Plague Minnow or Mosquito Fish? A Review of the Biology and Impacts of Introduced *Gambusia* Species

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INTRODUCTION

The names plague minnow and mosquitofish, by which *Gambusia affinis* and *G. holbrooki* have been known, indicate widely divergent attitudes toward these two fish species. Since approximately the beginning of the twentieth century, both species, which feed on mosquito larvae and pupae, have been introduced into water bodies throughout the world in efforts to control mosquitoes and the human diseases they carry (Pyke 2005). The name mosquitofish arose in this context (Jordan et al. 1930, Seale 1917). More recently, concern has arisen with regard to possible negative impacts that these fish may have on a variety of other animals, including fish, frogs, and aquatic invertebrates. The name plague minnow has arisen in this context (Pyke & White 2000, Richard 2002).

A large and diffuse literature exists with regard to *Gambusia*. My bibliographic database contains approximately 1800 documents that relate to *Gambusia*, including 51 university theses with a focus on *Gambusia*, plus articles from approximately 400 scientific journals and many book chapters. The journal *Copeia* features most prominently in my database with 86 articles, but this represents only approximately 5% of the 1666 journal articles.

Despite the divergent attitudes toward these two species and the large literature concerning them, there has so far been no comprehensive review of their biology and impacts (Lloyd et al. 1986). Such a review should consider their biology, reasons for their very successful spread throughout the world, their effectiveness as mosquito control agents, any impacts they may have on other animals, and their management. It should also be comprehensive, identify gaps and limitations in our knowledge, and be reasonably easy to revise whenever additional information becomes available (Pyke 2001). I have developed such a review using the strategy recommended by Pyke (2001), but with a focus on the impacts of *Gambusia* on other species and on aspects of their biology that are related to these impacts. The species are considered together because they are closely related and very similar biologically, and because it is difficult to separate these two species in the literature, as it is not always clear which species is being discussed. I have elsewhere reviewed other aspects of the biology of these fish (Pyke 2005).

Various aspects of the biology of *Gambusia* are relevant to evaluating their impacts on other species. A comparison of past and present distributions, for example, indicates the extent to which these species have invaded areas occupied by other species. Their range of occupied habitats and elements of general biology will determine their patterns of co-occurrence with other species and the nature of any interactions they have with them. Patterns of abundance will influence the magnitude of such interactions. To control their numbers (positively or negatively), it is necessary to understand their population biology, especially those factors that determine distribution and abundance. I review each of these aspects and the available evidence on interactions with other species.

RELEVANT BIOLOGY

Comparison of Past and Present Distributions

The original natural distributions of *G. affinis* and *G. holbrooki* were very different from the current combined artificial distribution.

The natural distributions lie within eastern North America. That of *G. holbrooki* extends along the east coast of the United States, east of the Appalachian Mountains, between Delaware in the north (approximately 39° N) (Moore 1922), Mobile Bay in Alabama to the west, and southern Florida to the south (approximately 25° N) (Rosen & Bailey 1963, Smith et al. 1989). *G. affinis* originally occurred within the very large drainage system associated with the Mississippi River, which lies to the west of the Appalachian Mountains and east of the Rocky Mountains, and other rivers draining into the Gulf of Mexico (Jordan et al. 1930). Its distribution reached as far north as southern Illinois to a latitude of approximately 40° N, west to Texas, east through Mississippi, and as far south as the Rio Panuco basin in northern Veracruz, Mexico (approximately 22° N) (Jordan et al. 1930, Rosen & Bailey 1963). The original distributions of the two species were almost contiguous, with a relatively small area of overlap around Mobile Bay and few sites where both species were present (Wooten & Lydeard 1990).

Today *G. affinis* and *G. holbrooki* are collectively the most widespread freshwater fish in the world, having been successfully introduced to most of the world. They are present and widespread on all continents except Antarctica (Lloyd 1986). With human help, the combined range of these two species has also increased within North America and now includes most of the United States, one site in Canada, and expanded parts of Mexico (Crossman 1984, Follett 1961, Lachner et al. 1970).

The present distribution of *Gambusia* is, however, restricted to relatively low elevations within the warmer parts of the world. Neither species generally occurs north of approximately 40° N latitude (Krumholz 1944) or south of approximately 38° S latitude (Arthington 1991, Krumholz 1948). Introductions of *Gambusia* further north and south have been unsuccessful except where water has been geothermally or artificially heated (Crossman 1984, Vooren 1972), although *Gambusia* occasionally survive cold winter conditions at high latitude (Smith 1960). *Gambusia* do not generally occur in highland areas (Weatherley & Lake 1967).

The present distributions of *G. affinis* and *G. holbrooki* are complex and difficult to separate with certainty. Taxonomic ambiguity makes species identification uncertain in many locations and translocation pathways for the two species have been different and tortuous, with the result that some places reasonably close together have different species. One pathway, for example, involved *Gambusia* taken from Georgia, within the natural distribution of *G. holbrooki*, to Italy and thence to other locations in Europe and Australia (Dulzetto 1928). This resulted in *G. holbrooki* being the only *Gambusia* species in Australia (Lloyd & Tomasov 1985). Another pathway involved *Gambusia* taken from Texas, within the natural distribution of *G. affinis*, to Hawaii and thence to other Pacific islands, including New Zealand (Jordan et al. 1930, Phillips 1930). This resulted in New Zealand acquiring only *G. affinis* (McDowall 1990). Documentation relating to translocations of *Gambusia* is generally poor and some regions may have received both *Gambusia* species.

Habitat Use

Gambusia generally occur in water that is shallow, is still or slow-moving, and has dense aquatic vegetation (Arthington & Lloyd 1989, Johnson & Hubbs 1989). In water bodies that are moderately deep, *Gambusia* are generally found along the shallow edges, especially where they are well-vegetated (Moyle & Nichols 1973).

Gambusia are otherwise extremely flexible and hardy in terms of their habitats. They have occurred in water with temperatures from approximately 0 to 45°C (Cherry et al. 1976), salinities from approximately 0 to 41 ppt (Hubbs 2000), pH from approximately 4.5 to 9.0 (Keup & Bayliss 1964), dissolved oxygen from approximately 1 to 11 mg l^{-1} (Cherry et al. 1976, Odum & Caldwell 1955), and turbidity from approximately 3 to 275 Jackson Turbidity Units (Cherry et al. 1976). They occur in environments that range from almost completely undisturbed swamps, lakes, and streams to highly disturbed water bodies including urban drains with various water quality problems such as pollution and dense growth of aquatic and surface weeds (Arthington & Lloyd 1989, Cherry et al. 1976, Moyle & Nichols 1973). They are often extremely abundant in disturbed habitats near urban areas (Lloyd et al. 1986). Recorded substrates include sand and mud (Cadwallader 1979). *Gambusia* have even been observed to survive under ice in some locations (Krumholz 1944). *Gambusia* will penetrate thick barriers of vegetation (Phillips 1930), although thick aquatic vegetation can also impede movement and access by this fish (Rees 1979).

Despite this amazing ability to tolerate widely ranging conditions, *Gambusia* are more abundant where the water is relatively warm (Arthington & Lloyd 1989) and have not greatly colonized estuaries, although they are clearly able to survive there (Arthington & Lloyd 1989). *Gambusia* are unable to survive in a water body that dries up or is drained completely, and hence do not occur in ephemeral aquatic environments (Myers 1965). The presence of larger predatory fish may also prevent *Gambusia* from occurring or from being abundant in some situations (Hildebrand 1919a).

General Biology

Gambusia are very flexible species with considerable variability within and between individuals, and from one time and place to another. The gestation period is, for example, usually 22 to 25 days (Krumholz 1948) but can extend from 15 to 50 days depending on water temperature, season, and locality (Gall et al. 1980). Other phases of growth and development are similarly variable in duration (Meffe 1992). The annual breeding cycle sometimes varies with local water temperature (Galat & Robertson 1992). Average clutch sizes range from 5 to 104 (Brown-Peterson & Peterson 1990, Hoy & Reed 1970). *Gambusia* diets include an exceptionally wide array of different food types and may vary considerably from one time and place to another (Rees 1958, Specziar 2004). They sometimes exhibit considerable variation between populations in life history traits (Specziar 2004).

Some of this variability may arise from the flexibility within each individual and from responses of individuals that depend on ambient conditions. For example, *Gambusia* can store fats or lipids in ways that give them flexibility in terms of survival and reproduction (Meffe & Snelson 1993). Temperature, photoperiod, and state of maturity have all been found to influence individual reproduction in *Gambusia* (Fraile et al. 1994). Female *Gambusia* can store viable male sperm and may adjust the point in time at which their eggs are fertilized (Haynes 1993). Males can mate successfully at any time during the breeding season (Fraile et al. 1992). Clutch size increases with increasing food availability and female body length or weight (Gall et al. 1980). *Gambusia* are selective foragers and their diet depends on the nature and extent of available foods (Lawler et al. 1999, Murdoch & Bence 1987). There are also genetically based differences in biological traits between different populations (Stearns 1983).

Whether through basic abilities, physiological adaptation to environmental conditions, or genetic changes at the population level, *Gambusia* are thus able to survive a wide range of physical conditions. Furthermore, their ability to survive relatively extreme environmental conditions is generally enhanced if they are first acclimated to more moderate conditions or if conditions change gradually (Cherry et al. 1976).

Just as *Gambusia* tolerate a wide range in the physical properties of their water habitat, they are also highly resistant, compared with other fish, to the effects of toxins and adverse conditions (Lloyd et al. 1986). In addition, *Gambusia* from populations that have had a long history of exposure to toxic chemicals such as herbicides, insecticides, or industrial pollutants show less mortality when experimentally exposed to these chemicals than *Gambusia* from relatively unaffected populations (Boyd & Ferguson 1964).

Abundance

When present, *Gambusia* are generally abundant (Webb & Joss 1997). They are often the most abundant fish species captured or observed (Arthington & Milton 1983, Kilby 1955) and may constitute more than 80% of the fish sampled (Morton et al. 1988). However, with few exceptions, there has been no quantitative estimation of *Gambusia* population size or density, and differences in approaches and methods in these studies make comparisons difficult (Lawler et al. 1999, Pen & Potter 1991, Schaefer et al. 1994, Zulian et al. 1993).

Gambusia density or abundance typically varies seasonally, with numbers greatest just after the breeding season and lowest when breeding has just begun. In most places, whether in the Northern or Southern Hemisphere, *Gambusia* have a spring/summer breeding season, and peak numbers generally occur in autumn and lowest numbers in spring (Barney & Anson 1921, Morton et al. 1988, Zulian et al. 1993). However, in parts of southwestern Australia, where rainfall tends to occur during winter and conditions are dry during spring and summer, *Gambusia* have a winter breeding season and peak numbers are found in spring (Pusey et al. 1993). Breeding generally occurs when it is mild and wet (Pyke 2005).

There is, however, little available information with regard to interannual variation in *Gambusia* numbers. Dramatic declines associated with sudden changes in habitat have been observed (Duryea et al. 1996, Self 1940). *Gambusia* can increase in numbers very quickly, and hence either repopulate areas after reductions in abundance or rapidly colonize new areas (Hildebrand 1919b, Lloyd et al. 1986, Self 1940). Less dramatic and longer-term variation in *Gambusia* numbers has not been reported.

Population Biology: Mortality and Recruitment

Gambusia potentially reproduce rapidly. Females may mature at just 18 days and subsequently have five or more consecutive clutches at intervals of just 4 to 5 weeks throughout a single season (Meffe 1992). Some females may also breed in a second season (Maglio & Rosen 1969) and clutch sizes of 50 to 100 are not uncommon (Brown-Peterson & Peterson 1990, Hoy & Reed 1970). The fact that female *Gambusia* give birth to live young may result in higher survival of these young than occurs in egg-layers. Population size may therefore increase very rapidly (e.g., Spencer et al. 2000).

Predation, parasites, and disease could be significant sources of mortality for *Gambusia*, although there is little quantitative information available. *Gambusia* are eaten by many different predators including wading birds, kingfishers, larger fish, snakes, bats, large crustaceans, and various other aquatic invertebrates such as water-striders, water-boatmen (Corixidae), and odonate nymphs (Arthington 1989, Levin et al. 2006, Meffe & Snelson 1989a, Meffe & Snelson 1993). Although parasites of *Gambusia* have been little investigated, at least 24 different parasite species have been recovered from *Gambusia* (Arthington 1989, Dove 2000, Lloyd 1989a, Umadevi & Madhavi 2006). *Gambusia* may sometimes be diseased (Bowser 1982), but the identities of these diseases are apparently unknown.

Gambusia populations may also be affected by unpredictable events such as floods and droughts. Numbers have declined dramatically during periods of high water flow, as may occur when streams flood or when water is discharged from a reservoir into a stream (Courtenay & Meffe 1989), and during periods of drought (Self 1940).

Little is known about mortality in wild *Gambusia* populations. Mortality is higher during winter than in warmer months and may be as high as 99% (Haynes 1993). Because mortality rates of 20% to 50% have been recorded for laboratory populations of *Gambusia* over periods of approximately 3 months (Stearns & Sage 1980), much higher mortality rates are likely under less benign natural conditions.

There is little quantitative information concerning recruitment in wild populations of *Gambusia*. Recruitment occurs mostly during the breeding season (Barney & Anson 1921), but how many young join the population at different times is unknown.

Average annual levels of mortality and recruitment must be high because maximum longevity in wild *Gambusia* seldom exceeds 12 to 15 months. Maximum longevity in wild *Gambusia* could possibly reach 18 months because individuals have lived this long in captivity (Hildebrand 1919b). In the wild, maximum longevity must be at least 9 months, as some individuals born in one breeding season are found breeding during the next (Pen & Potter 1991). Cadwallader & Backhouse (1983) estimate 15 months for maximum longevity. Vargas & Sostoa (1996) found that all males and most females lived less than 12 months, whereas a few females lived 2 to 3 years.

Population Biology: Population Regulation and Dynamics

Gambusia populations are potentially regulated by food availability and competition with other species. Food availability can regulate *Gambusia* in experimental ponds, as the application of commercial fertilizer increased primary productivity and numbers of *Gambusia* produced per pond (Goodyear et al. 1972). That *Gambusia* breed and increase in numbers when it is relatively mild and wet (Pyke 2005), which are times when their food organisms are also breeding and abundant, suggests that food availability may influence abundance in the wild. However, there is currently no available information concerning the role of food in regulating wild *Gambusia* populations. Competition with other species could reduce food availability, although its importance is also unknown.

Predation may also regulate *Gambusia* populations, especially in native habitats. *Gambusia* numbers, in the presence of larger fish that feed on them, sometimes decline dramatically, and the species may even be eliminated (Duryea et al. 1996, Nowlin et al. 2006). Numbers may be low in native habitats where *Gambusia* feature prominently in diets of native fish and water snakes (Hildebrand 1919b, Lachner et al. 1970, Meffe & Snelson 1989b, 1993), yet extremely abundant in feral habitats where they constitute only small proportions of the diets of ecologically comparable predators (Daniels 1987, Kilby 1955, Lloyd 1989a, Vooren 1972, Webb & Joss 1997).

Parasitism of *Gambusia* is similarly more prominent in their native habitats than elsewhere. In the United States, *Gambusia* host at least 23 parasite species (Arthington 1989, Lloyd 1989a), and sometimes a high percentage of individuals are heavily infested (Aho et al. 1975, Zuckerman & Behnke 1986). In Australia, however, there are few records of parasites of *Gambusia* (Arthington 1989, Arthington & Mitchell 1986, Dove 2000) and native fish are more heavily parasitized (by native parasites) than *Gambusia* (Lloyd 1989a). There are also few records of parasites on *Gambusia* from other parts of the world (Umadevi & Madhavi 2006, Yang et al. 2005).

Food availability, predation, or parasitism could have regular, seasonal effects and hence might explain observed seasonal variation in densities. Although any of these factors could regulate *Gambusia* populations, quantitative understanding of population dynamics is poor (Meffe & Snelson 1989b).

INTERACTIONS WITH OTHER SPECIES

Gambusia potentially interacts with many plant and animal species, including various invertebrates, amphibians, and other fish (Barrier & Hicks 1994, Kilby 1955). These interactions have been widely discussed because of long-term interest in *Gambusia* as mosquito-control agents and relatively recent interest in possible negative impacts of *Gambusia* on the natural environment.

Impacts on Mosquitoes and Mosquito-Born Disease

Since the discovery in the late nineteenth century that mosquitoes carry and transmit diseases (Herms & Gray 1940; Howard 1901, 1910), there has been considerable interest in controlling them and in the impacts of *Gambusia* and other fish on mosquito populations. In 1904, David Starr Jordan discovered that *Gambusia* would devour mosquito larvae in laboratory trials and recommended their use in mosquito control (Phillips 1930). Other early investigators reinforced this observation (Hildebrand 1919a,b; Howard 1901, 1910; Moore 1922; Seal 1910; Seale 1917).

Investigations of the impact of *Gambusia* on mosquito populations have evolved over the last 100 years, along with scientific protocols in general. Initial observations were anecdotal, consisting of qualitative observations of ponds with *Gambusia* added, or comparisons between ponds with and without *Gambusia* (Howard 1901, 1910; Moore 1922; Seale 1917). At this stage, sample sizes were very small, with sometimes only one or two ponds observed, and experimental studies lacked controls. Such anecdotal observations have continued until recently (Duryea et al. 1996). Since approximately 1920, studies of the impacts of *Gambusia* on larval mosquitoes have generally included control as well as experimental treatments, but for the most part sample sizes have remained small (i.e., <10) and different water bodies have not been randomly assigned as experimental or control (Blaustein 1991, Green & Imber 1977, Hildebrand 1925, Hoy & Reed 1970, Miura et al. 1984). Only one study so far has had 10 or more replicates of the experimental treatment, 10 or more controls, and random assignment of experimental and control treatments (Hoy et al. 1972).

Initial anecdotal observations suggested that *Gambusia* added to a pond with abundant mosquito larvae will drastically reduce or eliminate them (Hildebrand 1919a, b; Moore 1922; Seale 1917), and that ponds with *Gambusia* will have few or no mosquito larvae, whereas ponds with few or no fish may have abundant mosquitoes (Hildebrand 1919a, Hildebrand 1925, Howard 1920, Howard 1901, Moore 1922, Seale 1917). Anecdotal observations since then have supported these views and indicated that abundance of mosquito larvae increases after *Gambusia* removal (Duryea et al. 1996, Krumholz 1944, Murdoch & Bence 1987).

Initial anecdotal observations also suggested that *Gambusia* less effectively reduced mosquito larvae when aquatic vegetation was present, especially if it was thick (Hildebrand 1925; Howard 1901, 1910; Moore 1922; Seal 1910; Valli 1928). Clearing of the aquatic vegetation sometimes resulted in decreases in abundance of mosquito larvae through increasing the effectiveness of *Gambusia* (Valli 1928). Similar anecdotal observations have been reported in subsequent years (Duryea et al. 1996, Herms & Gray 1940, Rees 1958). Recent experimental studies have shown that predation by *Gambusia* on mosquito larvae is reduced by the presence of aquatic vegetation (Willems et al. 2005).

By the 1920s, it was widely accepted that *Gambusia* provided effective control of both mosquitoes and mosquito-borne diseases, and that this had been achieved in many parts of the world (Jordan 1926, Moore 1922, Phillips 1930). However, *Gambusia* was judged less effective in places where it died out during winter (Rees 1934) or where clearing water of vegetation was difficult or impossible (International Health Board 1924, Valli 1928). *Gambusia* were credited with a dramatic drop in the incidence of malaria in Mississippi in 1918 (Howard 1920) and striking reductions in deaths from malaria and yellow fever in other locations (Howard 1910). This positive assessment of *Gambusia* was associated with rapidly increased introductions of *Gambusia* into water bodies worldwide as a mosquito control agent (International Health Board 1924). *Gambusia* were even introduced into New Zealand, where mosquitoes were not considered a serious problem (Phillipps 1930).

The initial (and some subsequent) results of controlled experiments have generally provided further evidence of reductions in abundance of larval mosquitoes by *Gambusia*. Water bodies stocked with *Gambusia* have generally had lower densities of larval mosquitoes than controls (Blaustein 1991, Green & Imber 1977, Hildebrand 1925, Miura et al. 1984) and the density of larval mosquitoes decreased with increasing *Gambusia* density in a number of cases (Hoy & Reed 1970, Hoy et al. 1972).

For some of the other early controlled experiments, no difference in density of larval mosquitoes has been apparent between the water bodies with *Gambusia* and those without (Reed & Bryant

1975, Washino 1968), but the interpretation of these results has varied. To some, chosen stocking rates of *Gambusia* were considered too low for reduction in larval mosquito numbers, and this result would have been achieved through higher initial stocking rates or waiting until the fish had reproduced and increased in density (Reed & Bryant 1975, Washino 1968). To others, they indicated that *Gambusia* are generally ineffective at controlling mosquitoes (Lloyd 1986).

More recently, studies with adequate sample sizes and random assignment of treatments have generally failed to demonstrate that *Gambusia* control the abundance of mosquito larvae. For example, Hoy et al. (1972) found that water bodies stocked with *Gambusia* at low densities (i.e., 2 lb/acre) developed higher densities of larval mosquitoes than did either control ponds or ponds with a higher stocking rate of *Gambusia* (i.e., 6 lb/acre). They attributed the relatively low mosquito levels in control treatments to predation by notonectids and the higher mosquito levels at the low stocking rate of *Gambusia* to the fish concentrating their feeding on notonectids and some other invertebrates and tending to ignore the mosquito larvae (Hoy et al. 1972). *Gambusia* stocked at the higher rate ate both mosquito larvae and other invertebrate prey (Hoy et al. 1972). Similarly, both Kramer et al. (1987) and Blaustein (1992) found no significant difference in abundance of mosquito larvae between ponds with and without *Gambusia* and suggested that a depressive effect of *Gambusia* on the abundance of notonectids, which prey on mosquito larvae, may have been responsible for the neutral effect. Such indirect enhancement of mosquito populations by *Gambusia* has often been suggested (Hurlbert & Mulla 1981, Hurlbert et al. 1972).

A polarized view of *Gambusia's* effectiveness at controlling mosquitoes and mosquito-borne diseases has developed since approximately 1960. One group derives support from studies that indicate some reduction in larval mosquito abundance associated with introduction or presence of *Gambusia*. This group judges *Gambusia* as generally effective in controlling larval mosquitoes (Green & Imber 1977, Hoy et al. 1972, Russell 1993) and credits *Gambusia* as having significantly reduced irritation and disease risks from mosquitoes (Ghosh & Dash 2007, Russell 1993). The second group points to the often low levels of mosquito larvae in the diet of *Gambusia* and the studies that have "failed" to demonstrate reduction in numbers of larval mosquitoes by *Gambusia* and claims that *Gambusia* are generally ineffective in controlling larval mosquitoes (Arthington & Lloyd 1989; Courtenay & Meffe 1989; Lloyd 1986, 1989b; Service 1983). The only apparent middle ground has been the suggestion that the effectiveness of *Gambusia* at controlling larval mosquitoes varies widely between habitats (Wurtsbaugh et al. 1980), but so far no relationship between *Gambusia* effectiveness and habitat has been determined.

Widely used methods, other than *Gambusia*, for controlling larval mosquitoes include draining water bodies, placing an oil film across the water surface, introducing other fish species, releasing pathogens (biotoxins) or parasites of larval mosquitoes, and insecticides. Draining water bodies was highly recommended and much used from the late nineteenth century until approximately 1935, when the devastating environmental consequences of this strategy were acknowledged (Eigenmann 1923; Howard 1910, 1920; Moore 1922). Placing a layer of kerosene or other light oil on the water surface has been widely used from approximately 1812 to the present (Eigenmann 1923; Howard 1901, 1910, 1920; Phillipps 1930), although its adverse impacts on the environment have also been recognized (Moore 1922, Williams et al. 1939). Naturally produced bacterial toxins have been used since approximately 1974 (Homski et al. 1994, Laird 1977, Morton et al. 1988, Service 1983). Synthetic insecticides have been used since the 1940s (Lounibos & Frank 1994) but can lead to increases in mosquito numbers through decreases in natural invertebrate predators of mosquitoes (Laird 1977).

Many other fish species, from many different parts of the world, have been suggested as alternative or additional control agents for larval mosquitoes (Eigenmann 1923, International Health Board 1924, Lloyd 1986, Phillips 1930). The best fish for mosquito control were considered to live in quiet or open water, to swim amid aquatic and semiaquatic vegetation, to be active, top-feeding carnivores, especially with regard to mosquito larvae, not to harm other fish species, and to be found in high numbers where there are mosquito larvae (Moore 1922).

Many investigations of different fish species as control agents for larval mosquitoes were conducted throughout much of the world between approximately 1912 and 1922 (International Health Board 1924, Moore 1922). Like the early evaluations of *Gambusia*, these investigations were anecdotal, not very rigorous by today's standards and not well documented (International Health Board 1924, Moore 1922). However, some fish species were found to include mosquito larvae in their diet to a substantial extent and to reduce numbers of larval mosquitoes (Moore 1922).

By the end of this period, *Gambusia* had emerged as "the fish" for control of larval mosquitoes and was already the principal fish used in this manner (Eigenmann 1923, Howard 1920, Krumholz 1948, Myers 1965). Rather surprisingly, this view prevailed despite investigators agreeing that it was best to use indigenous fish for mosquito control (International Health Board 1924). Hence *Gambusia* were translocated throughout the world in the interests of mosquito control.

Since then, there has been little serious comparison of *Gambusia* and other plant or animal species as control agents of larval mosquitoes, although more than 300 fish species worldwide have been identified as being potentially suitable for mosquito control (Ghosh & Dash 2007, Lloyd 1986, Wilson 1960). It has also been recognized that many aquatic invertebrates eat mosquito larvae and may consequently help control mosquitoes (Laird 1977) and that some cnidaria such as *Hydra* feed on or otherwise inhibit mosquito larvae (Russell 1993). *Gambusia* nonetheless became virtually the only species used (Homski et al. 1994), and between approximately 1930 and 1960 there were few if any comparisons made between *Gambusia* and other fish species in terms of impacts on mosquito numbers.

Since 1960, most comparisons of *Gambusia* and other fish species have found considerable variation in the extent to which mosquito larvae feature in diets of individual fish and that other fish sometimes feed on mosquito larvae as much as or more than *Gambusia*. The proportion of mosquito larvae in the diet has ranged from close to 0 to more than 50% for *Gambusia* and other fish species, and other food types have sometimes been preferred over mosquito larvae (Harrington & Harrington 1961, Washino 1968). This proportion has often been lower for *Gambusia* than for other fish species (Harrington & Harrington 1961, Lloyd 1986).

The few comparisons that have been carried out between *Gambusia* and other fish species indicate that *Gambusia* sometimes, but not always, reduce larval mosquito abundance, but they are insufficient for an overall assessment of *Gambusia* in relation to other fish species. In experiments, numbers of mosquito larvae have often been lower with *Gambusia* or another fish species relative to controls (Rees et al. 1969), but numbers of mosquito larvae have sometimes been lower with *Gambusia* than with other fish species (Rees et al. 1969), and sometimes higher (Castleberry & Cech 1990).

Despite the lack of sufficient information for a comparison of *Gambusia* and alternative strategies for controlling larval mosquitoes, many have argued that *Gambusia* are no more and often less effective than other strategies, especially the use of indigenous fish (Arthington & Lloyd 1989, Wilson 1960). These researchers generally gain support for their view from studies that show larval mosquitoes are a relatively small component in diets of individual *Gambusia*, especially in comparison with other fish species (Lloyd 1986).

The extent to which introduction of *Gambusia* has resulted in reductions of adult mosquitoes or mosquito-borne diseases is not clear. *Gambusia* have been credited with the reduction of mosquito-borne diseases in several parts of the world (Ghosh & Dash 2007, Howard 1920), but other researchers have concluded that there is no unequivocal evidence that *Gambusia* have ever reduced mosquito density sufficiently to control mosquito-transmitted disease (Lounibos & Frank 1994, Service 1983). Lardeux (1992) was unable to detect any effect of larval mosquito control in one location on the subsequent observed rate at which humans in the area were "bitten" by adult mosquitoes. Olson et al. (1979) found a correlation between population indices of adult mosquitoes and the incidences of encephalitis and encephalomyelitis in California, but there remains no evidence to link differences in abundance of adult mosquitoes to larval control.

Impacts on Other Invertebrates

Several studies, mostly since the 1970s, have documented negative impacts of *Gambusia* populations on invertebrates other than mosquitoes. In many experiments, water bodies with *Gambusia* have had, compared with controls, reduced densities of aquatic invertebrates such as rotifers, crustaceans, backswimmers, water beetles, and odonate larvae (Blaustein 1991, Hurlbert & Mulla 1981, Hurlbert et al. 1972, Lawler et al. 1999, Miura et al. 1984). Declines in the invertebrate fauna have also been recorded after introduction of *Gambusia* to previously fishless water bodies (Schaefer et al. 1994).

Positive or neutral impacts of *Gambusia* populations on some invertebrates have also been recorded, as might be expected through compensation of the direct effects of predation by *Gambusia* with the indirect effects of predation on their competitors or predators. Hurlbert et al. (1972) found, for example, that experimental ponds with *Gambusia* had higher densities of one annelid worm species in comparison with control ponds. Hurlbert & Mulla (1981) found that experimental ponds with *Gambusia* had higher densities of various rotifers than control ponds. Miura et al. (1984) found no reduction in densities of copepods, ostracods, dragonflies, belostomatids and aquatic beetles associated with the experimental *Gambusia* introduction.

Some studies have recorded both positive and negative impacts of *Gambusia* on invertebrate populations, with resulting effects on phytoplankton and/or zooplankton. For example, Jassby et al. (1977a,b) concluded that, with *Gambusia* present, there was a shift from larger to smaller zooplankters owing to selective predation by *Gambusia* on large ones, a concomitant increase in bacteria, phytoplankton and rotifer number in tanks with fish owing to decreased grazing pressure on phytoplankton by larger zooplankters, and a fluctuating phytoplankton community directly influenced by abundances of larger zooplankters. Similarly, Rees (1979) found a shift in zooplankton type from large to smaller sizes in the presence of *Gambusia* as well as a grazer-controlled, fluctuating phytoplankton-zooplankton community that was also influenced by *Gambusia* presence.

Impacts on Amphibians

Concern about the potential impacts of *Gambusia* populations on amphibians first appeared in the literature in the early 1970s, with a large increase in publications since approximately 1990.

Gambusia have been implicated, through spatial and temporal comparisons, as responsible for declines and disappearances of a number of amphibian species, and experimental studies demonstrate negative impacts of *Gambusia* populations on frogs. For example, historical comparisons of amphibian records at several locations have shown a loss in amphibian species associated with *Gambusia* introduction (Ghate & Padhye 1988). On a shorter timescale, Dankers (1977) found that tadpoles were observed in ponds in years when *Gambusia* densities were relatively low but not in years when *Gambusia* were abundant. Spatial increases in *Gambusia* abundance have been associated with reduced amphibian abundance and diversity (Hurlbert & Mulla 1981, Webb & Joss 1997). Many experiments have found that tadpole survival, rate of development, or size at metamorphosis is lower in water bodies containing *Gambusia* than in controls or when *Gambusia* density is relatively high (Hurlbert & Mulla 1981, Lawler et al. 1999). On the other hand, some experiments have also shown that predation by *Gambusia* is moderated by the presence of aquatic vegetation and frogs can sometimes survive and breed in water bodies with *Gambusia* (Ghate & Padhye 1988, Lawler et al. 1999, Maglio & Rosen 1969, Webb & Joss 1997).

The effects of *Gambusia* on frogs may vary with frog species and habitat use. Frog species most likely to suffer negatively from *Gambusia* predation may be those whose eggs and/or tadpoles overlap extensively with *Gambusia* in space and time and are not protected by being distasteful or toxic. Eggs or tadpoles generally found near the surface where *Gambusia* also occur may be at greater risk of predation than those near the bottom of the water column (Ghate & Padhye 1988). Eggs and tadpoles that generally occur among thick aquatic vegetation may be at less risk than those in more open water because *Gambusia* forage mostly in relatively open water (Morgan & Buttemer 1996). Frogs that breed during the summer when *Gambusia* numbers and appetites are greatest may be at greater risk than other species that breed mostly at other times (Pyke & White 2000). Frogs that usually breed in temporary fish-free water bodies may be less distasteful or toxic to fish than frogs from more permanent water bodies, and hence more susceptible to *Gambusia* predation when these fish are able to gain access to their breeding areas (Grubb 1972).

Interactions with Other Fish Species

Where two or more *Gambusia* species coexist, competitive interactions between them would be expected. *G. affinis*, *G. holbrooki*, and other *Gambusia* species are very similar ecologically and overlap extensively in habitat utilization, and would therefore compete for any components of the habitat that are in limited supply. However, it is rare to find two *Gambusia* species coexisting in the same water body (Hubbs & Peden 1969, Meffe & Snelson 1989b, Wooten & Lydeard 1990), and when this happens they tend to occupy different habitats (Hubbs & Peden 1969). Hence competition between *Gambusia* species may be a strong force that has already affected the nature and extent of overlap among them.

There has been interest in the possible impacts of *Gambusia* on other fish species, beginning in approximately 1950 and increasing after approximately 1960, but only scant, relatively recent interest in the potential impacts of other fish species on populations of *Gambusia* (Blaustein 1991, Nowlin et al. 2006, Schaefer et al. 1994). There has also been considerably more interest in the possible negative impacts of *Gambusia* on other fish species than on other aquatic fauna apart from mosquitoes.

Spatial and temporal comparisons have implicated *Gambusia* populations as being responsible for declines and disappearances of a number of fish species of similar size and habitat. As *Gambusia* have increased, some other fish species have declined, even to local extinction (Arthington 1989, Courtenay & Meffe 1989, Galat & Robertson 1992). Following reduction (natural or artificial) in *Gambusia*, some other fish species have increased (Galat & Robertson 1992, Meffe 1983). Where *Gambusia* abundance has been relatively high, the abundances of some other fish species have been lower (Arthington 1989).

Since approximately 1985, experimental studies have demonstrated negative impacts of *Gambusia* on other fish species that are similar in size and habitat, but few have considered possible impacts in the opposite direction. For several fish species, survival and recruitment were found to be lower, with consequent reduction in population, when more *Gambusia* were present than in controls or when *Gambusia* density was relatively high (Blaustein 1991, Schaefer et al. 1994). In most cases, survival was reduced, especially for relatively small individuals, through predation or physical injury by *Gambusia* (Schaefer et al. 1994). The impact on *Gambusia* from other ecologically similar fish species has been neutral or negative (Blaustein 1991, Schaefer et al. 1994).

Recent experimental studies have similarly demonstrated negative effects of *Gambusia* on populations of other fish and shown that these effects may result from a complex interplay of age/size and habitat dependent competition, predation, and agonistic interactions. For example, *Gambusia* adversely affected the least chub (*Iotichthys phlegethontis*) through predation that decreased with increases in chub size relative to *Gambusia* size, agonistic interactions whereby relatively small chub were forced into refuge habitats where they suffered relatively high invertebrate predation, and agonistic interactions that resulted in reduced growth in all size classes of chub (Mills et al. 2004). However, these two species have exhibited complex spatial and temporal patterns of habitat use, with chub able to grow and reproduce better than *Gambusia* in relatively cool microhabitats, thus enabling coexistence in some situations (Ayala et al. 2007). Recent studies have highlighted the roles of predation and physical injury by *Gambusia*, and shown that aggression by *Gambusia* can force other fish into habitats where there is increased exposure to other predators or decreased access to food (Ayala et al. 2007).

Other Impacts

Because *Gambusia* are at intermediate trophic levels of complex trophic connections, they may affect many different trophic levels, and these impacts can be positive or negative. Experiments have shown, for example, that *Gambusia* may affect zooplankton community composition with flow-down effects on phytoplankton (Angeler et al. 2007, Cardona 2006) and that *Gambusia* may consume terrestrial insects on the water surface, thus enhancing primary productivity through increase of allochthonous nutrients (Hargrave 2006). Abundance of pupfish (*Cyprinodon macularius*) may sometimes be positively correlated with *Gambusia* abundance (Martin & Saiki 2005), even though *Gambusia* negatively affect pupfish populations and have contributed to their decline (Schoenherr 1981). As mentioned above, *Gambusia* can sometimes increase the abundance of mosquito larvae through predation on other mosquito predators (Blaustein 1992, Hoy et al. 1972, Kramer et al. 1987). In the same way, rotifers can benefit from *Gambusia* predation on microcrustaceans and chironomids (Miracle et al. 2007).

MANAGEMENT

Mosquito Control versus Wildlife Conservation

The perceived value of *Gambusia* has changed considerably. For the 50 years since *G. affinis* and *G. holbrooki* were first described until the beginning of the twentieth century, *Gambusia* were considered worthless and, thus, not exploited (Jordan & Gilbert 1882). For the subsequent 100 years many have viewed *Gambusia* as beneficial for controlling mosquitoes and mosquito-borne diseases and otherwise harmless (Phillips 1930). However, starting in approximately 1950 and increasing greatly since approximately 1970, some have seen *Gambusia* as an environmental scourge because of their negative impacts on other animal species (Arthington 1989, 1991; Lloyd et al. 1986). Views concerning *Gambusia* have consequently become polarized.

Since the beginning of the twentieth century, *Gambusia* have featured prominently in mosquito control programs that have affected the spread of *Gambusia*. Until approximately 1935, the general approach to mosquito control was to drain as many as possible of the wetlands where they breed and to convert the land to agriculture. At the time some could see no reason why 'swamps' should be retained, recommending canalizing all streams and draining all swamps and seepage areas (Howard 1920), and legislation was enacted that mandated mosquito-control work in general and draining of swamps in particular. The initial spread of *Gambusia* took place during this period with translocations to many parts of the world but, as far as mosquito control was concerned, the introduction of *Gambusia* was apparently seen as a backup strategy (Howard 1920). Major changes in approach occurred in the late 1930s and around the time that World War II began. There was then considerable resistance to continued draining of water bodies, because of the perceived environmental costs (Williams et al. 1939), and much concern about the risks of mosquito-borne disease faced by military personnel (Herms & Gray 1940, Lee et al. 1980). So, for approximately the next 20 years, introduction of *Gambusia* became the major mosquito-control strategy, and their distribution and overall abundance were greatly enhanced through the combined efforts of the military, government health agencies, and private individuals (Herms & Gray 1940, Lee et al. 1980, Myers 1965). This strategy was seen to eliminate conflict between mosquito abatement and wildlife conservation (Herms & Gray 1940).

In the 1960s, there was increasing concern about human impacts on the environment generally and about impacts of *Gambusia* and other introduced fish on native fauna. This concern resulted in legislation as early as 1960 in both the United States and Australia restricting the stocking, transport and release of *Gambusia* and other fish (Hubbs & Deacon 1964, Wilson 1960). The first attempt was also made to remove *Gambusia* from a water body as part of a recovery strategy for an endangered fish (Hubbs & Brodrick 1963). However, the American Fisheries Society and others did not recognize the problem of introduced nonnative fish species until approximately 1979 (Zuckerman & Behnke 1986), and it was only later that more significant legislation was enacted (Russell 1993). Recently, because of its perceived impact on several endangered frog species, *Gambusia* have, for example, been declared a "threatening process" in New South Wales, Australia and, under this state's Threatened Species Conservation Act of 1995, the development of an appropriate 'threat abatement plan' was required (Haering 2001). Since approximately 1960, mosquito-control strategies have also changed, with general use of *Gambusia* decreasing, introduction of *Gambusia* into natural water bodies avoided in some areas, and natural and synthetic larvicides increasingly used (Federici 1995). *Gambusia* are, however, still regarded as an important component of integrated mosquito control programs (Ghosh & Dash 2007).

Reducing Impacts of *Gambusia*

Any negative impacts of invasive *Gambusia* on native species could be reduced either by lowering numbers of *Gambusia* or by reducing average impacts per *Gambusia* individual. Methods that might be used to decrease *Gambusia* abundance include applying poison and introducing pathogens, parasites, or larger predatory fish. Piscicides are likely to be most effective in small water bodies where high concentrations of the poison can be achieved and where fish cannot easily escape its effects; otherwise other biological methods might be more broadly applicable. Impacts per individual *Gambusia* on another species might be reduced by either enhancing thick aquatic vegetation in water bodies that contain *Gambusia* or otherwise manipulating the habitat so as to render the *Gambusia* either less inclined to pursue this species or less successful in these pursuits.

Any method to decrease *Gambusia* abundance should clearly be target-specific, highly effective, and should not lead to further environmental problems. For example, a new predatory fish that preyed on native aquatic fauna instead of feeding on *Gambusia* or did so after it had reduced the numbers of *Gambusia* would certainly not be a welcome addition. However, a fish that could be introduced into a water body containing *Gambusia* in spring, would feed on the *Gambusia* to a high degree and to the almost complete exclusion of other prey, and would die during the winter as water temperatures decrease might prove beneficial (White 2001).

Despite the great concern about impacts of feral *Gambusia* on native fauna and flora, only few attempts to control *Gambusia* or its impacts have been documented, and all involve poison. Poisons that have been used include rotenone (Hubbs & Brodrick 1963), Antimycin A (Meffe 1985), liquid chlorine, and calcium hydroxide, supplied as 'lime' (G.H. Pyke, personal observation). There are so far no documented attempts to use biological methods to control *Gambusia* or their impacts.

Recorded attempts to eliminate *Gambusia* with poison have had mixed results. Hubbs & Brodrick (1963), for example, used rotenone unsuccessfully to eliminate *Gambusia* from some warm springs in Texas where they had been introduced. A sequence of liquid chlorine, then builders' lime, and finally rotenone, has been used in vain to remove *Gambusia* from a small pond in Sydney, Australia, measuring roughly 20 m × 10 m and up to approximately 50 cm deep (G.H. Pyke, personal observation). Attempts, using liquid chlorine, to remove *Gambusia* from a larger pond that measured roughly 40 m in diameter and up to approximately 2 m in depth were similarly unsuccessful (J. Weigel, personal observation). However, rotenone has successfully eliminated *Gambusia* from several other relatively small ponds in and near the Sydney area (A. Hamer, personal observation; C. Webb, personal observation) and from a pond in Utah with a surface area of 320 m^2 (Mills et al. 2004). Reducing the water in a pond may increase the effectiveness of any piscicide (Mills et al. 2004). In addition, removal of *Gambusia* from water bodies may only be temporary if they are able to reinvade later, as may occur, for example, during floods.

DISCUSSION

It is not surprising that *Gambusia* (i.e., *G. affinis* and *G. holbrooki*) have successfully colonized most parts of the world. They are hardy, flexible, and adaptable, with an extraordinary ability to tolerate and use a wide range of natural and artificial conditions. Their high reproductive potential and ability to store sperm enable them to colonize new areas rapidly, possibly from just a single impregnated female. Their broad diet and small size allow them to often achieve exceptionally high densities. They can alter their life history to adapt to particular environments. They have largely escaped their natural predators, parasites, and pathogens as they have spread around the world. In locations where *Gambusia* are a natural food source, native predators and parasites have presumably evolved to avoid or circumvent their defenses, whereas this may not have happened in habitats to which *Gambusia* have been translocated and potential predators and parasites do not use *Gambusia*.

Although *Gambusia* have been lauded for approximately 100 years for their alleged prowess in controlling mosquitoes and the diseases they carry, it is hard to separate legend from reality. Early investigations of their ability to reduce the numbers of larval mosquitoes and comparisons in this regard with other fish species were not satisfactorily rigorous by today's standards and were not well documented. Few observations were reported with regard to the potential impact of *Gambusia* on mosquito-borne diseases, and these were anecdotal. Yet the legend began and introduction of *Gambusia* was generally accepted as the best method for controlling mosquitoes and their diseases. Little further evaluation of this view was subsequently carried out, and the legend became entrenched.

The recent views that *Gambusia* is not very effective at controlling mosquito larvae and that other indigenous fish species are generally much better also lack a sound base. Few rigorous experimental evaluations of these assertions have been made and results have been equivocal.

Whatever benefit may arise from introducing *Gambusia* for mosquito control, it is clear that, when *Gambusia* are introduced into or escape into natural water bodies, the environmental cost can be high. Rigorous experimental studies have almost unanimously demonstrated negative impacts of *Gambusia* on a wide range of aquatic animals including aquatic invertebrates, amphibians, and other fish species. It is therefore not surprising that attempts have begun to arrest further spread of this fish and to remove it from some locations. It also seems likely that these results have encouraged some to doubt the effectiveness of *Gambusia* in terms of mosquito control. Polarization of views toward *Gambusia* has, I think, been inevitable.

This polarization seems unlikely to disappear soon. Given the complexity of the situation with very high numbers of mosquito species, even higher numbers of other animal species that might be affected by *Gambusia*, a diverse array of locations and habitats throughout the world where humans and mosquitoes overlap, and an understandable concern regarding impacts of disease on the human population, no small set of studies can be expected to settle the issue. Any study can always be argued to be just a special case or somehow flawed by those who do not favor its conclusions, in similar fashion to what has happened in the long-standing controversy concerning impacts of the honeybee on native plants and animals in locations where it has been introduced (Pyke 2000).

It is enigmatic that *Gambusia* can be so widespread and abundant, considered by some to be a savior and by others to be a scourge, and yet be so poorly understood in a number of respects. There is, for example, little available information with regard to just how abundant *Gambusia* actually are, and almost no available information concerning what factors control their distribution or abundance and how these factors operate, all seemingly essential knowledge. There is likewise little available quantitative information concerning the factors that influence behavior of individuals, especially with regard to where, when, and what they eat and to any underlying mechanisms or reasons for their behavior. Our knowledge of other aspects of *Gambusia* biology is also surprisingly patchy and limited. *Gambusia* can hardly be judged to be particularly well-known and understood species, despite the relatively vast literature that has been devoted to them.

Our knowledge of the impacts of *Gambusia* on other components of the environment also remains poor. There is overwhelming evidence on negative impacts of feral *Gambusia* populations, yet a paucity of information concerning the mitigation of such impacts. There is an equally overwhelming lack of good evidence with regard to the legendary abilities of *Gambusia* to control mosquitoes and their diseases, yet, in some quarters at least, the legend continues. All these areas deserve further attention.

The names mosquitofish and plague minnow promote essentially opposite attitudes toward these fish and hence contribute to the polarization of views. Adoption of the name mosquitofish for both *G. affinis* and *G. holbrooki* contributed to the unquestioned acceptance of these fish as the 'logical choice for mosquito control' and resulted in little evaluation of either the effectiveness of these or other fish in controlling mosquitoes or of the impacts of such control measures on other components of the environment (Arthington & Lloyd 1989; Lloyd 1986, 1989b). The obviously derogatory name plague minnow draws attention to their adverse environmental impacts. The names eastern and western *Gambusia* lack bias in either direction, and have been recommended or accepted by some researchers (Lloyd 1989b, Meffe 1989). Perhaps general adoption of these latter names would lead to a more balanced approach regarding these fish.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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