007). While detailed information on these attributes is best referred to the aforementioned, we present a brief summary of this information to aid the subsequent chapters of this review.

3.1 Taxonomy and morphology

Family: Poeciliidae
Scientific name: Gambusia holbrooki (Girard 1859)
Common names: Eastern gambusia, Gambusia, Mosquito fish, Plague minnow, Top minnow

The generic name Gambusia is derived from a Cuban word Gambusino, meaning nothing, or a joke or farce. Additionally, in Latin the word also means nothing (Clunie et al. 2002; Pyke 2005) suggesting the genus was viewed as a somewhat irrelevant group of fishes. The common names applied to Gambusia appear to reflect aspects of the species behaviour, for example the name top minnow reflect its tendency to swim near the surface, plague minnow referring to the species negative impacts on native fauna, and mosquito fish referring to its reputation for controlling mosquito populations.

Multiple changes in taxonomic classification of the G. affinis and G. holbrooki species complex as well as poor records of global transfers lead to much speculation over whether the species existing in Australia was G. holbrooki, G. affinis, both, or a hybrid [see McKay et al. 2001]. It has been confirmed that the species present across the whole country is in fact G. holbrooki (Pyke 2005) and for the purposes of this report, will be referred to as eastern gambusia [unless otherwise stated].

Eastern gambusia are a small (< 60 mm) poeciliid fish distinguished by their stout body, large cycloid scales, and a flattened upper head with a small up-turned mouth (Karolak 2006). They possess strong conical teeth and a shortened oesophagus and intestine, which are typical traits of predatory fish (Pyke 2005). They usually have an olive-brown back, blue-grey sides and are white-silver on their underside (Lintermans 2007). They are a sexually dimorphic species with females larger and much deeper bodied than males, possessing a large dark spot near the vent (Figure 1.). Males, which cease to grow after maturation, are generally slimmer and possess a slender elongated anal fin used for copulation (McKay et al. 2001; Karolak 2006).
3.2 Biology and ecology

3.2.1 Age structure
Eastern gambusia are typically a short lived species, generally living for a few months and dying in the same season in which they mature (McKay et al. 2001). Females maturing towards the end of the season have been recorded living up to 15 months (Cadwallader and Backhouse 1983, McKay et al. 2001) while Karolack (2006) reported a lifespan of up to three years for the species. Males and females generally mature at about the same body length (17-20 mm), at one and two months of age (Pyke 2005). Growth and maturation rates are highest when water temperatures are between 25-30 °C (Pyke 2005).

3.2.2 Reproduction
Like most Poeciliines, fertilisation in eastern gambusia is internal and young develop inside the mother until they are born as free swimming fish (Parenti and Rauchenberger 1989; Pyke 2005). Both male and female fish have an annual reproductive cycle with a distinct breeding season from spring until autumn, peaking during the warmest times of the year. Females can store viable sperm in their oviducts for several months, having considerable flexibility in the timing of egg fertilisation (Pyke 2005). A single previously fertilised female can colonise a new site but seasonal timing and duration of spawning is strongly governed by water temperatures and daylength with temperatures over 16 °C and daylengths over 12–13 hours required to initiate spawning (Pyke 2005).

Female eastern gambusia can have several broods in a single breeding season, with large females reported having up to 9 broods in the wild (Milton and Arthington 1983), although 2–5 broods per season is more typical (Pyke 2005). The clutch size of each brood is extremely variable, and dependant on age, time of season, food availability, female size, and geographic location (Pyke 2005).
2005). Clutches are typically around 50, but have been reported as high as 375, and as low as a single offspring (Cadwallader and Backhouse 1983; Milton and Arthington 1983; Rowe et al. 2008). The gestation period for each brood can range from 15–50 days depending on water temperatures but is usually around 22–25 days (Milton and Arthington 1983). With females unable to be fertilised until after a litter is released, and a delay of 2–14 days between birth and fertilisation, broods can be produced every three to four weeks (Pyke 2005). Maglio and Rosen (1969) reported that on average, females produced a brood every 25 days. Such information on the average number of broods and clutch size of a population allows an estimate of its total lifetime fecundity (Rowe et al. 2008). While not accounting for factors such as predation and resource availability, Maglio and Rosen (1969) calculated that 10 adult females could produce a population of 5 million individuals in a six-month period, such is the reproductive potential of the species.

Eastern gambusia often assume plague proportions in favourable habitats due to its rapid breeding ability (Lintermans 2007). Rowe et al. (2008) reported large aggregations reaching hundreds of fish per square meter can occur in surface waters of lakes and ponds during summer months (Figure 2). Much lower densities of eastern gambusia are observed in the winter, although it is unclear whether this is due to reduced population sizes due to mortality, or to sheltering behaviour that makes them less observable (Pyke 2005).

Figure 2. High densities of eastern gambusia in a shallow backwater environment.  
Photo: Tarmo Raadik.
3.2.3 Habitat and behaviour

Typical of a successful alien fish species, eastern gambusia can exist in a range of habitat types, including large rivers, creeks, wetlands, lakes, channels and bores. They are poor swimmers and prefer still waters to flowing waters (Rowe et al. 2008), and therefore are most commonly found in areas such as wetlands, weir pools, lakes and backwaters (Figure 3). Eastern gambusia tends to prefer shallow areas (often less than 15cm) within these macro-habitats, mostly around the littoral margins, in surface waters or amongst freshwater plants (Karolak 2006; Lintermans 2007; Rowe et al. 2008). Additionally, Stoffels and Humphries (2003) reported that larger fish preferred the benthic areas around macrophyte beds. Water velocity barriers such as those formed by rapids, chutes and falls limit its upstream penetration because it is not able to tolerate fast-flowing areas (Rowe et al. 2008).

Eastern gambusia are not known to undertake active migrations. Individuals generally move within relatively small areas (Pyke 2005; Rowe et al. 2008). Exceptions include downstream displacement during flooding, and perhaps seasonal movement to deeper water before the onset of winter (Pyke 2005). Although Lyon et al. (in review) reported movement of eastern gambusia between the main river channel and off-channel environments, with the highest numbers of fish moving during the day. It is not known whether this was an active migration, or given their diurnal feeding pattern (see below), just part of daily feeding behaviour into off-channel habitats.

Eastern gambusia have a remarkable ability to withstand adverse conditions (McKay et al. 2001). The species is extremely tolerant of poor water quality in particular high turbidity, extremes of temperature and salinity ranges, and low dissolved oxygen (Karolak 2006), reflecting its success as an invasive species in Australian floodplain habitats. While eastern gambusia can tolerate a wide range of temperatures (1.8-38°C), its preference and reproductive requirement for high temperatures (see above) indicate it is a warm water species (Pyke 2005; Rowe et al. 2008). McNeil and Closs (2007)
reported eastern gambusia's extreme tolerance of low dissolved oxygen levels in both controlled conditions and MDB floodplain habitats, demonstrating the species ability to comfortably utilise aquatic surface respiration through severe hypoxia and into anoxia. The authors suggested the species flattened head and upturned mouth indicate eastern gambusia are morphologically adapted for this aquatic surface respiration.

Disturbed habitats are particularly susceptible to eastern gambusia invasion given their extreme tolerance of poor water quality [Arthington et al. 1983; Kennard et al. 2005; King and Warburton 2007]. This is evident in many urban systems that have suffered extreme habitat alteration. For example, habitat alteration and subsequent water pollution have contributed to the decline of native fishes and successful establishment of eastern gambusia in urban Brisbane waterways [Arthington et al. 1983]. Additionally, the construction of dams and weirs reduce water discharge and subsequent flow velocities, creating additional favourable habitat for eastern gambusia [McKay et al. 2001]. Alternatively, undisturbed lotic systems with naturally variable discharge regimes are not favoured by eastern gambusia with higher river discharges reducing, and in some cases, almost eliminating populations [Arthington and Lloyd 1989; Arthington et al. 1990; McKay et al. 2001; Chapman and Warburton 2006].

Eastern gambusia exhibit both social and anti-social behaviour (Pyke 2005). On one hand they are a schooling fish, often occurring in large aggregations. Yet on the other hand, the species is well known for both intra- and inter-specific aggression towards other fish, often chasing and nipping the fins of fish much larger than themselves (Lintermans 2007). The effect of this behaviour is discussed in chapter 3.3.

3.2.4 Diet and feeding

Eastern gambusia feed during daylight hours and rely on sight to detect and attack prey [Swanson et al. 1996; McKay et al. 2001]. The species is primarily carnivorous (as indicated by their dentition and digestive organs), with a generalist diet including a range of aquatic macro invertebrates, terrestrial insects and arachnids, and the early life history stages of fish and anurans [Arthington and Marshall 1999; Ivantsoff and Aarn 1999; Stoffels and Humphries 2003; Pyke 2005]. Cannibalism of young is also known to occur [Maglio and Rosen 1969; Maynard et al. 2008]. Eastern gambusia are best described as an opportunistic or generalist omnivore as the species has also been reported to consume filamentous algae, fragments of fruit and other plant tissue [Arthington and Marshall 1999; McKay et al. 2001; Maynard et al. 2008]. McDowall (1996) described eastern gambusia as an adaptable generalist predator, able to vary its diet according to available prey. For example, researchers conducting seine netting surveys in a floodplain billabong observed large female eastern gambusia attacking and then ingesting recovering juvenile carp gudgeon that had been released after sampling [Tonkin pers. obs.]. Indeed, the generalist or opportunistic nature of eastern gambusia’s feeding habits is another reason for its success as an invasive species.

The flattened head and upturned mouth of eastern gambusia, coupled with its tendency to occupy surface waters indicate that a large proportion of its diet is sourced from or near the surface. Given the relatively small mouth of eastern gambusia, prey size is typically small, but increases with increasing fish size (Pyke 2005). Therefore, larger females can be expected to have a wider diet.

While mosquito larvae are consumed by eastern gambusia, they have been shown to make up a very small proportion of their overall diet [Lloyd 1986; Arthington and Lloyd 1989]. Furthermore, while used extensively throughout the world as a mosquito control agent, there are no striking examples of its effectiveness in reducing mosquito populations [Lloyd 1990].

3.2.5 Predators, parasites and disease of eastern gambusia

In its native range, eastern gambusia are susceptible to numerous predators, parasites and diseases [see Swanson et al. 1996]. In Australia however, it appears there are very few control agents. Other than the introduced Lernia, few species parasitise eastern gambusia in Australia compared to native species, which may carry at least two or three parasite species. This relatively light parasite burden may have also contributed to its success as an invader in Australia [Lloyd 1990].
There has been little work on predation of eastern gambusia in Australia although predators are likely to include birds such as cormorants and egrets [e.g. Boulton and Brock 1999, cited in Rowe et al. 2008], aquatic mammals [e.g. Lloyd 1987], invertebrates such as crayfish [e.g. Beatty 2006] and fish. In particular, another introduced fish, redfin perch (Perca fluviatilis) are thought to prey heavily on eastern gambusia, with Stoffels and Humphries (2003) and McNeil (2004) suggesting presence of this exotic predator may govern the densities of eastern gambusia in Australian floodplain billabong habitats. The level of predation by these organisms on eastern gambusia is largely unknown. For example, while the introduced redfin perch has been documented to influence eastern gambusia numbers by direct predation, both native and exotic fish predators avoid eastern gambusia as prey when given a choice, implying that the species still has the ability to establish large populations in the presence of large predator populations (Lloyd 1990).

3.3 Global distribution and spread into Australia and the MDB

Eastern gambusia are native to the south-east of the United States of America and Northern Mexico (McKay et al. 2001), but it was not until they were recognised as a potential biological control agent that they became one of the most widespread genera of fish species in the world. The genus is now present in all continents except Antarctica (Courtenay and Meffe 1989).

After the discovery that mosquitoes were responsible for the transmission of diseases such as malaria and yellow fever, health authorities began searching for mosquito control techniques, including the new concept of biological control [Lloyd 1990; McKay et al. 2001]. During the early 1900s, scattered anecdotal evidence of eastern gambusia successfully controlling mosquito populations led to their widespread use as a biological control, despite limited research into their capabilities or the utility of native species as mosquito control agents (Lloyd 1990; McKay et al. 2001). This resulted in widespread introductions of eastern gambusia into freshwater environments throughout the world, particularly from 1920–1940, including the first introduction into Australia in 1925 [Rowe et al. 2008].

Shortly after the initial introduction of eastern gambusia into the Botanic Gardens, Sydney, the species spread throughout New South Wales to the point that they were established in most of the state by the early 1940s (McKay et al. 2001). At this time, fish were released in north Queensland, parts of the Northern Territory, South Australia, Victoria and Western Australia, all for the purpose of mosquito control (McKay 1984; Maynard et al. 2008). Eastern gambusia were recorded in Tasmania in 1992, believed to be a result of an unauthorised release into a private dam (Maynard et al. 2008). Arthington and McKenzie (1997) reported the species was still being spread about Australia for mosquito control during the late 1990s, despite substantial evidence that native species were more effective at mosquito reduction than eastern gambusia (Lloyd 1990). Most states have since adopted legislation that has meant the species is no longer advocated as a mosquito control agent [see Chapter 5.1] and therefore unlikely to be intentionally distributed. Further spread of the species is most likely to occur during widespread flooding dispersing individuals from existing populations [e.g. McKay 1984] and from populations existing in irrigation channels and bore drains (McKay et al. 2001).

Currently, eastern gambusia are present in all states, having established populations throughout most of the major drainage divisions across the country (Rowe et al. 2008). This includes most of the eastern drainage division, from Port Douglas in Queensland’s north, extending south to Adelaide (McDowall 1996; Arthington and McKenzie 1997; Rowe et al. 2008). In Western Australia they are extremely abundant in the south-west, southern Pilbara and a small population has been discovered in an isolated region of the Kimberley (Morgan et al. 2004). Several populations have been discovered in Darwin, several eastern catchments draining into the Gulf of Carpentaria and in central Australia’s Lake Eyre drainage region (Rowe et al. 2008). Isolated populations have also established in northern Tasmania’s Tamar basin (Maynard et al. 2008).

Eastern gambusia are now present in all river basins of the MDB (MDBC 2008), being common and frequently present in very high abundances in farm dams, slow flowing waters and shallow wetlands (Lintermans 2007). They have been recorded at altitudes from 20–1120 m although most fish have been recorded below 300 m (Faragher and Lintermans 1997; McKay et al. 2001) which is not surprising given their preference for warm water and low flow. The only areas where they have not been recorded are the higher altitudes in the south-eastern alpine areas, and the upper reaches of parts of the Condamine and Warrego basins (Lintermans 2007).
4. IMPACTS OF GAMBUSIA AS AN ALIEN SPECIES

4.1 Introduction
Eastern gambusia’s aggressive nature, high reproductive potential, fast maturation rate, flexible behaviour and broad environmental tolerances have contributed to their success as invaders, and the species is considered to pose a serious threat to native fishes in Australia and overseas (Courtney and Meffe 1989; Howe et al. 1997; Caiola and de Sostoa 2005; Rowe et al. 2008). Eastern gambusia also have a demonstrated ability to negatively affect frogs (see Webb and Joss 1997; Gillespie and Hero 1999; Goodsell and Kats 1999; Komak and Crossland 2000), influence macroinvertebrate, zooplankton and phytoplankton communities (Hurlbert et al. 1972; Margaritora et al. 2001; Cardona 2006; Angeler et al. 2007), and enhance primary productivity through increasing allochthonous nutrient loads (Hargrave 2006). Such impacts can also indirectly affect native fishes by reducing or removing available prey resources, and altering physiochemical properties such as turbidity, water temperature and phosphorous cycles (Hurlbert et al. 1972). Changes to these variables may interfere with normal feeding, sheltering or reproductive strategies of native fishes and alter ecosystem level processes (Cardona 2006). Recently, Pyke (2008) completed a thorough review of the impacts of the eastern and western gambusia on aquatic systems, giving particular attention to the documented impacts of both species on mosquitos, other invertebrates, amphibians, planktonic communities and ecosystem functions. Accordingly, we have decided to focus the following discussion on the impacts of Gambusia species on native fishes alone, and draw attention to Pyke (2008) for further information on indirect effects and ecosystem level responses, and to Gillespie and Hero (1999) and Rowe et al. (2008) for reviews on the effects of eastern gambusia on Australian native amphibians.

A substantial portion of the literature devoted to the impacts of Gambusia species has been based on studies conducted in the USA and Australasia, focussing on the closely related western gambusia (e.g. Laha and Mattingly 2007; Rowe et al. 2007). Given the similarities of the two species in body size, diet, feeding rates, reproductive capacity and habitat requirements (Rehage et al. 2005), their mechanisms of impact may be similar; notwithstanding the potential for such mechanisms to be strongly mediated by the local physical environment, and the diversity and abundances of fish species present (Courtney and Meffe 1989; Rowe et al. 2008). In order to provide a global perspective on the impacts of Gambusia species on native fishes, we first discuss the types of impacts documented for both species and the main mechanisms underlying them. We then focus more specifically on the impacts of eastern gambusia in Australia and the MDB.

4.2 Impacts on native fishes across the world
Western and eastern gambusia have been introduced to over 60 countries in total (Garcia-Berthou et al. 2005), with populations of eastern gambusia now established in 21 of these (Froese and Pauly 2007 – Fishbase). Direct predation on native fishes (Myers 1965; Meffe 1985; Lloyd et al. 1986; Barrier and Hicks 1994; Ivantsoff and Aarn 1999; Rincón et al. 2002; Laha and Mattingly 2007); competitive exclusion from food resources and habitat resulting in displacement of native fishes from optimal niches (Arthington et al. 1983; Meffe 1985; Lloyd 1987, 1990; Howe et al. 1997; Rincón et al. 2002; Caiola and de Sostoa 2005, but see Becker et al. 2005) and aggressive interactions in confined environments (Barrier and Hicks 1994; Howe et al. 1997; Gill et al. 1999; Knight 1999; Warburton and Madden 2003; Laha and Mattingly 2007; Rowe et al. 2007) have been well documented, with implications ranging from reduced condition of native fishes (e.g. stunted growth, reduced ovarian weight and low fecundity; Howe et al. 1997; Mills et al. 2004; Ling and Willis 2005) and increased susceptibility of individuals to secondary infection through damage to skin and fins (i.e. via fin-nipping) (Meffe et al. 1983), to mortality-/competitive interference-driven reductions in population size and distribution (see Galat and Roberston 1992).
Combinations of these mechanisms may be acting simultaneously, and the magnitude of impacts on a given species may vary between day and night, seasonally, and with ontogeny (Mills et al. 2004; Ayala et al. 2007). For example, in mesocosm experiments in Utah, USA, predation by western gambusia upon least chub (Iotichthys phlegethontis) was found to decrease as least chub size increased; yet western gambusia were aggressively dominant over least chub and negatively affected growth over all young-of-the-year size classes (Mills et al. 2004). However, in a related study in natural spring systems, Ayala et al. (2007) observed that the extent of impacts may also be mediated by changes in seasonal and diel habitat use of these two species. Greater overlap in use of shallow, warmer habitats during the spring coincided with the least chub spawning period. The authors attributed the marked reduction in recruitment of least chub in spring to increased predation pressure driven by resource overlap at that time. During the summer months, least chub exploited cooler, deeper habitats, free of western gambusia, and/or moved to shallow, warmer habitats at night when western gambusia were less active. The availability of such habitats, even though sub-optimal, may have acted as a buffer, reducing the magnitude of impacts and promoting coexistence of chub with western gambusia. Asynchrony in spawning times may also provide such a buffering effect. Pen and Potter [1991] found no evidence of predation or aggressive behaviour by eastern gambusia on eggs or larvae of native nightfish (Bostokia porosa), western minnow (Galaxias occidentalis) and western pygmy perch (Edilia vittata) during their study in the Collie River, Western Australia. They attributed these findings to the pre-summer spawning period of the three natives, a time when eastern gambusia densities were still at low over-wintering levels.

The nature of interactions between Gambusia species and sympatric fish species may also strongly depend on the relative densities, and behaviour of the species present. In a series of tank experiments investigating behavioural interactions between eastern gambusia and several small Australian native fishes, Knight (1999), Breen (2000) and Conte (2001) demonstrated that interference competition and aggression towards Pacific blue-eye (Pseudomugil signifer), Duboulay’s rainbowfish (Melanotaenia duboulayi), ornate rainbow fish (Rhadinocentrus ornatus) and firetail gudgeon (Hypseleotris gali) increased with relative densities of eastern gambusia. With regard to Pacific blue-eye, these aggressive interactions were manifested in substantial physical damage (i.e. fin-nipping and skin damage) and changes in the schooling behaviour of the species. By contrast, Miles (2001) recorded reduced levels of aggression on olive perchlet (Ambassis agassizii) at higher eastern gambusia densities, as did Cronin (2001) for oxleyan pygmy perch (Nannoperca oxleyana) and firetail gudgeon. While these studies provide useful information on the nature and extent of potential interactions in confined environments, tank experiments clearly do not reflect conditions in natural systems, or account for the inherent environmental variability within them. The complexity of micro-habitats in natural systems, for example, may allow some native fishes with high trophic niche flexibility to shift niches to those not utilised by Gambusia, thereby potentially reducing resource overlap and competitive interactions, and tempering the impacts of high Gambusia densities.

Native fishes have displayed avoidance mechanisms by exploiting vacant dietary or habitat niches in response to localised population expansions of eastern gambusia (Lloyd and Walker 1986; Lloyd 1987, 1990; Arthington 1991; Keller and Brown 2008). Pitman and Tinkler (2007) recorded eastern gambusia in 54% of sites in which dwarf galaxias occurred in a recent investigation into the status of dwarf galaxias (Galaxiella pusilla) populations in West Gippsland, Victoria. Aggressive interactions were intensified at sites with high eastern gambusia densities, often resulting in the marked reduction in weight and body condition of dwarf galaxias (Figure 4). Abundant aquatic vegetation appeared to provide a refuge in some of the sites where the two species co-existed that mitigated these interactions and allowed reasonable populations of dwarf galaxias to persist. Further, in small aquaria, Keller and Brown (2008) documented differences in the response of populations of...
ornate rainbowfish (Rhadinocentrus ornatus) that had previously lived in sympatry or allopatry with eastern gambusia. Sympatric populations of ornate rainbowfish appeared to display a niche shift, with individuals utilising alternative micro-habitats to eastern gambusia and therefore reducing the occurrence of aggressive interactions. This niche shift was not evident in the allopatric populations. Individuals occupied open-water habitats that overlapped substantially with the dietary and habitat niches preferred by eastern gambusia. Consequently, a higher frequency of aggressive encounters between the species was observed. Keller and Brown (2008) suggest that sympatric populations have developed or evolved behavioural responses to the presence of eastern gambusia that facilitate coexistence between the species. If this is the case and there is some time lag before such avoidance mechanisms take effect, it follows that the impacts on some native fishes may be greatest during the period immediately after colonisation by eastern gambusia (Keller and Brown 2008).

Variation in physicochemical and environmental parameters such as dissolved oxygen (DO) concentration, the extent of macrophyte cover and complexity, the size and depth of the waterbody, salinity and temperature may also influence the nature of interactions between eastern gambusia and sympatric fishes (McNeil 2004; Rincón et al. 2002). In a study examining the hypoxia tolerance of 10 fish species (including eastern gambusia) inhabiting the Ovens River floodplain billabongs, in north eastern Victoria, McNeil (2004) suggested that the physicochemical environment, particularly DO levels, may influence the composition and abundance of species partly through the exclusion of intolerant species from environmentally harsh habitats. This in turn may mediate potential predatory and competitive interactions, advantaging highly tolerant species like eastern gambusia, particularly in small, shallow lentic systems. By contrast, high salinity has been suggested to limit the invasive success of eastern gambusia (Nordlie and Mirandi 1996; Alcaraz and García-Berthou 2007). In a study examining the role of salinity in mediating the competitive interactions between eastern gambusia and an endangered Mediterranean cyprinodont (Aphanius fasciatus), eastern gambusia decreased aggressive behaviour towards the cyprinodont and captured less prey at higher salinities (~ 25 ppt). This allowed the salt tolerant cyprinodont to capture more prey as salinity increased (Alcaraz et al. 2008). In a related study, Alcaraz and García-Berthou (2007) reported that female eastern gambusia presented earlier maturation and higher reproductive investment at high versus intermediate salinities, but this was associated with a significant reduction in body condition and abundance.

Seasonal alteration to natural or managed flow regimes and associated changes to aquatic ecosystem processes can increase spatial and trophic overlap in habitat and feeding niches among Gambusia species and native fishes, potentially magnifying competitive interactions (McNeil 2004). This may be particularly evident in small enclosed waterbodies during drying periods. As demonstrated by Fairfax et al. (2007) in the Great Artesian Basin, impacts of eastern gambusia on fishes such as the endemic red-finned blue-eye (Scaturiginichthys vermeilipinnis) may be exacerbated in closed habitats such as off-channel wetlands, springs and billabong systems, particularly during late summer when these areas experience receding water levels, coinciding with and immediately following the major eastern gambusia spawning period. Furthermore, in New Zealand, (see Hayes et al. 1992; Chisnall and West 1996; Glova and Sagar 2000) the marked reduction in condition and survivorship of Galaxias maculatus (via fin-nipping in tank experiments) documented by Rowe et al. (2007) implies that in shallow lagoons, ponds and wetlands with an absence of deep water habitats, and where the two species coexist, Gambusia species may potentially threaten the persistence and fitness of G. maculatus populations.

It has been well documented that the loss of genetic diversity and reduction in fitness resulting from reduced/fragmented populations pose major risks to biodiversity and native fish species worldwide (Weigel et al. 2002). Yet the associated processes hybridisation and introgression can also be beneficial to particular species and may contribute to the evolutionary process (Rowe et al. 2008). Rowe et al. (2008) defined hybridisation according to Arnold (1997) “natural hybridisation involves successful mating between individuals from two populations, which are distinguishable on the basis of one or more heritable characteristics.” The probability of hybridisation and introgression increases with the species’ relatedness, habitat and behavioural overlap, and reproductive compatibility. When defining a level of genetic threat posed by eastern gambusia to Australian native fishes, Rowe et al. (2008) discussed the likelihood of such processes occurring in Australian freshwater systems. They
concluded that due to the marked differences in the ecology of native species and alien species, the potential for hybridisation between them is relatively low [see also Arthington 1991].

Perhaps of more concern is the potential for eastern gambusia to reduce or fragment populations of native species to levels where negative factors associated with small population size, such as inbreeding depression, and loss of allelic diversity and heterozygosity become existent [Rowe et al. 2008]. The negative effects of inbreeding are well documented [see Gall 1987; Rowe et al. 2008 for review] and include decreases in fitness and increases in deformed offspring (Kincaid 1976), and extinction probability [Saccheri et al. 1998]. There are currently six species of the family Poeciliidae extant in Australia [see Rowe et al. 2008] and hybridisation between some of these species is possible and has been demonstrated in the wild [Rosenthal et al. 2003]. Despite the morphological and genetic differences reported across the distributional range of Australian populations [Arthington 1991; Renae Ayres unpublished data], the risk of processes such as hybridisation and introgression negatively impacting native fish communities has recently been rated as low [see Rowe et al. 2008].

Figure 4. Fin-nipping and weight loss to dwarf galaxias as a result of eastern gambusia aggression and competition. The fish below and on the left (respectively) was collected from an area with high densities of eastern gambusia while the other individual was collected from a healthy population with low densities of eastern gambusia. Source: Pitman and Tinkler (2007).
A large number of Australian studies have inferred negative ecological impacts of eastern gambusia on small-bodied native fish species (e.g. Arthington et al. 1983; Merrick and Schmida 1984; Fletcher 1986; Lloyd et al. 1986; Arthington and Lloyd 1989; Lloyd 1990; Arthington 1991; Arthington and Marshall 1999; Pen and Potter 1991; Pen et al. 1993; Howe et al. 1997; Ivantsoff and Aarn 1999; Gill et al. 1999; Warburton and Madden 2003; Keane and Neira 2004; Fairfax et al. 2007; Pitman and Tinkler 2007). Others have documented no detrimental effects (e.g. Morton et al. 1988; Pusey et al. 1989).

An excellent review of these studies has been recently compiled by Rowe et al. (2008), and we do not intend to duplicate that review here. Instead, we provide a brief synthesis of existing information on the main species impacted, and discuss the key knowledge gaps, before focussing more closely on the known and potential threats to MDB species in the next section.

In analysing the existing ‘evidence of impact’ of eastern gambusia on Australian native fishes, Rowe et al. (2008) identified 23 native species (for which published information was available) that were adversely impacted. These species included several members of the families Galaxiidae, Gobiidae, Eleotridae, Melanotaenidae as well as an Ambassid (Olive perchlet) and a Retropinnid (Australian smelt) among others (see section 4.4). As Rowe et al. (2008) points out, much of this evidence is solely based on correlative field data (11 of 23 species), or on controlled tank experiments where predatory or competitive interactions may be intensified (4 of 23). Both field and mechanism-based evidence from tank experiments was available for only eight species. The mechanisms and consequences of impact documented in these studies reflect those reported in section 4.2 for small-bodied natives overseas (mechanisms: direct predation, competitive exclusion from essential food and habitat resources, aggressive interactions; consequences: increased mortality rates, decreased growth, condition, reproduction, population declines and population fragmentation) and are most likely driven by high levels of overlap in habitat use and trophic niches, mediated by the local physical environment. Quantitative information regarding the magnitude of impacts in Australia is still lacking; and caution is warranted in extrapolating tank-based experiments to larger-scale, natural systems (Ling 2004).

Eastern gambusia is one of the most widely distributed freshwater fishes in Australia and its range is still expanding. The species’ broad physiological tolerances, high reproductive capacity and proven ability to rapidly colonise degraded freshwater environments (Arthington et al. 1983; Kennard et al. 2005; King and Warburton 2007) implies that the level of impact on Australian native fishes is not stable and has the potential to increase (Rowe et al. 2008). Because invasions by alien species are generally population level processes, the most reliable ‘proof of impact’ may come from density manipulations under natural conditions, whereby eastern gambusia are depleted or removed entirely and the recovery of native fishes monitored post-removal and compared to control treatments (e.g. Peterson and Fausch 2003). Such experiments have never been attempted in Australia (Rowe et al. 2008).

### 4.4 Impacts on native fishes of the MDB

The native fish fauna of Australia’s MDB comprises approximately 46 species, with current reviews of the Retropinnidae, Galaxiidae and Eleotridae families potentially recognising several other species. This relatively poor species richness is typical of Australia’s depauperate freshwater fish fauna, which is a legacy of the continent’s long isolation, low rainfall and high proportion of arid areas (Unmack 2001; Lintermans 2007). Nevertheless, the MDB contains a variety of aquatic systems including upland and lowland rivers, wetlands, billabongs and lakes, each of which contain their own array of habitat types and associated fish communities.

Over half of the native species in the MDB are listed as rare or threatened according to state, territory or national listings (Lintermans 2007) with overall abundances thought to be around 10% of the levels prior to European settlement (MDBC 2004). Alien species make up one quarter of fish species diversity and in many areas account to 80–90% of the fish biomass. It is little wonder that alien species have been listed as one of the key threatening processes to the native fish fauna of the MDB (MDBC 2004). Furthermore, with the growing evidence of detrimental impacts on native fish fauna globally and its widespread distribution throughout the MDB, eastern gambusia has been
Impacts of gambusia as an Alien Species

identified as one of the key alien species contributing to the decline of a number of native fish within the MDB (MDBC 2004).

Despite the common view that interspecific interaction between eastern gambusia and MDB native fish is detrimental to the native species, support for such implications is largely circumstantial and like the Australia-wide evidence (see Rowe et al. 2008), is based largely on a limited number of speculative correlative studies and aquaria based experiments. While the strength of individual cases of such evidence is limited, particularly for the development of control strategies (see chapter 4.2), its collation and combination with biological information can provide a better understanding of the potential impacts of an alien species. Therefore, we must not only understand the biology of the alien species in question (identifying the reasons for its success as an invader), but also have an equally thorough knowledge of the biology and ecology of the native fish community it invades (Rowe et al. 2008). This enables the identification of mechanisms by which native species may or may not be directly impacted by the alien species, further recognising any potential indirect impacts on individual species and on the fish community as a whole. We will review any documented evidence in association with the relevant available biological information for each native fish species of the MDB to assess the impact of eastern gambusia on the fish fauna of the MDB.

The major mechanisms eastern gambusia directly impact native fish around the world is through interspecific competition for resources such as food and habitat (including aggression), and predation of eggs, larvae and juveniles. For eastern gambusia to directly impact native species by one of these mechanisms there must be some degree of overlap in ecological niches. We have identified that eastern gambusia have a preferred habitat niche of still and slow flowing waters, such as wetlands and backwaters, predominantly occupying the upper water column and littoral zone (while large individuals are associated with benthic areas of macrophyte beds - Stoffels and Humphries 2003). Additionally, they have a broad omnivorous diet that includes detritus, aquatic and terrestrial invertebrates as well as the eggs and larvae of fish and amphibians. By overlaying this information in dietary and macro- and micro-habitat niches with those of each native species (using available knowledge of each developmental stages of each native species) we identify the likelihood and mechanisms by which eastern gambusia may directly impact each species (Table 1).

4.4.1 Interactions and impacts on ‘high risk’ species
Using available biological information, we have identified that 16 of the 37 native freshwater species of the MDB may exhibit major niche overlaps for a number of developmental stages with eastern gambusia (Table 1), suggesting these species are most at risk of direct impacts such as predation of eggs and/or larvae, competition for food and habitat, and aggression. Specifically, it highlights a number of key families, in particular the Ambassids [glassfish], Nannopercids [pygmy perches], Melanotaenids [rainbowfishes], Atherinids [hardyheads], Eleotrids [gudgeons], and Retropinnids [smelt], which together, make up the majority of the MDB’s wetland fish communities.
Table 1. Potential macro-habitat, micro-habitat and dietary niche overlaps between eastern gambusia and native freshwater fish of the MDB.

Macro-habitat niche = still and slow flowing areas such as back waters, weir pools and wetlands; Micro-habitat niche = aquatic vegetation, upper water column, and shallow littoral areas. Dietary overlap includes detritus, micro- and macro-invertebrates, terrestrial invertebrates and fish eggs and larvae; E = Eggs, L = Larvae, J = Juveniles, A = Adult developmental stages; - = minimal overlap of all developmental stages; * carp gudgeon species complex. Grey shading indicates species that possess the highest overlap (i.e. high risk). This was defined as where there is niche overlap between eastern gambusia and all four developmental stages of the native species in one or more of the macro-habitat, micro-habitat or dietary niches, and overlap in at least three developmental stages of the native species in at least one other niche type.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species name</th>
<th>Common name</th>
<th>Macro-habitat niche overlap</th>
<th>Micro-habitat niche overlap</th>
<th>Dietary niche overlap</th>
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<td>E, L, J&lt;sub&gt;3,18&lt;/sub&gt;</td>
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<td>Un-specked hardyhead</td>
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<td>E, L, J, A&lt;sub&gt;3,6,18&lt;/sub&gt;</td>
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<td>E, L, J, A&lt;sub&gt;5,6,18&lt;/sub&gt;</td>
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<td>E,L,J,A6,32</td>
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The olive perchlet (Ambassis agassizii) is still widely distributed in coastal systems of northern NSW and QLD but has undergone a major reduction in distribution and abundance throughout the MDB (Lintermans 2007). Given preference of this small species for vegetated margins in areas of little or no flow (particularly in wetlands and backwaters) and dietary overlap across all developmental stages (Table 1), it is clear that eastern gambusia have been implicated as a possible reason for this species decline (Lintermans 2007). Arthington et al. (1983) reported an inverse relationship between numbers of eastern gambusia and olive perchlet in a Queensland coastal system.

Like the olive perchlet, pygmy perch (Nannoperca sp.) are also small bodied wetland specialists that occupy similar habitat and dietary niches as eastern gambusia. The southern pygmy perch has undergone a major decline in distribution and abundance throughout the MDB, particularly throughout NSW. During surveys across the lower Murray River, Lloyd and Walker (1986) found southern pygmy perch absent in sites of suitable habitat but with an abundance of eastern gambusia, suggesting the interaction between these species could be responsible. Similarly, recent surveys of the Wimmera River basin conducted during the Victorian component of the Sustainable Rivers Audit showed southern pygmy perch were in low numbers or absent in areas where eastern gambusia were collected (SRA 2007), although such trends may be also due to factors such as habitat degradation. Koster (1997) conducted tank experiments and reported that there was no influence of eastern gambusia on the growth of southern pygmy perch when food was not limiting. However, as was also found with western pygmy perch (Gill et al. 1999), Koster (1997) reported eastern gambusia nipping the fins of southern pygmy perch, although this did not result in any infections or death during the study. Results must be treated with caution given this study was conducted in winter when eastern gambusia are very inactive and only looked at adult fish interactions. The Yarra pygmy perch may also be directly impacted by eastern gambusia given its somewhat restricted distribution in the MDB (Wager and Jackson 1993; Lintermans 2007).

The three hardyhead species in the MDB also exhibit major overlap in dietary niche and habitat with eastern gambusia (Table 1). Lintermans (2007) suggests all three species may be threatened by eastern gambusia interactions, with the Murray hardyhead now reduced to a handful of highly saline wetlands. Very little is known about the interactions of these species with eastern gambusia although McKay (1984) reported hardyhead species were usually rare or absent in Queensland streams where introduced Poeciliids occurred. The mid-water schooling and feeding behaviour of hardyhead suggest they are extremely vulnerable to direct interaction with eastern gambusia, particularly the Murray hardyhead that occurs almost exclusively in wetlands.

The Galaxiidae family also exhibit this open water behaviour, however, with most species occurring in upland areas only the flat-headed galaxias and to some degree, the common galaxias appears to have major niche overlaps with eastern gambusia. While little is known about the life-history of the flat-headed galaxias, it occurs in still or slower flowing areas at lower altitudes (Table 1). Lintermans (2007) reported that the species suffered a decline across its range suggesting interactions with eastern gambusia as a possible threat to the species. Becker et al. (2005) reported that during tank studies G. maculatus exhibited some changes in positioning and distribution in the presence of eastern gambusia but overall, were not out-competed for food. Furthermore, G. maculatus spends much of its early life in estuarine environments suggesting direct impacts of eastern gambusia on this species would be minimal, at least during early life history.

Interactions between eastern gambusia and non-MDB rainbowfish species have been well documented (see Arthington and Marshall 1999; Arthington 1991), and given the morphological and behavioural similarities across species, we suggest these interactions are relevant for the two species of rainbowfish within the MDB. Lintermans (2007) suggests eastern gambusia may pose a threat to desert rainbowfish (Melanotaenia splendida tatei) given their declining numbers at some localities coincided with the spread of eastern gambusia throughout their range. Lukies (2004) undertook an analysis of the distribution and abundance for eight fish species collected in the Broken River between 1996 and 2000, establishing eastern gambusia were more likely to overlap in time and space with...
Impacts of gambusia as an Alien Species

Murray-Darling rainbowfish (Melanotaenia fluviatilis) than any other native species in the system. Like similar rainbowfish species, there was substantial overlap in diet and foraging depth between the species but there was enough of a difference in diet to suggest that interspecific competition resulting in a negative impact on Murray-Darling rainbowfish juveniles and adults would be minimal. While limited in its conclusions in larval dietary overlap (highlighting this as an area for further research), eastern gambusia did display a significantly broader dietary niche breadth than that of Murray-Darling rainbowfish (which displayed a high level of dietary specialisation) suggesting that eastern gambusia may have a greater ability to endure times of limiting resources.

Interestingly, Lukies (2004) also reported that while there were high numbers of juvenile and adult rainbow fish co-occurring with eastern gambusia in backwater habitats, high numbers of larval rainbowfish were always absent. Gut content analysis of eastern gambusia revealed high numbers of unidentifiable eggs of similar proportion to those of Murray-Darling rainbowfish. While the identification of the eggs was not confirmed, the author did suggest predation by eastern gambusia may be a reason for the low numbers of rainbowfish larvae where the species co-occurred. Ivantsoff and Aarn (1999) documented evidence of eastern gambusia consuming Melanotaeniid larvae (although not a MDB species), also highlighting the difficulty of detecting egg and larval consumption using traditional gut content techniques, given larvae were not identifiable after 6 hours (small larvae less than hours). This may indicate that the proportion of eggs and larvae reported in many dietary studies on eastern gambusia may be a severe underestimate. Pen et al. (1993) recorded no predation by eastern gambusia on eggs or larvae of coexisting native species in a south-western Australian River, suggesting the early spawning times of the latter was the reason for this. Native species in this region spawned in spring when eastern gambusia numbers were still at their low over-wintering levels. This suggests that native species such as the Murray-Darling rainbowfish that spawn later in the season (King et al. 2007), are more likely influenced by eastern gambusia predation of eggs and larvae, particularly in cooler areas of the MDB.

Like rainbowfish, many of the gudgeon species in the MDB often exhibit late summer spawning times (King et al. 2007) indicating the presence of their eggs and small pelagic larvae often coincides with the highest densities of eastern gambusia. Furthermore, it is likely there is considerable dietary overlap between eastern gambusia and these species, particularly in the early developmental stages. The purple-spotted gudgeon (Mogurnda adspera) has undergone a major reduction in range and distribution throughout the MDB with eastern gambusia suggested as one of the key threats to the species (Wager and Jackson 1993; Lintermans 2007). Lloyd and Walker (1986) attributed the scarcity of purple-spotted gudgeon in areas of the lower Murray River to the spread of eastern gambusia. The carp gudgeon (Hypseleotris spp.) species complex is still widespread throughout the MDB (Lintermans 2007), despite major overlaps in dietary and habitat niches with eastern gambusia. Stoffels and Humphries (2003) reported small carp gudgeons exhibiting high spatial overlap with eastern gambusia within surface habitats coupled with similar diets. However, all size classes of carp gudgeon and eastern gambusia showed significant partitioning of food resources. This may suggest that while similar, the trophic niche of smaller carp gudgeon is broad enough to accommodate eastern gambusia, perhaps being the reason for no apparent decline of this species complex. Additionally, this species complex also occupies a broad range of habitats (King et al. 2007) and this flexibility in trophic niche may buffer the species from being heavily impacted by alien fish.

This may also be the case for other species exhibiting high trophic overlap such as flat-headed gudgeon (Philypnodon grandiceps), spangled perch (Leiopotherapon unicolour), Australian smelt (Retroponna semoni), un-specked hardyhead (Craterocephalus stercusmuscarum fulvus) and bony herring (Nematalosa erebi), all of which are still relatively widespread throughout the MDB. Similarly, Ling (2004) reported that many of New Zealand’s small native fish occupy relatively broad niches and some degree of niche contraction due to eastern gambusia may be accommodated without severe consequences. Ling (2004) suggests a species is likely to become locally extinct only if the niche into which a species is forced is too narrow. This is not to say that eastern gambusia do not have a
localised impact on such species, indeed, given the documented niche overlaps it is probably likely. Furthermore, such localised impacts are likely exacerbated in areas of limiting resources such as habitat availability. Morgan et al. (2004) reported evidence suggesting lentic habitats lacking cover and containing eastern gambusia contained very few native species, while habitats that provided cover as well as eastern gambusia often contained native fish. Such situations of limiting resources occur on a more frequent basis in closed habitats such as off-channel wetlands and billabong systems, particularly during late summer when these areas experience receding water levels and subsequent higher densities of eastern gambusia. Fairfax et al. (2007) presented evidence of spatial segregation where native species and eastern gambusia co-occur, although they were forced together during seasonal dry periods. This adds further weight to negative impacts of eastern gambusia being most pronounced on wetland species. Additionally, the impacts of eastern gambusia may also be exacerbated in the current drought, which has severely limited available wetland habitats in many areas of the MDB (e.g. Tonkin and Rourke 2008).

So far the species discussed are those that we have identified as most at risk from detrimental direct impacts with eastern gambusia based on the literature and degree of biological niche overlap. These indicate that eastern gambusia are most likely to have the most detrimental impact on smaller species that occupy at least in part, slow or still water habitats and as suggested by Rowe et al. (2008), will be less severe in riverine environments. Eastern gambusia may also impact on other larger riverine species. Indeed, they may interact with early developmental stages of these species, which often occupy slackwater habitats (Table 1). Barlow and Bock (1981, cited in Howe et al. 1997) reported that the survival of golden perch fingerlings stocked into farm ponds was reduced by 50% when eastern gambusia were present, with surviving individuals showing signs of caudal fin damage. Indirect interactions are the most likely mechanism by which eastern gambusia can impact on these larger species occupying different habitat and dietary niches.

The indirect interactions of eastern gambusia on the MDB’s native fish community have been largely overlooked, mostly due to our poor understanding of the species’ overall ecological impact on Australian environments. Fletcher (1986) suggested large populations of eastern gambusia are likely to alter invertebrate communities by predation. This was documented by Hurlbert et al. (1972) who found algal densities in experimental ponds increasing as a result of eastern gambusia selectively feeding on zooplankton. As discussed, such localised reductions in zooplankton can directly limit the availability of food and subsequent survivorship of larval stages and in situ small native fish species (Wilson 2006) and is likely to also reduce the amount of food that is transported to other environments, for example, from wetland to river channel (e.g. the flood recruitment model, Harris and Gehrke 1994).

High numbers of small native fish species are also likely to impact zooplankton communities, particularly in wetlands. Such situations of high fish densities are a natural occurrence, acting as a key source of dispersive offspring to the broader catchment (Wilson 2006; Stuart and Jones 2002). This was documented by Lyon et al. (subm.) who reported large numbers of carp gudgeon (→175,000 individuals) as well as Australian smelt, flat-headed gudgeon and eastern gambusia, moving between off-channel sites and the main river channel. These smaller native species are important forage fish for larger riverine species such as Murray cod and golden perch, which have been shown to actively avoid eastern gambusia as a prey item (Lloyd 1990). Wilson (2006) suggested alien species have the potential for creating energetic blocks within aquatic food webs which would be pertinent for eastern gambusia if they result in a reduction (or in some cases replacement) of native fish fauna, or their prey. Such energetic blocks have the potential to cause an indirect impact on larger riverine species of recreational significance such as Murray cod and Golden perch, by reducing the amount of food (such as zooplankton for larvae, and forage fish for adults) entering the broader environment. Given these iconic species support a lucrative inland recreational fishery, eastern gambusia may also have the potential for both social and economic impacts along with their obvious environmental influences.
5. MITIGATING THE IMPACTS OF EASTERN GAMBUSIA

5.1 Control and management
There is very little information available on mitigating the impacts of Gambusia species given the extensive literature relating to its invasion and global recognition of the threats Gambusia species pose to freshwater ecosystem function outside their native range. Pyke (2008) suggests there are two ways to reduce the negative impacts of invasive Gambusia species on native species: lowering their numbers (control), and reducing the impact per individual.

Wilson (2006) reported that virtually no information is available to guide managers in choosing the most appropriate control strategies in Australia, largely because traditional techniques including poisoning, exclusion, egg dehydration, direct removal, commercial harvest and habitat restoration have minimal chance of success for smaller species such as eastern gambusia, which occupy more cryptic habitats. Nevertheless, there is some documentation of Gambusia species control both internationally and within Australia. These activities predominantly focus on chemical techniques and drying of habitats, however, all call for extremely thorough treatment and extensive knowledge of the hydrology of the area.

In New Zealand, the Department of Conservation has invested substantial funding and effort in annual surveys and eradication of the species from selected waterbodies, particularly the Nelson/ Marlborough region, in recognition of the biosecurity threat western gambusia pose to freshwater ecosystems. Numerous techniques have been trialled in the region focusing on Rotenone in closed systems, and manual dip-netting in open systems (Elkington 2004; Elkington and Maley 2005). After mixed success across sites, the authors proposed that single treatment of a site may not be sufficient to achieve successful eradication, suggesting follow-up monitoring and treatment is required to establish the success of this program. Also in New Zealand, Willis and Ling (2000) assessed the use of Rotenone as a control method for western gambusia in the presence of a native wetland species, the black mudfish (Neochanna diversus). Given the higher toxicity of the piscicide to the native species the authors recommended treating small bodies of standing water during late summer when levels are at their lowest. It was reported that during these times mudfish were predominantly found aestivating in mud around wetland margins and not in the remaining pools where the western gambusia only are able to survive. It was suggested that these pool areas could be trapped prior to the application of the chemical to translocate any remaining native fish. This is a good example of the need for extensive knowledge of native fish ecology and behaviour along with that of the alien species in order to achieve successful control. Willis and Ling (2000) note the difficulties of chemical treatment alone as a means of eradication suggesting a single treatment is unlikely to completely eradicate a small livebearing fish such as western gambusia. They concluded that the application of rotenone to wetlands would control western gambusia numbers rather than eliminate them. If we consider the findings from Lydeard and Belk (1993), one must question the benefit of this.

Lydeard and Belk (1993) suggested two basic management strategies for Gambusia species. First is partial removal by seining to reduce population size. Second is complete removal by poisoning and subsequent reintroduction of native species. Using mesocosm experiments, the authors documented that the presence of eastern gambusia at both high and low densities had a negative effect on population growth of least killifish (Heterandria formosa). The experiment involved an initial stocking of mesocosms with zero, low and high densities of eastern gambusia, together with the native species. Eastern gambusia numbers in the low density treatment increased to levels present in the high density treatment in less than a month, finishing in higher abundances at the completion of the four month experiment, which is not surprising given the reproductive potential of the species (see Chapter 3.2.2). The authors suggested that eastern gambusia presence, and not abundance, is the
most important factor governing impacts on native fish fauna, concluding that complete removal of the species is the best management option for maintaining populations of native fishes.

In Australia, there has been little activity regarding control efforts for eastern gambusia, with most efforts for pest fishes, particularly in the MDB, focussed on carp [Wilson 2006]. Most states and territories have legislation listing eastern gambusia as a noxious or controlled species, which make it illegal for eastern gambusia to be kept, returned to the water or translocated (Queensland Fisheries Management Act 1995; New South Wales Fisheries Management Regulation 2002; Victorian Fisheries Regulations 1998; Northern Territory of Australia Fisheries Act 2005; Tasmania Inland Fisheries Act 1995; ACT Fisheries Act 2000; South Australian Fisheries Management Act 2007). In addition to such legislation, NSW have developed a threat abatement plan for eastern gambusia that proposes further research, reviewing existing legislation and control actions at feasible sites [NSW 2003]. While such legislation and planning is an important step in eastern gambusia control, particularly in slowing the establishment of new populations there is little, if any, on ground activities occurring in areas of established populations, particularly in the MDB. Those activities that have occurred have been focussed on two relatively new invasions, one in the Northern Territory, and the other in Tasmania.

In 2000, Waterwatch volunteers discovered a population of eastern gambusia in Ilparpa Swamp, Alice Springs. Realising the potential for the species to spread into some of the most pristine river systems in the country, Waterwatch volunteers, the community and government agencies worked together to develop and implement an eradication program which involved pumping the site dry (www. waterwatch.org.au). Furthermore, the publicity of this eradication prompted local residents to declare a number of other localised populations enabling aquatic pest management staff to coordinate further eradication using both pond pumping and Rotenone (www.nt.gov.au/dpifm/fisheries).

The largest eastern gambusia control operation occurring in Australia at present is being undertaken in Tasmania. Given the introduction of eastern gambusia to Tasmania is still relatively recent and restricted, the chance of statewide eradication of the species is still feasible. Consequently, The Natural Heritage Trust has funded a Priority Action Project investigating the distribution and control of eastern gambusia in the state’s north. The aims of the project are to raise community awareness of the alien species, determine the distribution of eastern gambusia in Tasmania and investigate control measures [Scurr 2007].

After gaining extensive knowledge of the distribution of eastern gambusia through the Tamar region coupled with an equally detailed knowledge of the region’s hydrology, numerous isolated populations of eastern gambusia (during low water levels or using manual isolation) were targeted using both chemical [rotenone and lime] and drying treatments [e.g. Freeman 2007; Scurr 2007]. While some of these eradication attempts have been unsuccessful [e.g. Nobelius Drive Dam which still contained eastern gambusia after three treatments of lime], many have proved successful. Freeman (2007) presents an example of one such successful eradication at Legana Dam. Methods adopting techniques developed in New Zealand were employed in March 2007 following several unsuccessful chemical treatments. In combination with a period of below average rainfall, the dam was first pumped down from around 1.8 m to 0.6 m maximum depth [out-flowing water was screened]. This was followed by a rigorous Rotenone application that involved multiple recirculation of the Rotenone/dam water solution through all habitats such as edges, reeds and damp sediment using petrol driven fire-fighting pumps. No eastern gambusia were found in the dam several weeks later during a post-treatment survey.

Researchers in Tasmania are also investigating the development of eastern gambusia specific traps to ultimately reduce the abundance of eastern gambusia to manageable levels [Maynard et al. 2008]. Laboratory trials established that eastern gambusia exhibit a positive phototactic response [attraction to light] and positive thermostatic response to heat [attracted to warm water] [Maynard et al. 2008]. The authors aim to exploit this behaviour by incorporating heat and/or light sources into a variety of trap designs to ultimately develop a trap and setting methodology that maximises the capture of
Mitigating the Impacts of eastern gambusia

While the success of these programs is dependent on the results of ongoing monitoring (and perhaps further treatment), they do suggest that with extensive biological and hydrological knowledge of an area and a coordinated approach, control of this invasive species within closed systems or in areas of new invasion is possible. Successful eradication of eastern gambusia using current methodologies is not likely to be feasible in larger open systems, such as many of the areas of the MDB. Minimising the impact of eastern gambusia on native fish may be an important strategy, particularly in areas containing threatened fish fauna, until new control strategies such as harvesting techniques and daughterless technology are developed. Pyke (2008) suggests that reducing any negative impacts of Gambusia species on native species can be achieved by a reduction in their numbers, and by reducing the impacts per individual. As documented (Chapter 3.2), lentic habitats that contain eastern gambusia and provided cover such as aquatic vegetation and snags, contain more native fish than areas without cover and eastern gambusia (Morgan et al. 2004). Furthermore, it appears that eastern gambusia have the greatest impact on native fish fauna during times of low water levels (e.g. Fairfax et al. 2007). Therefore, habitat maintenance such as enhancing thick aquatic vegetation (Pyke 2008) and watering during times of extreme low levels may reduce the impact of eastern gambusia on rare native fish fauna until improved control techniques are available.

5.2 Impacts of mitigation

The key objective of an alien species removal program is to reverse the negative impacts the species have had on native biota, and benefit native biological diversity (Zavaleta et al. 2001). One question that is often not considered in pest species management programs is ‘what negative effects will a reduction or complete removal of the target alien species have on ecosystem function’? There is evidence that successful eradictions of alien species can have unexpected and undesired impacts on native species and ecosystems, particularly in areas which have accommodated the alien species for long periods of time and where they are an established species in the food chain (e.g. Murphy et al. 1998). The type of species being removed, the degree to which it has replaced native taxa, and the presence of other non-native species can affect the eventual impacts of removal of an alien species (Zavaleta et al. 2001).

Maezono and Miyashita (2004) suggested two ways in which such undesired impacts may occur. First, the removal of an alien species can enhance secondary establishment, or increase the impact of other alien species. Secondly, negative impacts to native biota may occur if the alien species performs functions similar to those of native species that are no longer in the system. An example of the first mechanism was reported by Maezono and Miyashita (2004), who investigated the removal of introduced largemouth bass (Micropterus salmoides) on native communities in farm ponds. While removal of this alien species did result in an increase in native fish and shrimp, there was also a substantial increase in exotic crayfish, which resulted in a substantial reduction in macrophytes and associated rare odonate species. Zavaleta et al. (2001) suggest eradication of the alien prey species only can also cause problems by forcing the alien predator to switch to native prey. Indeed, such exotic predator and prey interactions may be relevant for areas containing both eastern gambusia and redfin perch. McNeil (2004) suggested eastern gambusia may be subject to selective predation by redfin perch in billabong habitats. This alien species predator-prey interaction was hypothesised as responsible for the dominance of small native species in habitats containing redfin perch and alternatively, the dominance of eastern gambusia in habitats without the exotic predator. This suggests that the removal of redfin perch alone may result in increased eastern gambusia dominated environments, or alternatively, the removal of eastern gambusia alone may result in increased predation pressure on the existing native fish community.
The second way Maezono and Miyashita (2004) suggested that removal of an alien species could result in undesirable impacts is if the alien species performs functions similar to those of native species that are no longer present in the system. In the case of eastern gambusia, these functions may include maintenance of plankton assemblages or acting as prey for native predators such as birds, invertebrates and fish. While there are numerous interactions across a variety of taxa that may occur with eastern gambusia, we suggest such effects are likely to be minimal and short-lived for the native fish community. This is primarily because the majority of species that eastern gambusia have theoretically out-competed are short-lived species, capable of rapid population establishment (e.g. rainbowfish, gudgeons and Australian smelt). Furthermore, the systems where eastern gambusia are most common (i.e. wetlands and billabongs) undergo frequent re-colonisation events associated, for example, with connection of wetlands to rivers during high flow events.

Nevertheless, to restore native biodiversity it seems essential to clarify the community-wide impacts by the exotic fishes, including any interactions between the exotic fishes and other exotic species prior to eradication (Maezono and Miyashita 2004). Zavaleta et al (2001) suggests pre-assessment including qualitative evaluation of trophic interactions between alien and native species to anticipate the need for special planning. Additional post-eradication monitoring is also suggested. These authors concluded that while invasive species eradication is an increasingly important component of conservation management, in natural systems a shift in focus is required from pure alien species control towards broader ecosystem restoration goals.
6. CONCLUSIONS

6.1 How should research be directed?
Despite the vast amount of literature devoted to the Gambusia species, there is a surprising lack of knowledge about their abundance; factors controlling their distribution and diet; their impact on native ecosystems and methods to mitigate such impacts (Pyke 2008). Studies examining trophic interactions (as suggested by Zavaleta et al. 2001) and subsequent ecological effects of small alien species such as eastern gambusia have received very little attention, particularly in comparison to larger species such as common carp (e.g. Wilson 2006). While we have documented a number of controlled experimental studies in this review, rigorous comparisons of control success under field conditions have not been undertaken. Rowe et al. (2008) recommended full BACI (before / after control/impact) and/or manipulation studies for the assessment of impacts of alien species on indigenous species. Such experiments have not yet been undertaken on eastern gambusia. Furthermore, information regarding how native species respond to reductions of an alien species in the wild is necessary before large amounts of money are spent on broad scale control strategies. Rowe et al. (2008) noted: ‘scientific proof of the impact of gambusia on indigenous biodiversity is likely to be required in the future as management efforts to control gambusia increase in number and size and therefore attract closer public scrutiny of cost’. Therefore, field based manipulation experiments will provide scientifically defensible information on an alien species’ impact (Rowe et al. 2008) and valuable information on controlling alien species populations to densities that result in measurable improvements to native fish communities.

A central tenet to integrated pest management is a focus on the reduction of impacts on ecosystem processes; not simply a reduction in numbers of the species (Lodge and Schraeder-Frechette 2003; Koehn and Mackenzie 2004). Given the ongoing threat eastern gambusia pose to native fish communities (Lintermans 2007), the lack of current effective control options (see McKay et al. 2001 and NSW National Parks and Wildlife Service 2003) and that the long-term detrimental impacts of the species on ecosystem function in the MDB remain uncertain, research into the feasibility of controlling eastern gambusia populations to densities where measurable improvements to native fish communities can be detected should be a priority. The continuation of existing and additional research should be directed to new control techniques for eastern gambusia given the current lack of successful and feasible control techniques. Trap designs are already being investigated in Tasmania (Maynard et al. 2008) and gene technology aimed at affecting the reproductive capabilities of eastern gambusia has been trialled (Fairfax et al. 2007). Rigorous investigation into possible biological controls are all areas where research needs to continue, expand or commence if eastern gambusia control or eradication is to be successful.

6.2 What is being done?
The Arthur Rylah Institute for Environmental Research has recently been commissioned by the MDBA to undertake a three-year program to address these research needs. This project takes a holistic approach by integrating quantitative experimental work in natural billabong systems throughout the MDB, with bioeconomic modelling approaches to address the question: does the cost (in effort and funding) of reducing eastern gambusia populations to defined levels, outweigh the ecological benefits to the sympatric native fish community? The work will provide initial correlative data on all alien fish species present in billabong habitats, and then using eastern gambusia as a model alien species in a controlled field-depletion experiment, will form a template to evaluate the relative costs of controlling other potentially harmful alien species across the MDB.

This work will be complemented by two other current projects. One of the projects aims to clarify eastern gambusia’s dynamic food-web effects relative to the abiotic disturbance factors common to wetlands.
Due to its high rate of feeding and densities, eastern gambusia is likely to exert some level of top-down control in many communities, particularly where high temperatures, lack of disturbance, and an absence of competitors promotes individual over-wintering survival and population growth throughout the year (S. Ho personal communication). The second project’s overarching objective is to quantify the nature and extent of aggressive interactions between eastern gambusia and some Australian native freshwater fishes in aquaria-based experiments (A. Moore personal communication).

Integrating data from all three projects will provide a strong platform for determining the level of ‘impact’ eastern gambusia may exert on native fish communities in the MDB. Ultimately, this will aid in the development of a truly integrated approach to management of this alien fish species in the MDB.
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Murray–Darling Basin Authority


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