

# Chapter 12 Evolutionary conservation biology

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## 12.1 Introduction

**P**OECILIIDS ARE OF PARTICULAR interest to conservation biologists for a number of reasons. First, they have become excellent models for conservation biologists due to their small size and rapid generation time (Quattro & Vrijenhoek 1989; Leberg 1990, 1993). Second, many poeciliid studies have provided important insights on the rate of evolutionary diversification (e.g., Endler 1980; Reznick et al. 1990; Reznick et al. 1997; see also Pires et al., **chapter 3**; Breden & Lindholm, **chapter 22**; Grether & Kolluru, **chapter 6**; Johnson & Bagley, **chapter 4**; Schlupp & Riesch, **chapter 5**), the ultimate source of biodiversity. Third, poeciliids are vulnerable to the same anthropogenic factors driving the current extinction crisis (e.g., habitat loss, invasive species). Paradoxically, one of the greatest threats to poeciliids is the spread of heterospecific poeciliids (Minckley & Deacon 1968; Meffe 1985b; Minckley & Jensen 1985; Courtenay & Meffe 1989; Belk & Lydeard 1994). Thus, poeciliids have been extensively evaluated in the context of conservation biology (Johnson & Hubbs 1989; Leberg 1990, 1993; Stockwell et al. 1996; Stockwell & Weeks 1999).

Johnson and Hubbs (1989) provided an overview of the conservation status of the poeciliids in the United States. Since that time, poeciliids have mirrored the decline of other freshwater fishes (see Jelks et al. 2008). Furthermore, our understanding of relationships among taxa has increased, allowing reevaluation of the systematics and distribution of poeciliid biodiversity (Rosen & Bailey 1963; Parenti 1981; Parenti & Rauchenberger 1989; Hrbek et al. 2007).

Much applied research has focused on endangered poeciliids (e.g., *Poeciliopsis* spp.) as well as common and invasive poeciliids (e.g., *Gambusia* spp., *Poecilia reticulata*). In fact, many poeciliids have been used as model systems to examine questions central to the field of conservation biology. Here, we provide an overview of the poeciliids from the perspective of conservation biology. First, we review the geographic distribution of poeciliid biodiversity as well as associated threats. We then consider the impact of nonnative poeciliids on native species and ecosystems. We conclude by summarizing the role of selected poeciliid species as models for studies in the emerging field of evolutionary conservation biology (as conceptualized by Ferrière et al. 2004).

## 12.2 Diversity, conservation, and threats

Poeciliid conservation status has changed considerably during the last few decades (Jelks et al. 2008). Here, we provide a brief overview of poeciliid biodiversity with special focus on the conservation status of these fishes. We also review the primary threats faced by poeciliids.

### 12.2.1 Poeciliid biodiversity and distribution

The *FishBase* data base (Froese & Pauly 2009) and recent reviews (Parenti 1981; Parenti & Rauchenberger 1989; Nelson et al. 2004; Hrbek et al. 2007; Eschmeyer & Fong 2008; Jelks et al. 2008; Scharpf 2008) recognize more than 250 species of poeciliids, belonging to 22–28 genera. The most species-rich genera are *Gambusia* (43 species),

*Poecilia* (34 species), *Xiphophorus* (28 species), *Poeciliopsis* (23 species), *Phalloceros* (22 species), and *Limia* (21 species) (table 12.1). The Poeciliidae family is widely distributed, occurring as native species from the southeastern United States to northeastern Argentina (Rosen & Bailey 1963; Nelson 2006). This clade of fishes originated in South America and dispersed to Central America and North America (Hrbek et al. 2007).

Our understanding of poeciliids in South America and parts of Central America has increased markedly in the last few decades (Meyer & Etzel 2001; Poeser 2002; Meyer et al. 2004; Lucinda 2005b, 2008; Lucinda et al. 2005;

Poeser et al. 2005; Lucinda et al. 2006). For example, a recent expedition in South America added 21 new species to the genus *Phalloceros*, which previously contained only 1 described species (Lucinda 2008). The known biodiversity of poeciliids (subfamily Poeciliinae = family Poeciliidae in Rosen & Bailey 1963) thus has grown from 194 species in the late 1980s (Rauchenberger 1989) to more than 262 valid species by 2008 (Eschmeyer & Fong 2008). This number is likely to grow as more areas are intensively sampled (Lucinda 2008).

Our knowledge of poeciliid diversity is further complicated by discrepancies among workers in the recognition of particular taxa. For instance, topminnows native to the Gila River and Yaqui River drainages were originally described as two species, *Poeciliopsis occidentalis* and *P. sonoriensis* but were synonymized by Minckley (1969) as *P. o. occidentalis* and *P. o. sonoriensis*, respectively. However, based on a series of studies including a variety of molecular markers, these two taxa are now considered distinct species (Vrijenhoek et al. 1985; Quattro et al. 1996; Minckley 1999; Hedrick et al. 2006).

Here, we follow Parenti (1981) in recognizing Poeciliidae as livebearing fishes excluding South American *Fluviophylax* and Old World relatives. Biodiversity of poeciliids should also consider the recognition of conservation units—evolutionarily significant units (ESUs)—although this concept has not been widely applied within Poeciliidae (but see box 12.1).

### 12.2.2 Poeciliid conservation status

The conservation status of poeciliid species is best known for populations in the United States; thus, knowledge of the threats faced by poeciliids is based largely on studies conducted for more northern species. For instance, the International Union for Conservation of Nature (IUCN 2008) evaluated the conservation status for a good portion of North American (including Mexico) poeciliids (22 species) but for only 1 species in Central America and 1 species in South America (table 12.2). This is mainly due to poor understanding of the diversity, distribution, and natural history of Central American and South American poeciliids (Lucinda et al. 2005; Lucinda 2008). Furthermore, the Endangered Species Committee of the American Fisheries Society (AFS-ESC) identified 37 imperiled poeciliid taxa from North America, including 32 (33% of total poeciliids) described species and 5 undescribed taxa/subspecies or populations (Jelks et al. 2008; fig. 12.1).

Unfortunately, the conservation status of poeciliids in North America has deteriorated in the last two decades, with the list of imperiled taxa growing from 21 to 37 (Williams et al. 1989; Jelks et al. 2008). Furthermore, the con-

**Table 12.1** Number of species and distribution of poeciliid genera in the world

Genus	Number of species	Distribution
<i>Alfaro</i>	2	CA, SA
<i>Belonesox</i>	1	NA, CA
<i>Brachyrhaphis</i>	12	NA, CA
<i>Carlhubsia</i>	2	CA
<i>Cnesterodon</i>	9	SA
<i>Gambusia</i>	43	NA, CA, SA
<i>Girardinus</i>	7	CA
<i>Heterandria</i>	10	NA, CA
<i>Heterophallus</i>	2	NA, CA
<i>Limia</i>	21	CA, SA
<i>Micropoecilia</i>	5	CA, SA
<i>Neoheterandria</i>	3	CA, SA
<i>Pamphorichthys</i>	6	SA
<i>Phallichthys</i>	4	CA
<i>Phalloceros</i>	22	SA
<i>Phalloptychus</i>	2	SA
<i>Phallotorynus</i>	6	SA
<i>Poecilia</i>	34	NA, CA, SA
<i>Poeciliopsis</i>	23	NA, CA, SA
<i>Priapella</i>	5	NA, CA
<i>Priapichthys</i>	7	CA, SA
<i>Pseudopoecilia</i>	3	SA
<i>Quintana</i>	1	CA
<i>Scolichthys</i>	2	CA
<i>Tomeurus</i>	1	SA
<i>Xenodexia</i>	1	CA
<i>Xenophallus</i>	1	CA
<i>Xiphophorus</i>	28	NA, CA

Source: FishBase (Froese & Pauly 2009).

Note: NA = North America; CA = Central America, and SA = South America.

**Box 12.1** Conservation units and the management of desert topminnows

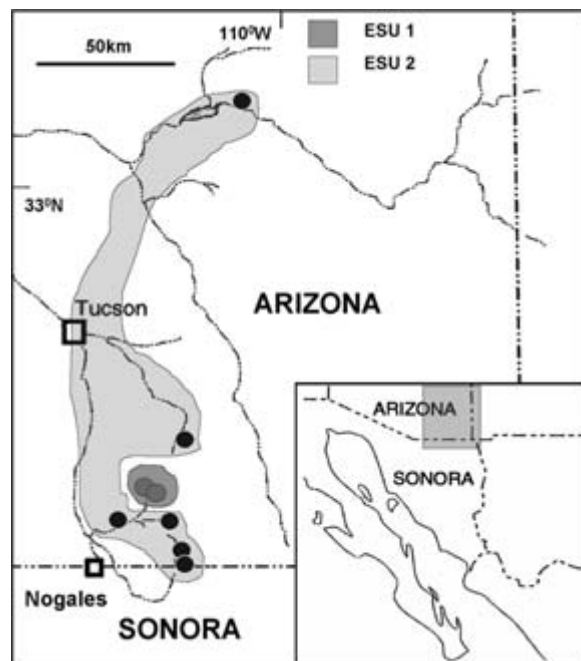
The Gila topminnow (*Poeciliopsis occidentalis*) provides an excellent opportunity to consider genetic management of protected species. This species was once widespread but is now restricted to a small number of remnant populations (Minckley 1999). Because gene flow must be accomplished by translocation of fish, delineation of evolutionarily significant units (ESUs) is of particular interest to managers.

Moritz (1994) proposed the operational yet restrictive criterion that ESUs be defined as taxonomic units that are reciprocally monophyletic at mitochondrial DNA (mtDNA) markers. Crandall et al. (2000) suggested that conservation units be considered along a gradient based on genetic and ecological exchangeability. Units that are nonexchangeable are thus unreplaceable, making them evolutionarily significant.

Fortunately, *Poeciliopsis* species have been well characterized with a wide battery of molecular markers. Vrijenhoek et al. (1985) observed low levels of genetic variation (allozymes) in remnant populations, leading them to recommend the experimental mixing of populations within the major groups as a means to increase genetic diversity (Vrijenhoek et al. 1985). Quattro et al. (1996) also observed no genetic diversity (mtDNA, RFLP) within the Gila River populations of topminnows and suggested that differences among Arizona populations of *P. occidentalis* were most likely associated with recent anthropogenic isolation. They nevertheless recommended caution in applying managed gene flow among these populations (Quattro et al. 1996). Significant differences at both microsatellites (Parker et al. 1999) and major histocompatibility complex (MHC; for more on MHC, see McMullan & van Oosterhout, chapter 25) loci, along with ecological differences, led Hedrick et al. (2001b, 2006) to argue that *P. occidentalis* was composed of two ESUs (box-fig. 12.1). However, these populations

of *P. occidentalis* exhibit no mtDNA variation (sequence data for 2626 bp) and therefore do not meet the criterion of reciprocal monophyly. Hedrick et al. (2006) argued that the requirement of reciprocal monophyly for ESU designation was too restrictive. In fact, the absence of mtDNA variation was consistent with the theoretical expectations based on the period of known divergence (10,000 years) (Hedrick et al. 2006).

Based on the ESU criteria set forth by Crandall et al. (2000), the two conservation units can be scored as ecologically and genetically nonexchangeable. Thus, a consensus seems to have emerged to recognize two ESUs of *P. occidentalis* (box-fig. 12.1) (Minckley 1999; Parker et al. 1999; Hedrick et al. 2006).



**Box-figure 12.1** The distribution of two ESUs of Sonoran topminnow (*Poeciliopsis occidentalis*). Monkey Spring and Cottonwood Spring populations were assigned to ESU 1, while all other populations within the Gila drainage were assigned to ESU 2 (Hedrick et al. 2001b; Hedrick et al. 2006).

ervation status has not improved for any of the species listed in 1989, and status has declined for 34% of the listed species (Jelks et al. 2008; table 12.3).

### 12.2.3 Threats to poeciliids

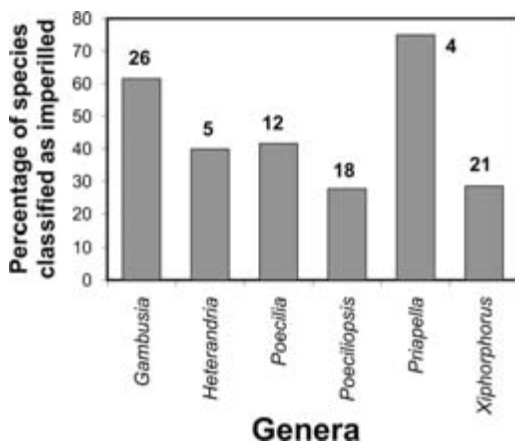
The primary threats to poeciliids fall into four broad categories: (1) restricted range, (2) habitat destruction/degradation, (3) overexploitation, and (4) impacts associ-

ated with nonnative species (Jelks et al. 2008; table 12.3). Many habitats are restricted in part due to natural, as well as anthropogenic, isolation. For instance, eight (73%) *Gambusia* species in the United States are endemic to small spring systems or restricted to portions of streams. Fish species with restricted ranges are more vulnerable to extinction. For instance, the construction of the Amistad Reservoir in 1968 caused the extinction of the Amistad gambusia (*G. amistadensis*) (Johnson & Hubbs 1989).

**Table 12.2** Poeciliid fishes evaluated according to IUCN Red List listing criteria

Species	Status	Distribution
<i>Poecilia latipunctata</i>	Critically endangered	Mexico
<i>Poecilia sulphuraria</i>	Critically endangered	Mexico
<i>Poecilia sphenops</i>	Data deficient	Mexico to Colombia
<i>Priapella bonita</i>	Extinct	Mexico
<i>Xiphophorus clemenciae</i>	Data deficient	Mexico
<i>Xiphophorus couchianus</i>	Critically endangered	Mexico
<i>Xiphophorus gordonii</i>	Endangered	Mexico
<i>Xiphophorus meyeri</i>	Endangered	Mexico
<i>Gambusia alvarezi</i>	Vulnerable	Mexico
<i>Gambusia amistadensis</i>	Extinct	United States
<i>Gambusia eurystoma</i>	Critically endangered	Mexico
<i>Gambusia gaigei</i>	Vulnerable	United States
<i>Gambusia georgei</i>	Extinct	United States
<i>Gambusia heterochir</i>	Vulnerable	United States
<i>Gambusia hurtadoi</i>	Vulnerable	Mexico
<i>Gambusia krumholzi</i>	Vulnerable	Mexico
<i>Gambusia longispinis</i>	Vulnerable	Mexico
<i>Gambusia nobilis</i>	Vulnerable	United States
<i>Gambusia senilis</i>	Lower risk/near threatened	Mexico, United States
<i>Gambusia speciosa</i>	Data deficient	Mexico, United States
<i>Gambusia nicaraguensis</i>	Data deficient	Guatemala to Panama
<i>Poeciliopsis monacha</i>	Data deficient	Mexico
<i>Poeciliopsis occidentalis</i>	Lower risk/near threatened	Mexico, United States

Source: IUCN 2008.



**Figure 12.1** The percentage of imperiled taxa for poeciliid genera. The numbers above the bars represent total imperiled taxa for each genus. Adapted from Scharpf 2008 and modified according to Jelks et al. 2008.

Likewise, the type locality of the Big Bend gambusia (*G. gaigei*), Boquillas Spring, dried up in 1957, causing the extirpation of this population (Hubbs & Springer 1957).

Habitat impacts are often associated with water management practices (dewatering, diversions) that have resulted in habitat loss and/or habitat fragmentation (Minckley 1999). For example, topminnows (*P. occidentalis*) probably functioned as large metapopulations that went through periods of isolation and connectedness (Minckley 1999). However, these habitats are now highly fragmented, resulting in widely dispersed, isolated remnant populations. The disruption of migration corridors now calls for managers to evaluate the costs and benefits of human-assisted migration to facilitate gene flow and recolonization (boxes 12.1 and 12.2) (Minckley 1999). Also, the only habitat for Clear Creek gambusia (*G. heterochir*) was dammed prior to the formal description of this species (Johnson & Hubbs

**Table 12.3** Imperiled poeciliid fishes of North America and their status

	Species	Status <sup>a</sup>	Status change <sup>b</sup>	Threats <sup>c</sup>
1	<i>Gambusia alvarezi</i>	E	stable	H R
2	<i>G. amistadensis</i>	X	stable	H I R
3	<i>G. clarkhubbsi</i>	E	new	H R
4	<i>G. eurystoma</i>	V	stable	H R
5	<i>G. gaigei</i>	E	stable	H I R
6	<i>G. sp. cf. gaigei</i>	E	new	H R
7	<i>G. georgei</i>	Xp	stable	H R
8	<i>G. heterochir</i>	E	declined	I R
9	<i>G. hurtadoi</i>	E	declined	H R
10	<i>G. sp. cf. hurtadoi</i>	E	declined	H I R
11	<i>G. krumholzi</i>	V	new	H R
12	<i>G. longispinis</i>	E	declined	H R
13	<i>G. nobilis</i>	E	declined	H I
14	<i>G. senilis</i>	T	declined	H I
15	<i>G. sp. cf. senilis</i>	E	declined	H R
16	<i>G. speciosa</i>	T	new	H I
17	<i>Heterandria jonesii</i>	V	new	H R
18	<i>H. sp. cf. jonesii</i>	V	new	H I R
19	<i>Poecilia catemaconis</i>	V	new	H O R
20	<i>P. chica</i>	V	new	H R
21	<i>P. latipunctata</i>	E	declined	H R
22	<i>P. sulphuraria</i>	T	declined	H R
23	<i>P. velifera</i>	V	new	H R
24	<i>Poeciliopsis catemaco</i>	V	new	O I R
25	<i>P. latidens</i>	T	new	H
26	<i>P. occidentalis</i>	E	declined	H I
27	<i>P. sonoriensis</i>	T	stable	H I R
28	<i>P. turneri</i>	V	new	H R
29	<i>Priapella bonita</i>	X	declined	H I R
30	<i>P. compressa</i>	T	new	R
31	<i>P. olmecae</i>	T	new	R
32	<i>Xiphophorus clemenciae</i>	T	declined	H R
33	<i>X. couchianus</i>	E	stable	H I R
34	<i>X. gordonii</i>	E	stable	H I R
35	<i>X. kallmani</i>	V	new	I R
36	<i>X. meyeri</i>	E	stable	H I R
37	<i>X. milleri</i>	E	new	H I R

Source: Jelks et al. 2008.

<sup>a</sup>V = vulnerable; T = threatened; E = endangered; X = extinct; Xp = possibly extinct .

<sup>b</sup>Compared with Williams et al. 1989 .

<sup>c</sup>H = habitat modification/destruction; O = overexploitation; I = impact of nonnatives; R = restricted range.

1989). Deforestation and associated habitat fragmentation remain an important threat to poeciliids in Central America and South America (Bussing 2008). These impacts are hard to quantify, as new poeciliid species have been recently discovered in South American Atlantic forests (Lucinda 2005b, 2008).

Habitat degradation is also associated with land use practices such as overgrazing, as well as with the introduction of various pollutants. Degradation of water quality associated with land use practices has contributed to the decline of some poeciliid populations (Minckley 1999). Pollution effects are often sublethal but are nevertheless important. Pollution associated with paper mill effluent has been shown to affect sexual development of eastern mosquitofish (*Gambusia holbrooki*) (Howell et al. 1980; Toft et al. 2004; Orlando et al. 2007). Females exposed to paper mill effluent were masculinized, developing a gonopodium-like anal fin (Howell et al. 1980). Furthermore, reduced pregnancy rates (Toft et al. 2004) and decreased embryo production (Orlando et al. 2007) were reported for paper-mill-exposed mosquitofish.

Pollution can also disrupt chemical communication and thereby facilitate hybridization (see Rosenthal & García de León, chapter 10). Fisher et al. (2006) provided experimental evidence that *Xiphophorus birchmanni* females preferred conspecific males in clean water but mated indiscriminately (*X. birchmanni* females and *X. malinche* males) in water polluted with agricultural runoff. This appeared to be mediated by humic acid, which results from degradation of organic matter. *Xiphophorus birchmanni* females exposed to elevated humic acid did not discriminate between conspecific and heterospecific males (Fisher et al. 2006).

Selected poeciliids have been threatened by overexploitation. The aquarium trade is the major cause for overexploitation, with 90% of freshwater aquarium fishes coming directly from the wild (Olivier 2001). For instance, both *Poecilia catemacensis* and *Poeciliopsis catemaco* are imperiled due to commercial exploitation (Miller 2005). The other threat of the aquarium trade is the release of ornamental fishes outside their native range (section 12.3).

The introduction of nonnative species has co-occurred with the rapid decline of many poeciliids, especially the topminnows. Minckley and Deacon (1968) suggested that the rapid decline of *P. occidentalis* is mainly due to the introduction of aggressive *Gambusia affinis*. Furthermore, Meffe (1985b) hypothesized that niche overlap combined with the predaceous nature and high reproductive rate of *Gambusia* explained the decline of *Poeciliopsis*. Collectively, it is important to note that the decline of many poeciliid species has been due to various combinations of the above-listed threats (table 12.3; Johnson & Hubbs 1989; Minckley 1999).

### 12.3 Impacts of poeciliids on native biota

Poeciliids have been introduced worldwide primarily through the ornamental-fish trade and their presumed ability to control mosquitoes. For example, poeciliids have been introduced to Australia (Arthington & Lloyd 1989; Morgan et al. 2004), Europe (Almaca 1995; Garcia-Berthou et al. 2005), the Mediterranean basin (Crivelli 1995; Goren & Ortal 1999), Africa (Welcomme 1988), and various countries in Asia (Ng et al. 1993; Pethiyagoda 2006). Two poeciliid species were introduced to Sri Lanka for malaria control, and two additional species were introduced via undocumented ornamental-fish releases (Pethiyagoda 1991). In Australia, five poeciliids escaped due to the ornamental-fish trade, while one species was introduced for biological control of mosquitoes (Lintermans 2004). The freshwater fish fauna in Singapore is dominated by four poeciliids and one cichlid introduced through the ornamental-fish trade (Ng et al. 1993). Moyle (1976, 2002) reported six nonnative poeciliids from California, five of which were introduced as ornamental-fish releases and one as a mosquito control agent.

Mosquitofish (*G. affinis* and *G. holbrooki*) have received much attention for their presumed value in controlling mosquito-borne diseases. These two species are native to the southeastern United States but now occur on every continent except Antarctica due to aggressive introduction programs which began in the early twentieth century (Van Dine 1907; Krumholz 1948; Welcomme 1988; Pyke 2008). For example, the western mosquitofish (*G. affinis*) was introduced from Texas to Hawaii in 1904 (Van Dine 1907, 1908) and to California in 1922 (Moyle 1976). Mosquitofish were subsequently introduced from Hawaii to the Philippines (Seale 1917) and New Zealand (McDowall 1990). Likewise, mosquitofish populations were rapidly established throughout the state of California, and by 1934 mosquitofish had been introduced to Nevada (Stockwell et al. 1996). Finally, mosquitofish introductions have often been facilitated by ordinary citizens attempting to control local mosquito populations (Stockwell et al. 1996).

Nonnative poeciliids have been very successful at invading new habitats. Garcia-Berthou et al. (2005) reported a 96.8% establishment rate of *Gambusia* species in Europe, the highest among the top 10 most frequently introduced aquatic species in the world. Establishment success of mosquitofish is associated with a number of key characteristics, including broad diet, broad physiological tolerance, rapid population growth rates, high genetic variability, high levels of aggression, and high dispersal tendencies (Arthington & Mitchell 1986; Ehrlich 1986; Arthington 1989; Courtenay & Meffe 1989; Leberg 1990;

Grether & Kolluru, **chapter 6**). Recent work has shown that dispersal tendencies are higher for invasive species of mosquitofish (*G. affinis* and *G. holbrooki*) than for noninvasive species of mosquitofish (*G. geiseri* and *G. hispaniolae*) (Rehage & Sih 2004). Furthermore, Alemadi and Jenkins (2008) reported that *G. holbrooki* readily dispersed in shallow water, increasing the likelihood that populations could establish themselves by traveling through networks of drainage ditches.

The efficacy of mosquitofish in controlling mosquitoes is controversial (Bence 1988; Pyke 2008), but their negative impacts on native biota have been well documented (Deacon et al. 1964; Minckley & Deacon 1968; Schoenherr 1981; Courtenay & Meffe 1989; Pyke 2005, 2008). Here, we briefly review the wide array of poeciliid impacts on native biota, focusing on invertebrates, fish, and amphibians.

### 12.3.1 Poeciliid impacts on invertebrates

Poeciliids are generally omnivorous, feeding on floating insects, chironomid larvae, zooplankton, odonate nymphs, mites, molluscs, crustaceans, ephemeropterans, and oligochaetes, as well as fish eggs and larvae (Hurlbert et al. 1972; Farley & Younce 1977; Rees 1979; Dussault & Kramer 1981; Hurlbert & Mulla 1981; Bence 1988). Hurlbert et al. (1972) provided one of the earliest experimental evaluations of mosquitofish impacts on ecosystems. Their controlled mesocosm experiments demonstrated that mosquitofish caused reductions of zooplankton (rotifers and crustaceans) and aquatic-insect populations and a subsequent increase in phytoplankton populations (Hurlbert et al. 1972). Thus, mosquitofish apparently can act in a top-down manner (Carpenter & Kitchell 1988) by causing a reduction in zooplankton densities, which in turn release phytoplankton from zooplankton grazing.

Mosquitofish can also affect the community composition and biodiversity of a system. For instance, *G. affinis* eliminated *Daphnia pulex* and *Ceriodaphnia* sp. populations and significantly reduced many other zooplankton and macroinvertebrate taxa in experimental ponds (Hurlbert & Mulla 1981). In another controlled study, back swimmer, damselfly, and dragonfly populations were significantly reduced in the presence of mosquitofish (Farley & Younce 1977). Also, *Megalagrion* damselflies native to Oahu, Hawaii, were absent from all lowland habitats occupied by introduced poeciliids: *G. affinis*, *Poecilia mexicana*, *Poecilia reticulata*, and *Xiphophorus hellerii* (Englund 1999). A Hawaiian native atyid shrimp was eliminated from its anchialine pool habitats within six months of the introduction of guppies (Brock & Kam 1997).

### 12.3.2 Poeciliid impacts on fish

The impacts of mosquitofish and other poeciliids on native fish have received much attention. In some cases the impacts have been well documented, but in many others impacts have been inferred from the simultaneous establishment of mosquitofish and decline of native fish(es). In fact, many authors have attributed the decline and extinction of native fishes to the concurrent introduction of nonnative mosquitofish (Miller 1961; Hubbs & Brodrick 1963; Deacon et al. 1964; Minckley & Deacon 1968; Pister 1974; Soltz & Naiman 1978).

Earlier work was largely correlative, yet the repetition of species replacement across a variety of systems provided convincing evidence for the negative impacts of nonnative poeciliids on native species. For example, endangerment of White River springfish (*Crenichthys baileyi*) and Moapa dace (*Moapa coriacea*) followed the establishment of introduced guppies (*P. reticulata*) and shortfin mollies (*P. mexicana*), respectively (Deacon et al. 1964; Scoppettone 1993). Likewise, Hubbs and Brodrick (1963) reported the loss of many populations of the endangered Big Bend gambusia (*G. gagei*) following the establishment of western mosquitofish (*G. affinis*).

There has been considerable experimental work evaluating the effects of poeciliids on native species (table 12.4). Experimental work and field surveys implicated heavy predation by mosquitofish (*G. affinis*) on Sonoran topminnow (*P. sonoriensis*) juveniles as the primary cause for the rapid replacement of topminnow populations by introduced mosquitofish (Meffe 1985b; Galat & Robertson 1992). The results of controlled mesocosm experiments showed that *G. holbrooki* had negative impacts via size-selective predation on experimental populations of the least killifish (*Heterandria formosa*) (Lydeard & Belk 1993; Belk & Lydeard 1994). More recently, Mills et al. (2004) reported that *G. affinis* caused reduced body growth and severely reduced survival of young of the year in least chub (*Iotichthys phlegethontis*). *Gambusia affinis* also caused reduced population growth of experimental populations of the White Sands pupfish (*Cyprinodon tularosa*) (Rogowski & Stockwell 2006a).

Mechanistically, impacts by mosquitofish are largely due to hybridization, resource competition, and predation on fish eggs, larvae, young, or even adults (Myers 1965; Moyle 1976; Shakunthala & Reddy 1977; Meffe 1985b; Courtenay & Meffe 1989; Kelley & Brown, **chapter 16**). In a few circumstances, nonnative poeciliids hybridized with native congeners, which increased risk of extinction for the native species. For example, Contreras and Escalante (1984) reported hybridization of introduced *X. hellerii* and *X. varia-*

*tus* with endangered *X. couchianus*. Furthermore, western mosquitofish (*G. affinis*) hybridized with endangered Clear Creek gambusia (*G. heterochir*) (Johnson & Hubbs 1989), although recent work has shown that this hybridization has been limited (Davis et al. 2006).

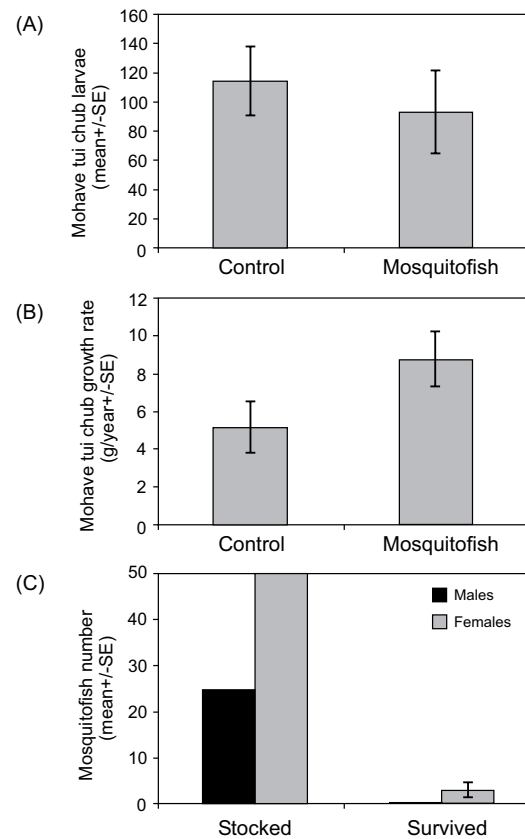
Predation by nonnative poeciliids on the eggs and larvae of native species has been shown to be important in many systems. For instance, Barrier and Hicks (1994) provided experimental evidence for *G. affinis* preying on fry of Australian black mudfish (*Neochanna diversus*). Rincon et al. (2002) reported evidence for heavy predation by *G. holbrooki* on juveniles of two endangered Spanish toothcarps (*Aphanius iberus* and *Valencia hispanica*).

Nonnative poeciliids have also been shown to be aggressive toward adult fish. For instance, Gill et al. (1999) conducted tank experiments to evaluate the impact of *G. holbrooki* on an endemic Australian fish. This work showed that the degree of caudal fin damage and mortality of western pygmy perch (*Edelia vittata*) was directly correlated with *G. holbrooki* density (Gill et al. 1999). Likewise, reduced growth of adults was reported for another Australian fish, *Pseudomugil signifer*, in the presence of *G. holbrooki* (Howe et al. 1997).

Another likely aspect of poeciliid impact on native fish is transmission of exotic parasites and diseases (Arthington & Lloyd 1989; Eldredge 2000). Native freshwater fishes in Hawaiian streams had helminth parasites but only in sympatry with exotic poeciliids such as guppies (*Poecilia reticulata*) and green swordtails (*X. hellerii*) (Font & Tate 1994). Furthermore, Font (1997b, 2003) showed that 4 out of 11 helminth parasites of native Hawaiian freshwater fishes originated from exotic poeciliids. Similarly, the Asian tapeworm (*Bothriocephalus acheilognathi*) was presumably co-introduced with mosquitofish (*G. affinis*) and now infects endangered Mohave tui chub (*Siphateles bicolor mohavensis*) (Archdeacon 2007).

Although most case studies reported negative impacts of introduced poeciliids on native species, neutral interactions and coexistence of nonnative and native fishes have been observed occasionally (Barrier & Hicks 1994; Maddern 2003; Ling 2004; S. Henkanaththegedara and C. Stockwell, unpublished data). It appears that coexistence can occur under special circumstances such as reciprocal predation and/or minimum niche overlap (Barrier & Hicks 1994; Ling 2004; S. Henkanaththegedara and C. Stockwell, unpublished data). In an unpublished thesis, Maddern (2003) reported no significant impacts of nonnative *Phalloceros caudimaculatus* on *Edelia vittata*, an Australian endemic species.

We recently found that nonnative mosquitofish (*G. affinis*) may not impact native populations of the endangered



**Figure 12.2** Mohave tui chub–mosquitofish interactions as measured during a controlled mesocosm experiment. (A) Mosquitofish presence had no effect on Mohave tui chub (*Siphateles bicolor mohavensis*) larval survival ( $t = 0.567$ ;  $P < 0.05$ ). (B) Mohave tui chub had higher growth rates in the presence of mosquitofish ( $t = 0.567$ ;  $P < 0.05$ ). (C) The number of surviving mosquitofish is depicted relative to the initial number of mosquitofish stocked (25 male and 50 female mosquitofish in each mesocosm). S. Henkanaththegedara and C. A. Stockwell, unpublished data.

Mohave tui chub (*Siphateles bicolor mohavensis*). These two species have coexisted for at least eight years at one site (S. Parmenter, California Department of Fish and Game, pers. comm.). Furthermore, a controlled mesocosm experiment revealed that mosquitofish presence had no effect on Mohave tui chub larval survival (fig. 12.2A). In fact, Mohave tui chub gained higher body mass in the presence of mosquitofish (fig. 12.2B). Interestingly, mosquitofish survival in experimental mesocosms was low, probably because of predation by Mohave tui chub (fig. 12.2C). Only large females that exceeded the gape size of Mohave tui chub survived the mesocosm experiment (S. Henkanaththegedara & C. Stockwell, unpublished data).

### 12.3.3 Poeciliid impacts on amphibians

Nonnative poeciliids also negatively impact native amphibians by preying on amphibian eggs and larval stages (Grub



**Table 12.4** Experimental evidence of negative impacts of mosquitofish (*Gambusia spp.*)

Taxa	Impact	Overall impact	Reference
<b>Impacts on invertebrates</b>			
<i>G. affinis</i>	Reduced zooplankton and insect populations; high algal densities	Negative	Hurlbert et al. 1972
<i>G. affinis</i>	Reduced aquatic macroinvertebrate abundance in rice fields	Negative	Farley & Younce 1977
<i>G. affinis</i>	Reduced pelagic aquatic invertebrates; increased algae and some benthic invertebrates	Negative	Hurlbert & Mulla 1981
<i>G. affinis</i>	Reduction of aquatic macroinvertebrates in rice fields	Negative	Bence 1988
<b>Impacts on fish</b>			
<i>G. affinis</i>	Replacement of <i>Poeciliopsis occidentalis</i> by predation	Negative	Meffe 1985b
<i>G. holbrooki</i>	Reduced population growth of <i>Heterandria formosa</i>	Negative	Lydeard & Belk 1993
<i>G. holbrooki</i>	Size-selective predation on small <i>Heterandria formosa</i> in experimental mesocosms	Negative	Belk & Lydeard 1994
<i>G. holbrooki</i>	Reduced growth and lack of egg survival of <i>Pseudomugil signifer</i>	Negative	Howe et al. 1997
<i>G. holbrooki</i>	Caudal fin damage and mortality of <i>Edelia vittata</i>	Negative	Gill et al. 1999
<i>G. holbrooki</i>	Heavy predation on <i>Aphanius iberus</i> and <i>Valencia hispanica</i> juveniles	Negative	Rincon et al. 2002
<i>G. affinis</i>	Reduced growth and survival of <i>lotichthys phlegethontis</i> young of year	Negative	Mills et al. 2004
<i>G. affinis</i>	Reduced population size and biomass of <i>Cyprinodon tularosa</i>	Negative	Rogowski & Stockwell 2006a
<i>G. affinis</i>	No impact on larval survival; increased body growth of <i>Siphateles bicolor mohavensis</i>	Neutral	Henkanaththegedara & Stockwell, unpublished data
<b>Impacts on amphibians</b>			
<i>G. affinis</i>	Elimination of <i>Hyla regilla</i> tadpoles	Negative	Hurlbert & Mulla 1981
<i>G. affinis</i>	Predation on <i>Taricha torosa</i> larvae	Negative	Gamradt & Kats 1996
<i>G. affinis</i>	Predation on <i>Hyla regilla</i> tadpoles	Negative	Goodsell & Kats 1999
<i>G. affinis</i>	Delayed metamorphosis and reduced growth rates of <i>Rana aurora draytonii</i>	Negative	Lawler et al. 1999
<i>G. holbrooki</i>	Reduced survival of endangered <i>Litoria aurea</i> tadpoles	Negative	Hamer et al. 2002

1972; Bradford et al. 1993; Brönmark & Edenhamn 1994). The decline of many amphibian populations has been correlated with the introduction of nonnative poeciliids to previously fishless water bodies (Gamradt & Kats 1996; Goodsell & Kats 1999; Hamer et al. 2002). Controlled laboratory experiments and field surveys have revealed neg-

ative impacts of mosquitofish on amphibians, as measured by the survival of tadpoles and larvae, delayed metamorphosis, and reduced larval growth rates (Gamradt & Kats 1996; Goodsell & Kats 1999; Lawler et al. 1999; Hamer et al. 2002). For example, Lawler et al. (1999) showed that *G. affinis* caused injury to the tadpoles of the endangered

California red-legged frog (*Rana aurora draytonii*) and caused reduced growth rates. Likewise, *G. holbrooki* reduced the survival of endangered green and golden bell frog (*Litoria aurea*) tadpoles in southeastern Australia (Hamer et al. 2002).

#### 12.4 Poeciliids as model organisms in conservation biology

As in evolutionary and ecological studies (e.g., see Schlupp & Riesch, **chapter 5**; Grether & Kolluru, **chapter 6**; Langerhans, **chapter 21**), poeciliids have been used extensively to test many important questions in the field of conservation biology. This is largely because their short generation time and small size make poeciliids excellent model organisms for controlled experimental studies. Furthermore, many poeciliid species have been extensively translocated (Hendrickson & Brooks 1991), allowing retrospective analyses of the factors associated with population persistence (Sheller et al. 2006), as well as the genetic and evolutionary consequences of historic translocations (Stearns 1983b; Stockwell et al. 1996; Stockwell & Weeks 1999).

Much of the work on the conservation biology of poeciliids has focused on population genetics. For example, understanding population structure is central to identifying appropriate conservation units (box 12.1). This information is particularly useful for managing metapopulations that have experienced recent habitat fragmentation, such as the case with desert topminnows (*Poeciliopsis* spp.) (Minckley 1999). The population genetic structure of poeciliids is influenced by the interactive effects of genetic drift, gene flow, and divergent selection (sexual and/or natural) (see Breden and Lindholm, **chapter 22**). Management practices that influence gene flow among population segments could potentially erode genetic structure, some of which may be adaptive (box 12.2). Thus, the benefits and costs of gene flow should be considered before establishing an artificial gene flow regime (boxes 12.1 and 12.2).

Poeciliids have also been used to examine questions central to the management of endangered species concerning the effects of inbreeding depression, outbreeding depression, and the loss of genetic variation (Leberg 1990, 1993; Stockwell et al. 1996; van Oosterhout et al. 2007b). For instance, Leberg (1990) reported that experimental populations of *G. holbrooki* with reduced genetic variation had lower population growth rates. More recently, van Oosterhout et al. (2007b) examined the effects of inbreeding during captivity on reintroduction success using captive and wild populations of Trinidadian guppies (*Poecilia reticulata*). Captive-reared and wild fish were released to a streamside mesocosm to evaluate population responses.

They found that captive-reared guppies were more vulnerable to gyrodactylid parasites (58% survival) than wild guppies were (96%). They attributed this effect to reduced variation at immune function genes due to inbreeding and lack of previous parasite exposure during captivity (van Oosterhout et al. 2007b).

Many workers have considered the importance of genetics to the conservation and management of poeciliids (Vrijenhoek et al. 1985; Quattro & Vrijenhoek 1989; Leberg 1990; Stockwell et al. 1996; Sheffer et al. 1997). For instance, Vrijenhoek et al. (1985) reported that the Monkey Spring population (located in Arizona) of the Gila topminnow (*P. occidentalis*) had no genetic variability as measured with 25 allozyme loci. These findings were striking because this population had been used as brood stock for extensive restoration efforts (Vrijenhoek et al. 1985; Simons et al. 1989). Theory indicates that populations with little to no genetic variability are not likely to survive over the long term when introduced to a variety of habitat types. Quattro & Vrijenhoek (1989) reported that the lower genetic variation of the Monkey Spring population was associated with lower fitness compared with other populations of *P. occidentalis* with greater genetic variation. This work was used to argue for changing the restoration brood stock from the Monkey Spring population to a population with greater genetic variation (Sharp Spring) (Quattro & Vrijenhoek 1989).

Subsequent work by Sheffer et al. (1997) compared these same populations and found no relationship between population genetic diversity and fitness. These contrasting results may in part be explained by different experimental environments. Sheffer et al. (1997) pointed out that mortality rates were substantially lower for their study than for Vrijenhoek et al.'s study (Vrijenhoek et al. 1985). Thus, it is possible that a correlation between genetic diversity and fitness can be observed only under harsh environmental conditions (Stockwell & Leberg 2002).

These two studies emphasize that factors other than genetic variation should also be considered in selecting brood stock for restoration efforts (Sheffer et al. 1997). For instance, Sheffer et al. (1997) recommended that managers use geographically proximate populations for restoration. Managers should consider the evolutionary history of the species when designing restoration plans. Thus, it is critical to have sound data concerning the evolutionary distinctiveness of subspecies and population segments to guide conservation and restoration efforts (see box 12.1).

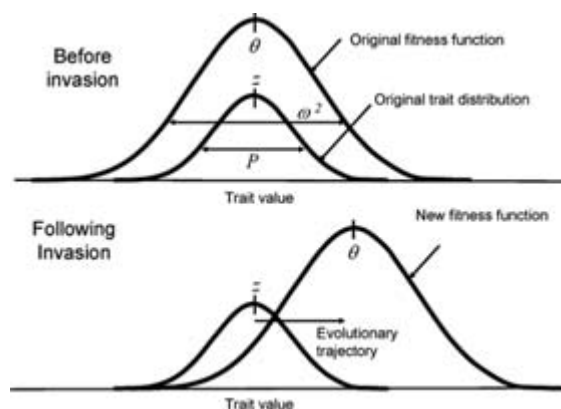
The persistence of translocated poeciliid populations has broad implications for conservation biology due to the extensive use of translocation as a tool for managing and restoring various protected species (Hendrickson & Brooks 1991; Sheller et al. 2006). For instance, the Gila topminnow (*P. occidentalis*) has been extensively translocated in

**Box 12.2** Evolutionary considerations in the replacement of native poeciliids by nonnative poeciliids

The rapid replacement of many native desert fishes by nonnative species has in part been explained by evolutionary constraints. Mosquitofish (*Gambusia affinis*) have replaced native Gila topminnows (*Poeciliopsis occidentalis*) throughout much of their range. However, some topminnow populations persist in the presence of mosquitofish (Meffe 1984), raising questions about the ecological and evolutionary factors that promote coexistence.

Meffe (1984) pointed out that topminnow populations often persisted in habitats vulnerable to flash flooding. Following such events, topminnows typically dominated the fish community, and mosquitofish increased in number until the next flood (Minckley 1999). Minckley and Meffe (1987) hypothesized that the evolutionary history of these two species likely selected for different responses to flooding. Whereas topminnows had evolved in an environment with periodic flash flooding, this was not the case for western mosquitofish (Minckley & Meffe 1987). Indeed, Meffe (1984) found that topminnows outperformed mosquitofish in swimming trials.

Evolutionary history may also have played a role in the response of native species to nonnative species (Miller 1961). Because topminnows evolved in species-depauperate habitats, the introduction of *G. affinis* represented a novel selective threat in terms of both predation and competition. Indeed, nonnative poeciliids seemed to have their greatest harmful effects as novel predators (section 12.3.2; Miller 1961; Courtenay & Deacon 1983). Thus, earlier workers have recognized the importance that evolutionary histories can have in determining the outcome of native and nonnative species interactions. The previous work essentially treated these species as evolutionarily static, although it is plausible that contemporary evolution plays an important



**Box-figure 12.2** A representation of trait variation and selection before and after the invasion of a poeciliid likely to prey on small larvae. The upper curve in each panel represents the fitness function acting on a trait (the higher the curve, the higher the fitness of a given trait value). The lower curve represents the frequency distribution of trait values in the population.  $P$  is the phenotypic variance for the trait,  $\theta$  is the optimal trait value,  $\omega^2$  is the strength of stabilizing selection around the optimum, and  $z$  is the mean trait value. Evolution for faster larval growth rates would be expected under this scenario. Figure adapted from Stockwell et al. 2003.

role in the persistence of native poeciliids in the face of novel selection pressures (Stearns 1983b; Reznick et al. 1997; Stockwell & Weeks 1999).

Here, we briefly describe how contemporary evolution can play a role in the demise or persistence of populations. The evolutionary response of a population  $\Delta z$  is the product of the selection gradient  $\beta$  and the additive genetic variance  $G$ :  $\Delta z = G\beta$  (box-fig. 12.2). Thus, we may ask if a native population of topminnows has sufficient genetic variation to evolve in response to novel selection pressure associated with nonnative mosquitofish. For instance, mosquitofish are highly piscivorous on fish larvae (Courtenay & Meffe 1989) and thus may exert strong selection pressure on early life-history traits. From previous poeciliid studies (Stearns 1983b; Reznick et al. 1990; Stockwell & Weeks 1999), we hypothesize moderate levels of additive genetic variation for poeciliid

an attempt to restore this species to its former range (Simons et al. 1989; Hendrickson & Brooks 1991; Minckley 1999). Sheller et al. (2006) found that a number of factors were important for the persistence of translocated Gila topminnow populations. For instance, populations founded late in the year (July–December) persisted up to five times longer than populations established in May or June. Most translocations occur early in the year, so persistence time may increase simply by translocating populations later in

the season. They also found that topminnows persisted longer when introduced to ponds/lakes than when introduced to streams, wells, or tanks. Finally, they found that populations established from Monkey Spring did not persist as long as populations exhibiting higher levels of heterozygosity (Sheller et al. 2006). By contrast, they did not find any evidence that initial population size had any effect on population persistence (Sheller et al. 2006). Collectively, they recommended that translocations should be conducted

life-history traits, suggesting that they should exhibit a response to selection due to predation (see Reznick et al. 1990).

Thus, we can envision an undisturbed topminnow population as being centered on an optimum value and the introduction of mosquitofish changing this optimum to a new location (i.e., larger embryo size). This creates a mismatch between current phenotype and optimal phenotypes (box-fig. 12.2), leaving the topminnow population subject to directional selection, which can be represented as

$$\beta = \frac{-(z - \theta)}{\omega^2 + P}$$

where  $z$  is the mean trait value,  $\theta$  is the optimal trait value,  $P$  is the phenotypic variance for the trait, and  $\omega^2$  is the strength of stabilizing selection around the optimum (the original optimum before disturbance, the new one after disturbance) (Arnold et al. 2001). An evolutionary response is expected if there is sufficient genetic variation.

Even evolving populations can go extinct if selection is too strong and/or there is insufficient genetic variation (Lynch 1996; Boulding & Hay 2001). Population size declines during the early phases of evolution. Thus, if selection is too strong or if the population is too small, population extinction is likely. In fact, a highly adapted population can go extinct due to demographic stochasticity (Gomulkiewicz & Holt 1995).

Gene flow can also have important effects on evolutionary potential. Gene flow has been characterized as the Jekyll and Hyde of conservation due to its potential benefits and costs (Stockwell et al. 2003). Gene flow can facilitate adaptive divergence by enhancing genetic variation and thus evolutionary potential (Frankham 1995). Alternatively, gene flow may limit adaptive divergence if the immigrants are not locally adapted (Lenormand 2002; but see also Räsänen & Hendry 2008). For ex-

ample, gene flow imposed across a predator selection gradient should be carefully considered (section 12.4). This example is especially relevant, as predators have repeatedly been shown to have important evolutionary effects on poeciliids (Reznick et al. 1990; Reznick et al. 1997; Johnson 2001a; Langerhans et al. 2005)

Therefore, from an evolutionary perspective, one may examine the role of these factors in topminnow population persistence in the presence of nonnative mosquitofish. For instance, population sizes and associated genetic variation vary among topminnow populations (Minckley 1999; Hedrick et al. 2001b). Thus, evolutionary potential is also likely to vary among populations. Furthermore, contemporary evolution can be facilitated or constrained by factors such as gene flow (see Räsänen & Hendry 2008).

It is also important to further examine the evolutionary response of invading species. Meffe (1984) pointed out that topminnows were evolutionarily adapted to periodic flooding, whereas mosquitofish had evolved in the absence of such selection pressure. We suggest that an important unresolved question is whether this relationship has been maintained. It seems plausible that nonnative mosquitofish populations may well have evolved in response to novel selection pressures associated with flooding (see Collyer et al. 2005). Thus, it seems prudent to assess whether mosquitofish swimming performance has evolved in response to the novel flow regime associated with desert aquatic systems: periodic severe flash floods.

We conclude that an evaluation of the evolutionary dynamics of both native and invasive poeciliids can provide important insights regarding species replacement and coexistence. Poeciliids are ideal for such studies, as a number of important life-history and morphological traits have been well studied (Stearns 1983b; Reznick et al. 1990; Reznick et al. 1997; Stockwell & Weeks 1999; Langerhans et al. 2005).

in late summer or later and utilize fish from sources other than Monkey Spring and target ponds and lakes as introduction sites (Sheller et al. 2006; see box 12.1). These data, combined with genetic data on conservation units (Hedrick et al. 2001b; Hedrick et al. 2006), have allowed for a rich scientific foundation for managing desert topminnows (see also box 12.1).

Poeciliids can also serve as useful models of the evolutionary consequences of translocating populations to new

habitats (Stockwell et al. 1996; Stockwell & Weeks 1999). Mosquitofish provide a best-case scenario for the retention of genetic diversity because females have multiply sired broods (Constantz 1989; see table 18.1 in Evans & Pilastro, **chapter 18**). Thus, translocated populations are likely to include the genes of males that were not actually relocated (Stockwell et al. 1996). Mosquitofish also have rapid population growth rates (Leberg 1990), greatly reducing the likelihood of prolonged genetic bottlenecks.

Many workers have conducted retrospective genetic surveys to determine the loss/retention of genetic variation of nonnative poeciliid populations (Scribner et al. 1992; Stockwell et al. 1996; Lindholm et al. 2005; Shoji et al. 2007). Scribner et al. (1992) examined genetic diversity for populations of *G. affinis* translocated from three sites in Texas to Hawaii in 1905. They found no evidence for a loss of genetic diversity. In another study, Stockwell et al. (1996) studied populations in California and western Nevada derived from the translocation of 900 fish from two populations in Texas in 1922. Despite predicting that the California and Nevada populations would retain high levels of genetic diversity, they found that allelic diversity was severely reduced, with the elimination of most rare alleles. These data combined with theoretical expectations (Allendorf 1986) suggested a severe initial bottleneck of fewer than 10 individuals (Stockwell et al. 1996). These findings were surprising and suggested that even under ideal conditions, genetic diversity of introduced populations can be compromised.

Lower levels of genetic diversity are expected to limit the evolutionary potential of managed populations (Frankham 1995). However, two poeciliid case studies have reported results contrary to this expectation. Stockwell & Weeks (1999) reported rapid life-history evolution for recently established populations of mosquitofish, despite the fact that these populations recently descended from a population that had experienced a severe bottleneck (Stockwell et al. 1996). Likewise, guppies introduced to Australia had low genetic variation as measured by microsatellites (Lindholm et al. 2005), despite the fact that these populations exhibit high levels of additive genetic variation for morphological traits (Brooks & Endler 2001a).

These case studies illustrate the importance of obtaining data sets that include both neutral markers and phenotypic variation. In fact, as Lynch (1996) pointed out, conservation of biodiversity is based on the preservation of phenotypic variation. These case studies also illustrate the importance of considering evolution on a contemporary time scale. In fact, it now appears that evolution on ecological time scales is rather common, requiring managers to take an evolutionary approach to the conservation of biodiversity (Stockwell et al. 2003; Kinnison et al. 2007). Studies of poeciliids have shown that the same factors associated with the current extinction crisis are also important selective factors that promote contemporary evolution: habitat destruction/degradation, habitat fragmentation, exotic species, and altered harvest schedules (Reznick & Ghalambor 2001; Stockwell et al. 2003; box 12.2).

Many cases of contemporary evolution have been documented for introduced poeciliid populations (Stearns 1983b; Reznick et al. 1990; Stockwell & Weeks 1999).

Thus, evolution may play an important role in the invasion dynamics of nonnative species (Stockwell & Weeks 1999; see also box 12.2).

Evolutionary dynamics should be also considered in the conservation and management of predators (Reznick et al. 2008). Following predator removal, certain key traits under natural selection are likely to evolve, such as size at maturity and escape performance (Reznick et al. 1990; Ghalambor et al. 2004). For instance, rapid life-history evolution toward later age of maturity has been observed for guppies released from high predation pressure (Reznick et al. 1990). By contrast, guppy populations exposed to increased predation pressure fared poorly. Simply stated, in these circumstances fish are often consumed before they reach maturity. These effects apparently increase the risk of extinction for naive prey species (Reznick et al. 2008). In fact, Reznick et al. (2004) found that guppy (*Poecilia reticulata*) populations adapted to predator absence were likely to go extinct when exposed to predators. These findings are consistent with observations of nonnative fishes severely impacting native fishes in the American Southwest deserts. In these regions, fishes that have evolved in the absence of predation have been extremely vulnerable to the introduction of nonnative fish predators (Miller 1961; see also box 12.2).

Environmental novelty is also of concern for the expected environmental changes associated with global climate change. For instance, increased sea levels are likely to have important consequences for coastal ecosystems. Purcell et al. (2008) examined evidence for local adaptation to salinity among coastal populations of *G. affinis*. They found variation among populations in salinity tolerance, suggesting that populations may vary in their response to rising sea levels (Purcell et al. 2008).

## 12.5 Conclusions and future directions

Poeciliids have received considerable attention from conservation biologists and evolutionary ecologists. This work has examined threats to protected species as well as the threat of nonnative poeciliids to native species and ecosystems. Poeciliids have been excellent model/surrogate species for addressing basic questions in conservation biology and evolutionary ecology.

Despite this attention, many poeciliid species are at risk of extinction, and little progress has been made in securing poeciliids in the last 20 years. Furthermore, the conservation status of poeciliids outside the United States is largely unknown, mainly due to poor understanding of species diversity, distribution, and natural history. Thus, one critical direction for further research is to obtain more data on the

taxonomy, distribution, and conservation status of poeciliids in Mexico, Central America, and South America.

Evolutionary theory and ecology should be integrated to address the issues concerning the invasion biology of poeciliids. Recently, workers have examined ecological factors such as niche breadth to determine habitat features that may be modified to promote coexistence between native species and invasive mosquitofish (Laha & Mattingly 2006; Ayala et al. 2007). A similar approach that incorporates evolutionary theory could prove profitable. For instance, additive genetic variation should be estimated for key traits (i.e., swimming performance, temperature tolerance, and early life-history traits) in both invasive and protected fish species to better predict the evolutionary prospects for species coexistence. Such evolutionarily enlightened manage-

ment may offer important insights regarding factors that will promote the persistence of poeciliid populations under the stress of novel anthropogenic induced selection.

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