A HANDBOOK OF GLOBAL FRESHWATER INVASIVE SPECIES

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Gambusia affinis (Baird & Girard) and *Gambusia holbrooki* Girard (mosquitofish)

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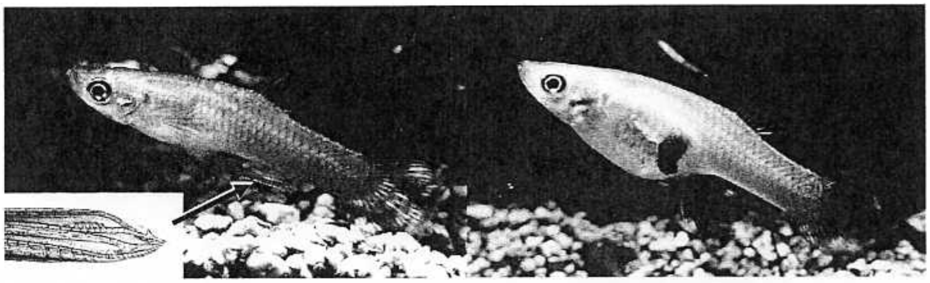
History of the Species and its Introduction

Two species of *Gambusia* are commonly referred to as mosquitofish and represent the most widespread freshwater fishes globally, occurring on all continents except Antarctica. *Gambusia affinis* was originally described in 1853. Placed within another genus by Baird and Girard, the species was reassigned within the genus *Gambusia* after the generic name was first assigned to a Cuban species (*G. punctata*) by Poey in 1854. The species name, *affinis*, denotes 'related' and is thought to refer to the similarity of the western form to an eastern species that had been characterized in an unpublished morphological description of a North American fish (Moyle, 2002). Girard formally described the eastern North American species of *Gambusia, G. holbrooki* in 1859 (Figure 22.1).

The western mosquitofish, *Gambusia affinis,* and the eastern mosquitofish, *Gambusia holbrooki,* are members of a genus of about 46 species (Moyle, 2002; Froese and Pauly, 2010) within the order Cyprinodontiformes and the family Poeciliidae, the top minnow live-bearers. Central America is the centre of poeciliid abundance (Moyle, 2002). Unlike the broad distributions of *G. affinis* and *G. holbrooki,* which are the result of introductions outside their native ranges for mosquito control, the 20 North American *Gambusia* species have comparatively restricted geographic ranges and are found in rivers and spring systems in the south-central US and eastern Mexico (Page and Burr, 1991; Moyle, 2002).

Morphological similarity of *G. affinis* and *G. holbrooki* has caused historical changes in the taxonomic status of the two species that confound published scientific findings and stocking records. Both fish were considered subspecies of *G. affinis* for an extended period and publications did not always distinguish between the two forms (Gerberich and Laird, 1968; Moyle, 2002). After about 1990, species status was re-established based on morphological differences (Rauchenberger, 1989), genetic studies and geographic distribution (Wooten et al, 1988). Adults of the two species can be distinguished by the numbers of dorsal and anal fin rays and the morphology of the male anal fin or gonopodium: *G. holbrooki* usually has seven dorsal rays, ten anal rays and a gonopodium with a series of prominent teeth on ray three; whereas, *G. affinis* has six dorsal rays, nine anal rays and lacks prominent teeth on ray three of the gonopodium. More recently, molecular diagnostic tools have been developed to distinguish between the two species (Vidal et al, 2010).

Beginning in the early 1900s, the two mosquitofish species were introduced as biological control agents for mosquitoes in temperate and tropical countries (Figure 22.2). Based on published accounts of mosquitofish stocking and research focusing on

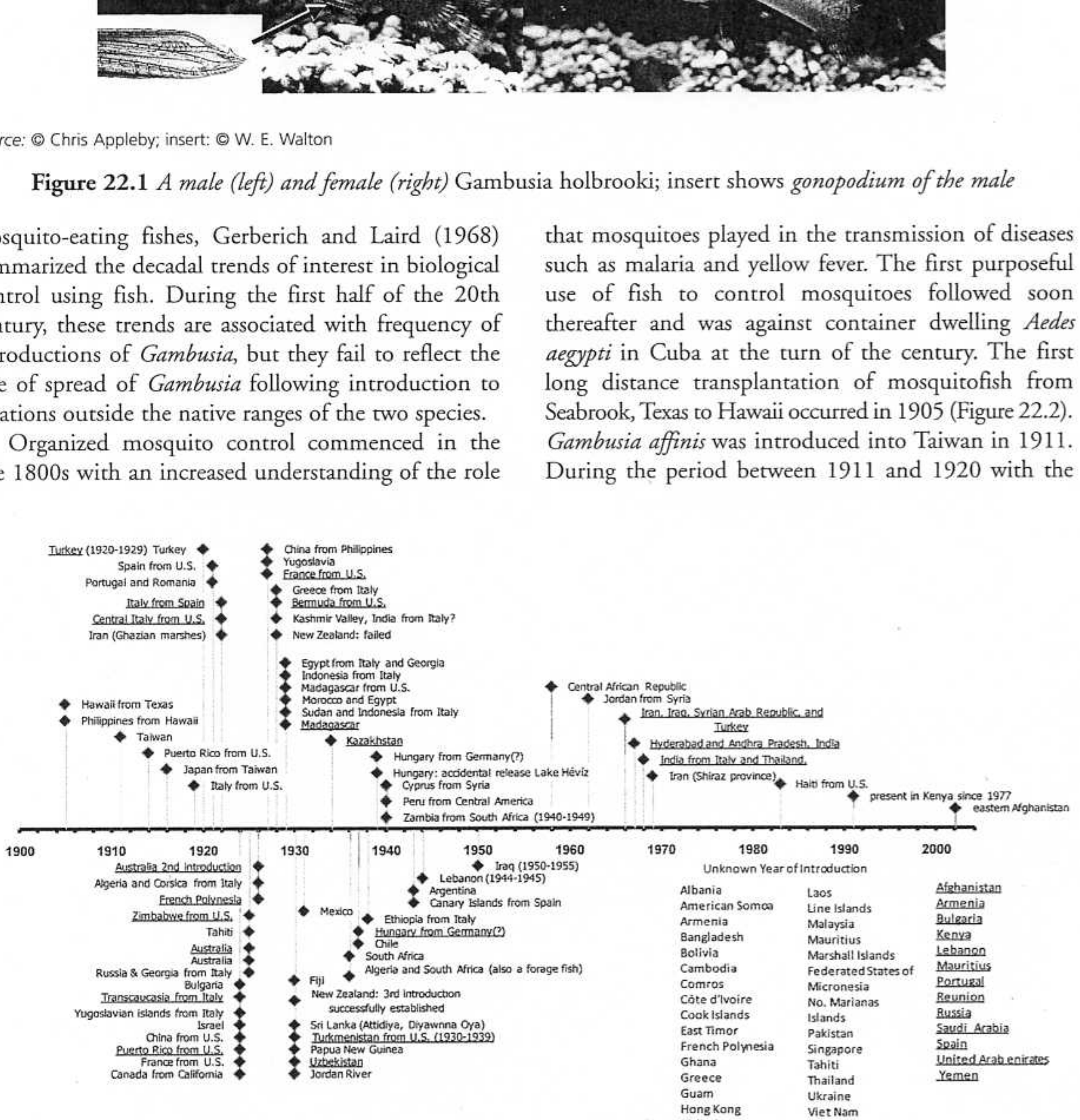


Source: © Chris Appleby; insert: © W. E. Walton

Figure 22.1 *A male (left) and female (right)* Gambusia holbrooki; insert shows *gonopodium of the male*

mosquito-eating fishes, Gerberich and Laird (1968) summarized the decadal trends of interest in biological control using fish. During the first half of the 20th century, these trends are associated with frequency of introductions of *Gambusia*, but they fail to reflect the rate of spread of *Gambusia* following introduction to locations outside the native ranges of the two species.

Organized mosquito control commenced in the late 1800s with an increased understanding of the role that mosquitoes played in the transmission of diseases such as malaria and yellow fever. The first purposeful use of fish to control mosquitoes followed soon thereafter and was against container dwelling *Aedes aegypti* in Cuba at the turn of the century. The first long distance transplantation of mosquitofish from Seabrook, Texas to Hawaii occurred in 1905 (Figure 22.2). *Gambusia affinis* was introduced into Taiwan in 1911. During the period between 1911 and 1920 with the



Note: The data represent a compilation of introductions listed in Gerberich and Laird (1968), Welcomme (1988), Haering (2005), ISSG (2006) and Froese and Pauly (2010). A question mark indicates uncertainty in a record.

Source: Timeline developed using Wittwer (2005)

Figure 22.2 *A timeline for the introduction of* Gambusia affinis *and* Gambusia holbrooki *(underlined) outside the US* completion of the Panama Canal (in 1914) and during World War I, large numbers of men from North America were moved into the tropics and regions where mosquito-borne pathogens were present. At this time, *Gambusia* and guppies (*Poecilia reticulata*) were the primary species being transplanted for vector control.

During the following decade 1920–1930, interest in the use of larvivorous fish for vector control increased appreciably. During the 1920s, *Gambusia* were transplanted from eastern and south-central North America to Mexico, Central and South America (Figure 22.2) as part of a yellow fever reduction campaign sponsored primarily by the philanthropic efforts of the Rockefeller Foundation. The focus was still primarily on the control of mosquitoes inhabiting man-made containers such as rainwater storage jars. *Gambusia* also were transplanted to New Zealand, Australia and Europe. Recent genetic studies (Vidal et al, 2010) confirmed stocking records that indicated *G. holbrooki* was exported from North Carolina (US) to Spain in 1921. From Spain, the mosquitofish was introduced into Italy in 1922. The Italian population served as the primary source of *Gambusia* introductions to countries of Europe, western Asia, northern Africa and islands of the Mediterranean Sea between 1924 and 1930.

During this same time period, *Gambusia* were stocked outside (e.g. northern Illinois, California, Canada) its native range in North America. *Gambusia affinis* was introduced into California from Texas in 1922 (Dill and Cordone, 1997). By 1926, *G. affinis* had been introduced into 30 counties by the California State Board of Health and had spread rapidly from the introduction sites (Moyle, 2002). Pflieger (1975) notes that the distribution of *G. affinis* changed appreciably over 30 years. In survey collections from the 1940s *G. affinis* was restricted to the lowlands of south-eastern Missouri and waters adjacent to the Mississippi River. During a 30 year period the geographic distribution expanded to include central Missouri and two river systems in the south-western portion of the state as a consequence of widespread stocking for mosquito control.

Gerberich and Laird (1968) conclude that some of the *Gambusia* introductions during the 1920s had sound ecological bases, but others lacked consideration of the ecological conditions of the habitat relative to the physiological and ecological needs of the fish. The latter introductions either failed or gave equivocal results for mosquito control. During this time period, *Gambusia* and other mosquito-eating fishes also were being used in abatement campaigns against vectors of malaria whose immature stages do not occur in container habitats; impact on non-target fauna was probably given little consideration. Mosquito-eating fish were naïvely thought to provide a long term solution for vector control that was a favourable alternative to the labour-intensive and ecologically damaging approaches that had been effective to date. Prior to this period the predominant approaches for mosquito control outside of residences and buildings were to drain and fill wetlands, to construct parallel ditching systems for draining standing water above the high tide line with no regard for natural drainage patterns and ecological interactions in coastal marshes, and to spread oil across the surface of large water bodies and slow moving sections of rivers and streams.

During the next two decades, interest in the use of biological control agents (based on the number of published papers) declined. However, in the 1930s, studies of the relationship between ecological conditions and the efficacy of biological control using mosquito-eating fish and of the evolutionary changes in fish stocks (i.e. cold-adapted and salinity-adapted strains of *Gambusia*) were carried out in regions of the former Soviet republics and North Africa (Gerberich and Laird, 1968). *Gambusia* were introduced into South Africa in 1936 and into various countries of South America during the late 1930s and early 1940s.

Interest in the use and the introductions of non-native fishes declined further during the 1940s after the realization in 1939 of the insecticidal properties of an organochlorine compound originally synthesized in 1874. Dichlorodiphenyltrichloroethane (DDT) was being used widely to reduce the populations of agricultural pest and public health insects. DDT provided the primary means of controlling malaria and other arthropod-borne diseases during World War II. During this time, interest in using fishes in biological control programmes against mosquitoes waned. However, *Gambusia* were introduced to Lebanon and Cyprus during the mid-1940s.

Interest in mosquito-eating fishes reached a nadir in the 1950s; nevertheless, *Gambusia* introductions occurred within western Asia. Following the discoveries of insecticide resistance to DDT and other synthetic insecticides in the mid-1950s, and the realization that these chemicals could not by themselves provide a viable long term strategy for mosquito control, interest in integrated mosquito control programmes that utilized a multifaceted approach to mosquito control increased during the 1960s and 1970s. The interest in use of larvivorous fish as components of integrated mosquito control programmes increased concomitantly. *Gambusia* were transplanted into additional countries in Eurasia and western Asia, the Middle East and India during the 1960s. Introductions slowed during the second half of the 20th century, but the end result was the spread of *G. affinis* and *G. holbrooki* across six continents (Figure 22.3).

Ecological Niche in Native and Introduced Ranges

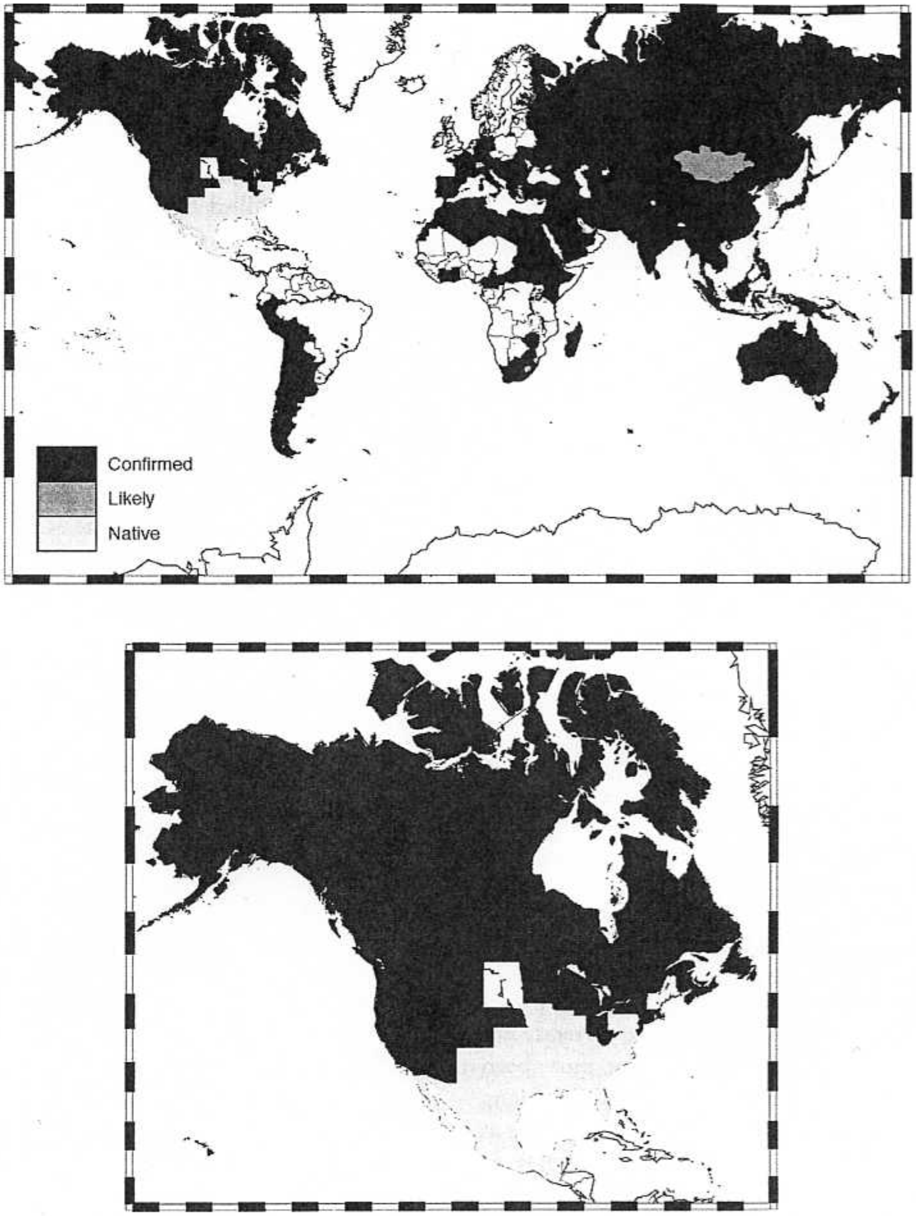
The two *Gambusia* species that have been transplanted worldwide are native to the Atlantic and Gulf Coast drainages in eastern North America (Page and Burr, 1991; Nico and Fuller, 2010, Nico et al, 2010) (Figure 22.3). The eastern mosquitofish, *G. holbrooki*, occurs from southern New Jersey to Florida and to the eastern Mobile Bay, Alabama. The western mosquitofish, *G. affinis*, is native to the Gulf Slope drainage from central Indiana and southern Illinois to eastern Mexico and from the western Mobile Bay, Alabama to Texas and into eastern Mexico. The western extent of the native range in the south-central US was never adequately defined prior to the widespread movement of the fish by man. Intergrades of the two species can be found in the Mobile Bay basin.

The ecological niches of both species are similar. *Gambusia* spp. are common and locally abundant, often in vegetation along the periphery of lakes and ponds, and in backwaters and pools of streams within their native ranges. Mosquitofish are common in submerged and emergent plants, but tend not to penetrate dense plant beds preferring to reside near the vegetation-open water interface. They are occasionally found in brackish water. Both species are adapted for life in shallow, slow moving, warm water where piscivorous fish are absent or rare (Moyle, 2002).

Mosquitofish are omnivorous, opportunistic feeders. Diets typically include both plant and animal matter. *Gambusia* feed mostly at the water surface, but foraging is not restricted to the hypopneustic zone of the water column. Animal food includes insects, spiders, small crustaceans, rotifers and snails. Plant material is less important in the diet than is animal material but provides an important food when animal food is rare. It is common for diets to change during ontogeny from predominantly rotifers and micro-crustaceans in the diets of young individuals to mosquito larvae, other aquatic insects and organisms trapped in the surface film in the diets of adults. Cannibalism and predation on the eggs and immature stages of other co-occurring vertebrates are known to occur.

The two *Gambusia* species are hardy, capable of surviving broad ranges of environmental conditions, are comparatively tolerant of pesticides and exhibit high reproductive capacities. These characteristics, along with bearing live young (eliminating the need for nest building), omnivory, preference for habitats where predators are absent and mosquito larvae are present, and ease of culture, contribute to the success of *Gambusia* as mosquito control agents (Moyle, 2002). While these characteristics make them ideal candidates for mosquito control (Swanson et al, 1996), especially in the poor water quality and marginal habitats where mosquito production is typically greatest, many of these characteristics also are ideal for an invasive species (Lloyd et al, 1986; Moyle and Marchetti, 2006).

A detailed presentation of the environmental tolerances of *Gambusia* can be found in Swanson et al (1996); we provide only an overview of the broad environmental tolerances of mosquitofish. *Gambusia* spp. can survive low oxygen saturations (~0.2mg O_2 litre^{-1}) by breathing at the air–water interface. They can survive a broad temperature range (0.5–42°C) but persist in habitats where temperatures typically range annually between 10 and 35°C. Optimal temperatures for growth and reproduction are 25–30°C. Survival is greatly reduced during prolonged exposure to cold (<4°C) and this characteristic limits the geographic distribution of these species. Acclimation, however, is possible and cold hardy *Gambusia* strains exist. *Gambusia affinis* can survive in a pH range of 4.7–10.2 but typically occurs in waters with pH 7–9. Mosquitofish exhibit a broad salinity tolerance ranging from 0 to 58 parts per thousand (ppt), but survive best in fresh water and slightly brackish water with salinities <25ppt. Given these broad environmental tolerances, it should not be surprising that the ecological niche of *Gambusia* does not change appreciably in habitats outside its native range.



Note: Mosquitofish populations do not persist in regions where winter temperatures are below freezing for extended periods such as high latitude temperate zones unless geothermal or anthropogenic processes enhance water temperature during winter. Note that although entire countries are highlighted this does not mean that *Gambusia* spp. are present throughout all regions within the country.

Source: G. J. Funning created the distribution map using the Environmental Systems Research Institute, Inc,'s Digital Chart of the World®, available at www.maproom.psu.edu/dcw (accessed 10 August 2010) and generic mapping tools (Wessel and Smith, 1998)

Figure 22.3 *The native and introduced geographic distributions of* Gambusia *spp. worldwide (upper panel) and in North America (lower panel)*

Management Efforts

Attempts to eradicate introduced *Gambusia* populations have been largely unsuccessful and, even if possible, the cost of such efforts in established populations is prohibitively expensive. A primary focus of management efforts for *Gambusia* is to prevent new introductions and to limit future spread of introduced populations. This approach is recommended for the management of potentially widespread, persistent alien species because eradication after establishment is improbable (e.g. Lodge and Shrader-Frechette, 2003).

Given the rapid reproductive rate of mosquitofish populations following introduction, aggressive interactions of *Gambusia* with other freshwater biota, comparatively broad physical and chemical tolerances of mosquitofish, and the current widespread distribution of the species outside their native geographic ranges, management efforts that affect *Gambusia* yet have a minimum impact on non-target fish species have generally been unsuccessful. Control efforts applied against invasive species worldwide include:

- chemical control;
- cultural control and sanitary measures;
- physical removal/mechanical control;
- biological control;
- integrated pest management;
- control by utilization;
- ecosystem restoration; and
- containment (e.g. dispersal and movement control).

While some of these control strategies are currently not viable against mosquitofish and have not been attempted, most control strategies have a minimal long term impact on established populations and provide at best a temporary measure of population reduction in most natural habitats.

Chemical control

Gambusia spp. often have greater tolerances of chemical control agents than native fish and other aquatic biota (Lloyd and Arthington, 2010). *Gambusia* are more tolerant of the organophosphate pesticide chlorpyrifos (Dursban) than are several native fishes in Australia (Pyke, 2005) and are comparatively tolerant of a broad range of insecticides and herbicides (Walton, 2007). The organic piscicide and insecticide rotenone has been used to attempt to control introduced mosquitofish, but because mosquitofish can often tolerate higher rotenone concentrations than native fishes, it may have detrimental effects on native fishes while concomitantly having little effect on mosquitofish. In Australia, most native fish are killed by a rotenone concentration of 0.5mg $litre^{-1}$ but *G. holbrooki* can survive this concentration (Pyke, 2005). Impact on native fishes and other native fauna has been mitigated by releasing potassium permanganate downstream of the rotenone release point in flowing waterways (Lloyd and Arthington, 2010).

In addition to physiological tolerance of chemical control agents, *Gambusia* can use behavioural mechanisms to avoid toxic dosages. Rotenone applications failed to eliminate *Gambusia* from a hatchery spring pond and conveyance ditch (Gurtin, S., Arizona Game and Fish Department, pers. comm.). During an attempt to eliminate *Gambusia* from Scotty's Castle Creek at the north end of Death Valley National Park (California, US), mosquitofish were observed stranding themselves on algal mats at the water surface following the detection of rotenone applications and thereby survived chemical control methods by avoiding a toxic dosage of the piscicide. The rotenone application caused mortality but eradication by this chemical method was deemed infeasible because the numbers of surviving *Gambusia* were sufficient for re-establishment (Pister, P., pers. comm.). In another creek in the south-western US (Corn Creek on the Desert National Wildlife Refuge north of Las Vegas, Nevada), a mosquitofish population was successfully eliminated using rotenone.

Cultural control and sanitary measures

Introduced fishes often thrive in disturbed habitats (Lloyd and Arthington, 2010) and the broad environmental tolerances of *Gambusia* provide a selective advantage over native fauna in such habitats. In hypereutrophic lentic habitats that are isolated from native habitats and that would be either stressful or potentially detrimental for native fishes (Walton et al, 2007; Peck and Walton, 2008), there is little reason not to utilize extant mosquitofish for vector control. As a component of integrated mosquito management programmes for such nutrient-enriched ecosystems, *Gambusia* can reduce larval and adult mosquito abundance by an order of magnitude or more as compared to the same control measures without larvivorous fish (Walton, W. E., unpublished data).

Arthington et al (1990) recommend that maintaining the natural flow regime and habitat characteristics of aquatic systems provides an effective management strategy to reduce the impact of introduced mosquitofish populations on native fauna. Non-native mosquitofish populations in the south-western US are detrimentally affected by disturbance from spates more than are native species with similar ecological requirements such as *Poeciliopsis* (Schoenherr, 1981; Minckley and Meffe, 1987). In addition to the potential negative effects of biotic interactions with *Gambusia* on native fauna, homogenization of flow regimes (Poff et al, 2007) probably also contributes significantly to the dominance of mosquitofish in some natural systems. In such systems, increasing the frequency and intensity of disturbance actually may be advantageous to native fishes (Bunn and Arthington, 2002).

Physical removal/mechanical control

Physical removal of mosquitofish requires a concerted effort to eliminate a substantial portion of the population, if not the entire population, in a water body or watercourse. The size (i.e. length, area) of the inundated habitats within a watershed, as well as the physical characteristics of the aquatic ecosystem under consideration, will determine the effort and cost of a well-planned and well-executed mosquitofish removal programme. *Gambusia* cannot be allowed to recolonize sites from which it was extirpated while control efforts are ongoing.

Physical removal programmes have required holders of scientific collection permits and persons carrying out research projects to sacrifice individuals of any exotic species taken during census and research activities. In Australia, *Gambusia* collected as bycatch in ecological research programs must be sacrificed immediately. Introduction to another water body or household aquaria is not permitted (Lloyd and Arthington, 2010). In the US, increasingly stringent regulations for the use of vertebrate animals in university-related research typically do not permit the elimination of bycatch in research programmes and, if euthanasia is permitted, then the number of specimens to be killed must be specified beforehand. The practical outcome of compliance with such regulations necessitates that extermination of individuals of exotic species is left to agents of the natural resource agencies. Because collection and research activities are rarely carried out intensively across all habitats containing invasive species, such measures probably fail to cause a significant reduction in the populations of invasive species such as *Gambusia*.

The insertion of devices that macerate biological material within pipelines carrying reclaimed water appears to have been effective at eliminating mosquitofish from reclaimed water supplies. *Gambusia affinis* has been added for vector control in constructed wetlands treating municipal wastewater that provide a source of reclaimed water in southern California. Physicochemical conditions in wetlands treating highly enriched municipal effluent often are not conducive for the survival and proliferation of native fishes (Walton et al, 2007) and sometimes even *G. affinis* (Popko et al, 2009). The maceration devices eliminate clogging of small diameter water conveyance structures within reclaimed water systems by decaying vegetation and other biological material drawn into high volume pumps at the outflows of the wetlands.

Draining standing water bodies (e.g. outdoor ornamental ponds) and closing pathways for recolonization (e.g. dispersal control within conveyance structures between habitats containing mosquitofish and natural waters) have been somewhat successful for reducing *Gambusia* populations in Australia (Lloyd and Arthington, 2010). Barriers to spread must obstruct dispersal pathways as shallow as 3mm depth because *Gambusia* can move through shallow water half of their body depth (Alemadi and Jenkins, 2008).

Biological control and IPM

At the present time, biological control and integrated pest management (IPM) control strategies hold little promise for introduced *Gambusia* populations. Biological factors such as parasites, pathogens and predators that potentially regulate *Gambusia* populations occur in habitats within the native and introduced geographic ranges (Arthington and Lloyd, 1989; Courtenay and Meffe, 1989; Nagdali and Gupta, 2002); however, the majority of these mortality factors are not specific to *G. affinis* or *G. holbrooki*. Crandall and Bowser (1982) report a microsporidian infection (*Glugea*) that may be unique to mosquitofish but that has an unknown impact on *Gambusia*. Unlike efficacious biological control programmes in agricultural systems in which a parasitoid is intimately linked to a particular host pest insect, such narrowly focused interactions are not present for *Gambusia* and its potential biological control agents, at least for the important mortality factors that are known currently.

Moreover, the economic threshold of damage that can be tolerated within IPM programmes is comparatively easily calculated based on market conditions and the crop yield for agricultural systems. The concept of permissible crop losses does not translate readily to the ethics requisite in public health programmes and the level of control required for problematic invasive species. It is considerably more difficult to: (1) assign monetary values to a human life lost and to time lost while recouping from disease; and (2), as Service (1985) notes, achieve the high levels of reduction required for pathogens and vectors causing public health concerns. These same arguments are applicable to biological control and IPM programmes intended for invasive species. The inability of current global economic policies to assign full, credible dollar values to ecosystem services and biodiversity of natural environments (Ehrlich and Ehrlich, 2008) exacerbates the differences between IPM programmes for agriculture vs. invasive species. In many instances, the goal of invasive species control programmes is the elimination of the exotic species from its introduced range; this is not the goal of biological control and IPM programmes.

Lloyd and Arthington (2010) suggest that biomanipulation may afford some measure of *Gambusia* control through top-down predation. The proposed strategy using predatory galaxid (*Galaxias maculatus*) fishes in small water bodies of Australia does not, however, provide long term regulation of the target species. The relative cost–benefit of repeated introduction of predators vs. long term control by another control method(s) still needs to be evaluated.

Besides the direct benefit of consumption of *Gambusia* by piscivores, native piscivorous fishes provide an indirect benefit to vector control by forcing *Gambusia* to seek refuge in the vegetated habitats that are most likely to contribute significantly to mosquito production. The ability of predators to regulate *Gambusia* populations and the outcome of interactions between mosquitofish and fauna (e.g. juveniles of other fish species, macroinvertebrates) residing in the emergent and submerged vegetation will need to be evaluated carefully when determining the merits of this control strategy. The potential 'bio-synergistic' interactions of multiple biotic agents (Gerberich and Laird, 1968) functioning on different trophic levels warrants additional consideration.

Control by utilization

Utilization is not a control strategy that has been applicable to mosquitofish. If anything, utilization of mosquitofish for vector control has exacerbated the invasive species problem through the purposeful release of *Gambusia* into inappropriate habitats or unforeseen colonization of ecosystems outside the native geographical range. Prior to their use for vector control, these fish were not highly valued by humans, perhaps other than as a bait fish. Poey's name for the genus reflects this derisive point of view as it is a reference to a provincial Cuban term *gambusino* that refers to 'nothing' in the mocking sense that one says he was fishing for *gambusinos* when one catches nothing (Poey, 1861).

Ecosystem restoration

Depending on the foci of restoration activities, ecosystem restoration can either reduce or enhance the abundance of *Gambusia*. Maintenance of natural processes in aquatic ecosystems will promote native biodiversity and is the best way to suppress alien fishes (Arthington et al, 1990; Bunn and Arthington, 2002). Increasing the variation of discharge of flow regimes seems to reduce *Gambusia* populations associated with lotic environments (Minckley and Meffe, 1987). Re-establishing the natural variation in discharge that occurred historically in many drainage systems within suburban and urban areas is probably not possible because of human activities in and adjacent to the floodplain.

Restoration activities in riparian zones sometimes promote aquatic features that encourage human uses or attempt to satisfy multiple habitat goals. Depending on the morphometry and numerical occurrence of lentic type features within the restored riparian system, such features could enhance *Gambusia* populations. For example, the inclusion and increased frequency of large ponds and lakes in restoration projects that dissipate the impact of spates on the fish community may provide favourable habitat for *Gambusia* and non-native predators. A hands-off 'let nature take its course' approach to ecosystem management under homogeneous or reduced discharge regimes often leads to the development of thick stands of emergent vegetation. This approach to ecosystem restoration also will favour *Gambusia*.

Containment (e.g. dispersal and movement control)

Containment efforts include regulations and practices that prevent the spread of extant populations of *Gambusia* and limit its introduction into habitats that currently lack mosquitofish. Such measures include the quarantine and prohibition of stocking mosquitofish into waters of natural ecosystems. Categorization of *Gambusia* as a noxious species restricts the movement of mosquitofish between habitats and among watersheds in Australia (Lloyd and Arthington, 2010). Australia utilizes quarantine, certification and prohibition as measures to prevent the further introduction and spread of mosquitofish (Lloyd and Arthington, 2010).

The movement of any fish species, native or non-native, is typically limited by regulations in most US jurisdictions that require approval of the fish and wildlife agency, conservation district or other entity charged with jurisdictional oversight of natural resources. In many instances, this approval is contingent on the outcome of an examination of a representative sample of the stock population for disease, parasites, etc. Where stocking of mosquitofish for mosquito control outside the native geographic range of the fish is still permitted by law, containment is the primary strategy used for limiting the spread of *Gambusia*. In many jurisdictions, stocking of mosquitofish is limited to aquatic features (i.e. neglected residential swimming pools, ornamental ponds, etc.) that produce mosquitoes but have no direct connection to natural aquatic environments. These policies provide an effective means to halt subsequent introductions and the spread of mosquitofish distribution.

Whereas the management of mosquitofish populations in self-contained man-made aquatic environments is straightforward and generally effective, management of *Gambusia* in approved uses for semi-natural environments is potentially more difficult. Mosquitofish are also used as a component of integrated mosquito management programmes for semi-natural aquatic environments such as seasonal wetlands used for waterfowl hunting and inundated agriculture such as rice fields. Containment is also the primary strategy used in semi-natural aquatic environments to limit additional introductions of mosquitofish into natural aquatic ecosystems. Seasonal duck-hunting wetlands typically lack an outlet for water and are dried rather than drained. Water in rice fields may be drained overland or using procedures (e.g. pumps, water and fish barriers) that greatly reduce the survival and potential dispersal of mosquitofish.

Public awareness is an important component of mosquitofish management programmes in many places. Public education campaigns and outreach have been used to inform the public about the ecological consequences of alien fish introductions. Besides the two *Gambusia* species that have been spread as part of public health efforts, other live-bearing fishes and organisms (i.e., fish, amphibians, reptiles) in the aquarium trade have been introduced on several continents (Arthington et al, 1999; Saiki et al, 2010). Zoological parks are increasingly adding exhibits on the plight of native fauna, including fishes, as part of their educational activities. Public education should be requisite for vector control programmes in places where the public has access to mosquitofish. Boklund (1997) provides an example of the oversight required by the vector control agency, coordination with the natural resource agency and education/agreement with the recipient requisite for distribution of *Gambusia*. Lloyd and Arthington (2010) suggest that community involvement in monitoring habitats provides an early warning system for incipient population explosions following an introduction as well as a sense of ownership of the pest fish issue, and an improved understanding of the complexities of managing alien fish species. A concerned and informed public can provide important supplemental detection of species introductions for natural resource agencies dealing with ever-present budgetary constraints.

As a result of public education and stricter regulation of the movement of organisms between watersheds and outside native geographic ranges, mosquito control agencies are more aware of the ecological impact of non-native species than they were previously. In most places, mosquitofish are not currently planted into waters of the states of the US for the purpose of mosquito control.

Controversies

The two primary controversies related to *Gambusia* are its efficacy as a biological control agent for mosquitoes and the magnitude of its impact on aquatic ecosystems and biodiversity (Lloyd et al, 1986; Gratz et al, 1996; Rupp, 1996; Pyke, 2008). These differences of opinion stem in part from the evidence used by each side of the two controversies as regards the applicability of anecdotal accounts, laboratory and field experiments that differ in design and statistical power etc. to predict what happens in nature. In many cases the positive effect of *Gambusia* on reducing mosquito numbers or a negative effect of *Gambusia* on particular fauna is caused by more than one factor. Rarely has the relative importance of the factors causing a particular outcome been adequately quantified.

There are aquatic systems where *Gambusia* can exert significant levels of mortality on immature mosquitoes. Mosquitofish clearly have demonstrable negative effects on mosquitoes in environments that typically lack physical structure and have low predation pressure from consumers of small fishes. It could be argued justifiably that, in such situations, most native species could achieve the same result. The efficacy of *Gambusia* as an agent of mortality for mosquitoes declines as the physical structure of aquatic environments becomes more complex. This fact is not unique to *Gambusia* or any native fish species for that matter. Mosquitofish, as well as other species with high reproductive rates, can be effective mosquito control agents in isolated man-made aquatic environments such as man-made wetlands, ponds enriched by organic matter or with inputs of limiting nutrients, urban and agricultural drains and other systems where mosquito production is high enough to merit abatement and where mosquito predator populations need to increase rapidly to be large enough to provide persistent levels of control.

There is disagreement among vector ecologists, mosquito control practitioners, public health biologists and others involved in mosquito control as regards the efficacy of fish for vector control (Rupp, 1996; Gratz et al, 1996). Service (in Gratz et al, 1996) questions the utility of larvivorous fishes for vector control and argues that reduction of larval mosquito numbers is not the appropriate metric for assessing the effectiveness of a control agent: the biting densities of mosquito females and/or reduction of disease prevalence should be evaluated. Others claim that mosquito-eating fish are a useful component of integrated mosquito control strategies that include other control methods (see the opinions of some authors in Gratz et al, 1996). Because mosquitofish are opportunistic, generalist feeders, predation is not limited to mosquitoes. The lack of a tight predator–prey interaction between *Gambusia* and immature mosquitoes could slow control and impact non-target taxa.

There is ample observational and experimental evidence that non-native *Gambusia* have strong negative effects on the fauna and function of some ecosystems. Mosquitofish can be damaging to native fish (Schoenherr, 1981; Arthington and Lloyd, 1989; Courtenay and Meffe, 1989; Minckley and Marsh, 2009) and amphibian species (Gamradt and Kats, 1996; Goodell and Kats, 1999; Hamer et al, 2002). Mosquitofish are thought to eliminate some native species through predation on juveniles and/or eggs and interference competition (e.g. aggressive behaviour) that reduces reproductive success (Moyle, 2002). *Gambusia* can be detrimental to small fish with similar ecological requirements (Meffe and Snelson, 1989) and their greatest negative effects appear to be on fishes of similar size in small or isolated habitats where the mosquitofish can become dominant (Moyle, 2002).

Clearly, judicious use of mosquitofish and a greater appreciation of the roles that native mosquito-eating fish and invertebrates can play in integrated mosquito management programmes have merit. An all-out ban on the use of mosquitofish for mosquito control is probably not warranted, but use of *Gambusia* should be limited to the places where the fish are currently found and in habitats where the probability of dispersal into natural systems is very low. New introductions outside the native range should be prohibited. Efforts to manage and possibly extirpate *Gambusia* from natural habitats outside its native range should continue. A better understanding of the factors that facilitate dominance of *Gambusia* in some ecosystems and limit its numbers in native habitats is needed and should facilitate better management strategies for mosquitofish.

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