AN ECOLOGICAL OVERVIEW OF POECILIID FISHES

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INTRODUCTION

Poeciliid fishes have been relatively well studied in areas such as genetics, reproductive physiology, and embryonic development, but ecological aspects of the group are less well known. Part of our ignorance stems from the historical use of **poeciliids** as important laboratory models for genetic, physiological or medical studies, wherein investigators were not primarily interested in poeciliids in natural settings. More recently, use of these fish in evolutionary and life history research, in context of relevant environmental parameters, has begun to close gaps in our ecological knowledge of the family. However, a great deal remains to be learned.

Only a small proportion of the approximately 184 species of **poeciliids** (Parenti and Rauchenberger, this volume) has been used at all in ecological studies. The mosquitofish (Gambusia affinis) is the best known member of the family from an ecological perspective, due to its widespread stocking as a mosquito control agent (see Courtenay and Meffe, this volume) and resultant studies of its diet, habitat and environmental tolerances. Some ecological information on other members of the genus has been gathered as well, as has information on Poecilia, **Xiphophorus**, **Poeciliopsis**, Heterandria and Belonesox. The vast majority of the family, however, is virtually unknown with regard to very basic aspects of their ecologies. Because other features of poeciliids are so well understood, an excellent opportunity exists for a synthesis of genetics, physiology, life histories, and development with ecology. Together with a comparative approach across species and genera, the family could facilitate a more comprehensive understanding of ecological and evolutionary processes.

We herein review basic ecological aspects of the Poeciliidae. This is likely a biased perception of ecology of the family, since most information comes from a few genera and species. The lack of good ecological understanding of the group is illustrated by combination of several important topics into one chapter. There are not enough data available to justify separate treatments of trophic, physiological, and community ecology, for example. Thus, pertinent information for poeciliids is spotty and uneven across taxa and disciplines, and only a very general treatment can be made here.

HABITAT USE

Macro-scale Habitat Use

Poeciliid fishes live in a broad array of habitats, occupying temperate and tropical zones, desert and mesic areas, rivers, lakes, springs, fresh and brackish marshes, and saline mangrove swamps. Within deserts alone, poeciliids cover a wide habitat range, including rocky and fluctuating arroyos, constant and chemically harsh springs, small to large rivers, productive cienegas, and a variety of man-made ecosystems. The diversity of habitats used by the family and individual species indicates that poeciliids are a robust and highly adaptive group.

There are two major reasons for the wide range of habitat use by poeciliids. First, they are excellent colonizers, and a single gravid female can found a new population. Consequently, poeciliids often occupy "fringe habitats" - geologically unstable and harsh areas with few other fishes. This is especially evident in arid regions, where poeciliids are one of few, or the only species in thermal springs or temporary headwaters of streams. In mesic regions they may also be the only fish to colonize isolated springs, shallow freshwater or brackish coastal ponds, or Carolina Bays, the semi-permanent depressions of southeastern United States.

The second reason for the success of poeciliids is high thermal and salinity tolerances, resulting in the ability to survive short periods of dispersal under poor conditions, and to maintain populations in sub-optimal habitats. For example, G. affinis can survive in salinities from fresh to full-strength sea water, and lives from semi-tropical Texas and Mexico to temperate Illinois and Indiana, where it over-winters below ice (Krumholz 1944). Likewise, Poeciliopsis monacha does well in barren, rocky mountain streams in Mexico that have low productivity, and warm, poorly oxygenated waters in summer (Vrijenhoek 1979).

Of course, not all poeciliids are so catholic in their habitat use. Many are confined to a few or single localities. This is exemplified by several Gambusia species in the Chihuahuan desert of Texas and Mexico that are springhead endemics and occur in only one or several localities (Lee at al. 1980; Minckley 1984).

Micro-scale Habitat Use

Poeciliids typically inhabit small, shallow bodies of water such as springs, marshes, and ponds, or shallow, marginal areas of larger bodies such as rivers and lakes. Even when they occur in marine systems, they occupy margins, in mangrove roots or shallow bays (Krumholz 1963). These shallow areas are typically slow-water habitats, and are often partially or heavily vegetated, or have other types of cover. A notable exception is Gambusia **puncticulata** monticola, described by Rivas (1971) as being "...collected in rapids over gravel bottom and around boulders, at an elevation of 1,250 feet, 198 km upstream from the sea." Rivas (1982) indicated that Poecilia hisnaniolana also occurs in fast current.

Several factors may result in use of shallow, marginal microhabitats. First, predation by larger fish may force **poeciliids** into shallow refugia. Haskins et al. (1961) found that smaller guppies (Poecilia reticulata) are more likely to stay in shallow stream margins, whereas larger individuals stayed in more central areas; they related this behavior to predation. Seghers (1974a & b) and Liley and Seghers (1975) demonstrated that guppies select shallow water in the presence of predaceous fishes, and deeper water when aerial predators are abundant. Goodyear (1973) discovered that mosquitofish use the sun to orient toward shore and away from predators in deeper water. In a laboratory study, Noltie and Johansen (1986) documented that guppies have a preference for shallow water, but there were differences in depth selection based on past experience and sex and age of other fish present.

The substrate over which a fish orients may also dictate shoreline orientation. Endler (1980) demonstrated that fish predation impacts the intensity and type of color patterns in guppies and Phalloceros caudimaculatus. Background coloration affected color pattern in both species through predation on less cryptic individuals. Two species of *Gambusia* in Belize appear to have different substrate/cover preferences. *G. sexradiata* prefers heavy cover of emergent vegetation and a substrate of rich organic material, whereas the sympatric *G. puncticulata yucatana* is found primarily over a clay-mud substrate with no vegetation (Greenfield et al. 1983a). Female reproductive condition may affect substrate use and shoreline orientation. Maglio and Rosen (1969) indicate that females near parturition moved into very shallow, sandy regions of their pond.

A third factor in use of shallows may be oxygen availability. Kramer and Mehegan (1981) and Weber and Kramer (1983) used guppies to demonstrate that gulping air at the surface is an adaptive response to hypoxic conditions. Juvenile guppies with access to the surface under experimental low oxygen conditions grew faster and had lower mortalities than those prohibited from using the surface. Mosquitofish initiate surface respiration between 20-65 torr PO_2 (12.5 - 40.8% saturation at 25 ^{o}C and 1 atm pressure) and it is obligatory below 20 torr at 20 C (Cech et al. 1985).

Temperature is also important in selection of shallow microhabitats. It is a common observation, for example, that during colder periods, shallow shorelines are frequented by poeciliids because these areas warm quickly on sunny days. Conversely, under artificially high thermal conditions, shallow regions may offer a refuge from lethal temperatures. In a nuclear reactor cooling reservoir in South Carolina, we repeatedly observe an abundance of mosquitofish in shallow water, adjacent to deeper, lethal water several degrees higher. In a New York pond, Maglio and Rosen (1969) found that mosquitofish sought the maximum available temperature up to 33 C, resulting in diurnal movements relative to the shoreline. Johnson (1976) demonstrated a diurnal pattern of critical thermal maxima in mosquitofish, further indicating diurnal change in microhabitat use as a function of temperature.

Other microhabitat preferences have been observed or documented in poeciliids, some only in anecdotal observations. In southwestern desert springs, native Sonoran topminnows (*Poeciliopsis occidentalis*) routinely use springhead habitats that have high concentrations of dissolved CO$_2$ and low pH. Introduced mosquitofish are usually at lower numbers or absent from immediate outflows, but swarm in large numbers downflow where conditions moderate (Minckley et al. 1977; Meffe 1983). The same situation occurs with mosquitofish and *Gambusia heterochir* in Texas (Hubbs 1971).

In a complex of unisexual-bisexual fishes of the genus *Poecilia*, Balsano et al. (1981) demonstrated that bisexual females were more prevalent in headwater locations, whereas unisexual frequencies increased downstream, although both types preferred shaded areas and a gravel substrate. Lanza (1983) reported that five members of a unisexual-bisexual species complex of *Poeciliopsis* changed microhabitat use dependent upon the presence of other species in an artificial stream. Even more subtle microhabitat partitioning occurs in other *Poeciliopsis*. Two distinct clones of *Poeciliopsis* 2 monacha-lucida specialize on different feeding microhabitats (Vrijenhoek, 1978) and therefore coexist in an unproductive desert arroyo. Other ecological specializations on limited space and food resources allow coexistence of a number of combinations of these fish "species" and their sexual ancestors (Vrijenhoek 1984; Schenck and Vrijenhoek 1986; Schenck et al. this volume).

TROPHIC ECOLOGY

Poeciliids as Consumers

As in their habitat use, poeciliids exploit a broad range of food types. Trophic types range from the highly piscivorous pike killifish, *Belonesox belizanus* (Miley 1978; Turner and Snelson 1984), to omnivorous mosquitofishes (Hess and Tarzwell 1942; Greenfield et al. 1983 a & b) to the largely herbivorous sailfin molly, *Poecilia latiRinna* (Harrington and Harrington 1961, 1982; Wetzel 1971). Most poeciliids examined are omnivores, however, and eat a mixture of terrestrial and aquatic invertebrates, detritus, algae, or vascular plant matter (Sokolov and Chvaliova 1936; Hess and Tarzwell 1942; Hunt 1953; Reimer 1970; Harrington and Harrington 1961; Schoenherr 1974; Dussault and Kramer 1981).

The diets of poeciliids are often reflected in morphology. Tooth structure and gut length relative to body size are good indicators of diet preference (Al-Hussaini 1949; Barrington 1957; Lagler et al. 1977). Strong, conical teeth and short gut lengths are typical of predators such as *G. affinis* or *B. belizanus* (Meffe et al. 1983; Turner and Snelson 1984), whereas omnivores/detritivores such as *Poeciliopsis* spp. have longer guts and weaker, spatulate teeth (Vrijenhoek and Schultz 1974;

Schoenherr 1981). Sensory canals of the head are also clues to diet, and are correlated with dentition and feeding behavior (Rosen and Mendelson (1960). Open sensory canals, with exposed neuromasts, are common in surface feeders with strong teeth; bottom feeders with movable teeth tend to have covered sensory canals. The open canals of the former are thought to aid in detection of live, moving prey near the surface.

Within a species, food choice may range from very narrow to broad and opportunistic. The piscivorous pike killifish eats a diet virtually restricted to fish. Miley (1978) reported that 99% of the diet of Belonesox from southern Florida was fish, and in laboratory experiments, they readily ate mosquitofish, least killifish (Heterandria formosa) and sailfin mollies. In its native habitat, the adult pike killifish only eats fish (primarily other **poeciliids**) but juveniles include a small percentage of insects in their diet (Anderson 1980). Belonesox accepted only fish in aquaria, even when offered tadpoles, insects or small frogs (Turner and Snelson 1984). Most other species, however, exhibit a broad range of food choice and will often take the most abundant item available. For example, both mosquitofish and sailfin mollies drastically changed diets in a Florida salt marsh when invertebrate prey declined after impoundment (Harrington and **Harrington** 1982). Gambusia went from a diet predominantly of insects to one largely of algae and plant detritus. **Poecilia** shifted from mostly vascular plants before impoundment to almost exclusively algae and detritus afterward.

Similarly, there may be large differences in trophic selection among different populations within a species (e.g., compare Sokolov and Chvaliova 1936; Hess and Tarzwell 1942; Walters and Legner 1980) or within the same population over time (Hunt 1953; Reimer 1970). Although great variation in trophic utilization over time or space is at least partly the result of changing prey availability, it nevertheless demonstrates the diet flexibility of many poeciliids.

Poeciliids have been used in several experimental studies dealing with the dynamics of predation and foraging. Gerking and Plantz (1980) found that P. occidentalis preferentially selected larger prey than was available at random. Wurtsbaugh et al. (1980) found the same pattern in mosquitofish, but Bence and Murdoch (1986) did not. In using G. affinis to test selected aspects of optimal foraging theory, they reported that mosquitofish actively chose small prey, which were more profitable. Reddy and Pandian (1973) tested relative predatory efficiencies of mosquitofish in different volumes of water; mosquitofish ate fewer mosquito larvae per time unit under conditions of less water. Grubb (1972) tested predation by mosquitofish on a series of anuran eggs and found that eggs from breeders in temporary ponds were preferred over those from permanent systems.

A number of researchers have focused on the impacts of mosquitofish on prey communities and ecosystems. In an experiment in California rice fields, Farley and Younce (1977) documented declines in populations of notonectids, odonates, hydrophilids, chironomids, corixids and ephemerillids in the presence of Gambusia. Walters and Legner (1980) reported that mosquitofish and the desert pupfish (*Cyprinodon macularius*) both reduced numbers of predaceous invertebrates in experimental earthen ponds, but pupfish were less damaging to other fishes. In experimental pools, mosquitofish reduced crustacean, insect, and rotifer populations, which in turn had positive effects on phytoplankton populations and changed physico-chemical aspects of the systems (Hurlbert et al. 1972). In another set of experimental ponds, Hurlbert and Mulla (1981) documented elimination of Daphnia *pulex* and *Ceriodaphnia* sp. populations and large changes in other zooplankter populations. This one species can thus have major effects on community and ecosystem structure through its predatory habit (see Courtenay and Meffe, this volume).

We wish to make one final point relative to food in poeciliids. In laboratory experimentation, investigators often evaluate the effects of food quantity but neglect food quality as a variable. Two examples from the poeciliid literature are instructive. Reddy and Shakuntala (19XX) found that adult female *G. affinis* and *P. reticulata* grew very poorly on a diet of mosquito larvae but grew much more quickly on a diet of Tubifex worms. The difference in the guppy was almost 10 fold. Both species appear to "prefer" worms to larvae and consumed 3-4 times more worms, by weight, per day. The conversion efficiency was also much higher for worms than for larvae, dramatically so for the guppy (32% versus 15%). Wurtsbaugh and Cech (1983) compared growth rates of juvenile mosquitofish fed to satiation with brine shrimp nauplii and tubifex worms. After 25 days, the mean weight of nauplii-fed fish was 22% greater than that of fish-fed worms.

Food quality can thus be a relevant factor in experimental studies of poeciliid feeding.

Cannibalism in Poeciliids

A particularly intriguing aspect of the diet of some poeciliids is cannibalism. Several species are known to cannibalize in nature, including *G. affinis* (Seale 1917; Krumholz 1948; Walters and Legner 1980; Harrington and Harrington 1982), *B. belizanus* (Belshe 1961; Miley 1978; Turner and Snelson 1984), and *P. monacha* (Thibault 1974a & b). Several others have been observed to cannibalize in the laboratory, including *P. reticulata* (Shoemaker 1944), *P. occidentalis* (Meffe 1984a) and *Poecilia sphenops*, *H. formosa* and *Xiphophorus maculatus* (Meffe, pers. observ.). Laboratory observation, of course, cannot be extrapolated to natural situations, but serves to demonstrate the physical capability of a species to cannibalize, including some that are more typically herbivorous.

Although we know very little about the evolution and maintenance of cannibalism in poeciliids (or other organisms) we do know that it has a genetic basis (Thibault 1974) and may serve to control population size (Moore and McKay 1971). It may also benefit the cannibal as a particularly good nutritive source, allowing enhanced growth and reproduction (Meffe and Crump 1987).

Poeciliids as Prey

Poeciliids have also been studied as prey organisms. Many poeciliids are routinely eaten by predatory fishes, snakes, birds, and even invertebrates. *Gambusia affinis*, *H. formosa* and *P. latipinna* were the top three prey items for four species of water snakes (genus *Nerodia)* in Louisiana bayous, constituting 66% of their diets (Mushinsky and Hebrard 1977). These same **poeciliids**, along with other fish species, were also documented as prey for *Nerodia* by Kofron (1978). Several predaceous fishes feed on several species of **poeciliids**. In particular, mosquitofish are common food items of black basses, and gars are known to eat mosquitofish, least killifish, and sailfin mollies (Hunt 1953).

There is a series of excellent studies documenting impacts of predation on **poeciliid** evolution and life histories. Endler (1980) studied color patterns in male Trinidadian guppies exposed to various predation intensities. Size of color spots in the field and laboratory closely matched background gravel size in the presence of predation, principally by the **cichlid** *Crenicichla* alta. Color spots were larger (due to sexual selection) in the absence of predation.

Reznick and Endler (1982) then documented that female life histories are also affected by predation intensity. Guppies exposed to dangerous predators had higher reproductive investments, reproduce sooner and have larger broods than fish from low predation habitats. Reznick (1982) demonstrated that these differences held up in second generation laboratory fish, and thus had a genetic basis. In a different system, Endler (1982) conducted a parallel study of predation by several piscivores on *P. caudimaculatus* in Brazil. Results were concordant with those in the guppy studies: predation resulted in less conspicuous fishes, with smaller and duller spots.

The only other quantitative study of predation on poeciliids involved mosquitofish as prey for herons in France (Britton and Moser 1982). Heron predation is heavy in marshes but light in ditches. Herons favor female mosquitofish, which are larger than males, consequently biasing sex ratios in marshes toward males, whereas ratios in ditches were close to unity. Thus, population parameters of poeciliids, as well as coloration or life history characteristics, may be affected by predation.

PHYSIOLOGICAL ECOLOGY

Salinity Tolerance

Based on current distribution and zoogeography, Rosen and Bailey (1963) argued that the family Poeciliidae is broadly euryhaline. Of course, many species are now confined to inland and montane areas and occupy exclusively freshwater habitats. are not aware that the salinity tolerance of any inland species has been evaluated in detail. Rosen and Bailey present limited evidence that two such species (*Girardinus uninotatus* and *guintana atrizona*) may retain the ability to survive elevated salinities, although there also is anecdotal evidence that some fresh water forms (e.g., *Gambusia nobilis*) may have low tolerance to elevated salinity (Hubbs and Springer 1957).

Other poeciliids occupy coastal or lowland situations and some species among this group occur across a broad salinity range. The "record holder" in this regard certainly must be *Poecilia sphenops*, a species characteristic of brackish-water habitats, but occurring naturally across a range of 0 to 135 ppt (Kristensen 1969; Feltkamp and Kristensen 1970). Other species occurring across a broad salinity range include *P. reticulata*

(Haskins et al 1961), P. latipinna (Hubbs 1964; Trexler 1986) and B. belizanus (Belshe 1961; Anderson 1980; Turner and Snelson 1984).

The genus Gambusia exhibits an especially broad salinity tolerance. Some species occur only in isolated desert springs (e.g., gaigei and alvarezi, Hubbs and Springer 1957) or other exclusively fresh water habitats (e.g., longispinis, Minckley 1969; marshi, Meffe 1985a). Other species appear to be confined to high salinities (e.g., 30 ppt for xanthosoma, Greenfield 1983; 28-40 ppt for manni, Krumholz 1963), and still other species occur across a broad salinity range (e.g., yucatana, Carter 1981; nicaraguensis, Greenfield et al. 1982).

Most of the experimental work conducted on salinity tolerance has been done with species of Gambusia. Carter (1981) examined the salinity preference and tolerance of four populations of three Gambusia species occurring naturally across a range of salinities in Belize. He found that all four forms had the ability to adjust to gradual changes in salinity regardless of their origin or acclimation, but there were differences in the ability of species to tolerate abrupt salinity changes. The marine G. yucatana survived direct transfer from seawater to freshwater. However, the three forms acclimated to fresh water were much less able to tolerate direct transfer from fresh to seawater, with survival ranging from 60% for brackish water yucatana to 0% for freshwater sexradiata. Gambusia yucatana from both marine and brackish populations showed a much greater ability to maintain stable plasma osmotic concentrations when transferred from fresh to salt water than did the species of freshwater origin, **luma** and sexradiata. The fishes selected positions in a salinity gradient tank consistent with the salinities they occupy in nature.

Gambusia affinis acclimated to freshwater exhibits high survival when transferred directly from fresh water to concentrations as high as 50% seawater. Mortality increases abruptly at test salinities above 50% and virtually no fish survive direct transfer from fresh to full seawater for more than 24 hours (Salibian 1977; Al-Daham and Bhatti 1977). There are a variety of other indicators that G. affinis, although broadly euryhaline, is best adapted to fresh water (Stearns and Sage 1980; Zimmerer 1983).

Salinity tolerance and/or preference has been examined in relatively few other species, including B. belizanus **(Belshe** 1961), P. reticulata (Gibson and Hirst 1955; Zimmerer 1983), and **P**. sphenops (Feltkamp and Kristensen 1970). In general, all three have been shown to tolerate a wide range of salinities but appear to prefer or "do best" at salinities near those most typically occupied in nature. **Poecilia** latipinna, although most characteristic of brackish water, is broadly euryhaline in nature (e.g., Gunter 1950; Large 1985; **Trexler** 1986). Although the salinity tolerance or preference of this species has not been tested, Evans (1973, 1975) and Gustafson (1981) have examined osmotic balance and both conclude that **P. latipinna** is physiologically best adapted to brackish waters.

Temperature Tolerance

Poeciliids occur across a broad range of thermal regimes.

Unfortunately, the thermal biology of only a few species has been examined in any detail. Unquestionably, the best studied species in this regard (perhaps one of the best studied of all teleosts) is the mosquitofish. This species has been of special interest because it occurs across such a broad temperature range, from northern, ice-covered lakes and ponds (Krumholz 1948; Otto 1973) to constant-temperature hot springs (Otto 1973; Winkler 1975) to thermally elevated environments whose temperature may change drastically over a short time (Ferens and Murphy 1974; Bennett and Goodyear 1978).

In general, thermal tolerance and preference are determined by a combination of acclimation temperature and genetic adaptation to native thermal environments (Hart 1952; Otto 1973). Otto (1973) found a lower lethal temperature of about 0.5 C for cold acclimated-cold adapted fish and an upper incipient lethal temperature of about 38 C for warm acclimated-warm adapted fish. He also reported that the thermal tolerance boundaries differed by about 2.5 C between cold and warm-adapted fish, with the shifts being in the direction predicted by genetic adaptation.

Specific results reported by other authors vary, depending on methodology used, the source of the fish, and acclimation procedures. Smoak (1959) found that mosquitofish from thermally altered environments did not withstand elevated temperatures any better than did fish from normal environments if the latter were briefly acclimated at elevated temperatures, but Hagen (1964) reported that survival was correlated with habitat temperature. Mosquitofish from Arkansas had a preferred temperature of 28-29 C and fish selecting different temperatures in a gradient varied little in their upper lethal temperature (Bacon et al. 1968). Winkler (1979) reported that G. affinis from Arizona had a preferred temperature of 31 C in both the field and laboratory, regardless of whether the source population had experienced acclimation temperatures above, below, or at 31 . He suggested that a temperature preference of 28-31 C was genetically determined.

The importance of acclimation history to the critical thermal maximum (CTM) of the mosquitofish was pointed out by Otto (1974). He found that short-term thermal heat tolerance was greatly increased in fishes subjected to an acclimation cycle which included brief exposure to temperatures at or above the upper lethal temperature. Since mosquitofish appear to behaviorally select a cycling acclimation regime in the field (Winkler 1975), most laboratory studies on the lethal temperature of this species probably are oversimplified. The species has been collected at temperatures as high as 42-44 C (Ferens and Murphy 1974; Otto 1974), although it undoubtedly ventures into such lethal temperatures only briefly.

The effects of thermal loading on the general ecology of mosquitofish have been evaluated in several studies. Aho et al. (1976) reported that metacercarial cysts of a parasitic trematode were more dense in the brains of mosquitofish from thermally elevated habitats than in those from normal habitats. The density relationship was reversed in a second species of trematode that encysted in the body cavity of the fish.

Ferens and Murphy (1974) and Bennett and Goodyear (1978) evaluated reproduction and population structure in thermally altered environments. In general, they found few meaningful differences in sex ratios, size structure, size at maturity, or size-fecundity relationships between stressed and ambient environments. Only two consistent differences were found: 1) females from thermally elevated habitats reproduced year-round whereas those from normal habitats reproduced only in the summer, and 2) the percentage of reproductively active females generally increased with increasing water temperature. These differences are not surprising since temperature appears to be the most influential environmental factor in "triggering" reproduction in this species (Medlen 1951).

No consistent relationship between fat content and environmental temperature has been found (Falke and Smith 1974; Bennett and Goodyear 1978), but Blaylock and Mitchell (1969) reported that mosquitofish were more resistant to gamma radiation at 25 C than at 30 C.

The thermal biology of other poeciliids has been examined, but none in the detail of *G. affinis*. *Gambusia gaigei*, whose native habitat is warm springs, was better able to survive at elevated temperatures than *Gambusia geiseri*, whose native habitat is cool springs (hagen 1964). Gelbach et al. (1978) reported that the CTM for *G. nobilis* was 38-39 C and that the preferred temperature was 21-25 C in the morning and 26-30 C in the afternoon. The guppy has an incipient upper lethal temperature of about 32 C (Gibson 1954). Males prefer a significantly cooler temperature (24.5 C) than females (28.2 C) or juveniles (28.2 C)

(Johansen and Cross 1980). However, sexual differences in guppy thermal tolerance are not clear cut. Tsukuda (1960) reported no significant difference in either heat or cold tolerance of males and females. Gibson (1954) found that the sexes were very similar at most lethal test temperatures except two; at 37 C males died more quickly than females but at 34 C males lived longer than females. In the preferred temperature range of 20-30 °C, the rate and intensity of male guppy courtship behaviors exhibit little variation with temperature after acclimation (Laudien and Schlieker 1981).

Shafland and Pestrak (1982) found the lower lethal temperature of *B. belizanus* in Florida to be 9-11 C and Angus (1983) found that temperature influenced the penetrance and expressivity of a mutation for melanism in *P. latipinna*. In unisexual-bisexual species complexes of the genus *Poeciliopsis*, the hybrid unisexuals are heterotic for temperature tolerance with respect to the bisexual parental forms (Bulger and Schultz 1979, 1982).

Photoperiod Responses

Photoperiod and temperature are usually considered to be the two most important environmental parameters influencing the reproductive cycle of fishes. Several studies have evaluated the relative effects of photoperiod and temperature on reproduction in poeciliids, producing mixed results. Colson (1969) found that *H. formosa* ceased reproduction during the winter in northern Florida both in "ambient" environments and in constant-temperature (21 C) springs. On this basis he hypothesized that photoperiod played the dominant role in the initiation and termination of reproduction. This was confirmed by laboratory experiments; there was no reproduction at a 8L:16D photoperiod, regardless of temperature.

Bowden (1970) examined the effects of temperature and photoperiod on the guppy and found that temperature was the extrinsic factor of greatest importance in regulating both the periodicity and intensity of reproduction. In fact, guppy reproduction is quite insensitive to photoperiods ranging from continuous light to continuous darkness. Both Bowden (1970) and Munro (in press) note that the interbrood interval (the rate of embryonic development) of the guppy is not significantly influenced by photoperiod treatments.

In the Tampa Bay area of Florida, reproduction of the sailfin molly ended abruptly in mid-September and then commenced again in January (Grier 1973). Laboratory studies indicated that ovary development ceased at a critical photoperiod somewhere between 12 and 14 hours of light per day, regardless of temperature. This would coincide well with the observation that field reproduction ceases at or near the autumn equinox, even though temperatures satisfactory for reproduction (20-22 C) extended beyond that time. The effect of photoperiod on the initiation of reproduction is less clear. Grier found that field reproduction began in the spring when day lengths were less than the critical 12-14 hour photoperiod, and he concluded that a complex combination of temperature and photoperiod influenced the initiation of reproduction in the spring.

Field reproduction of the molly in the Cape Canaveral area of Florida also terminates sharply in mid-September to early October, even in constant-temperature (21-23 C) springs (Large 1985). In contrast to Grier's results, the spring resumption of reproduction in east-central Florida normally does not occur until March or April (Wetherington 1982, Large 1985, Snelson, unpublished). However, there are unexplained exceptions. In one "ambient" study area, reproduction continued at a significant level throughout the winter of 1983 (R. E. Smith, unpublished). Large (1985) found that significant reproduction began in February in a constant-temperature spring as opposed to March or April in ambient environments.

The importance of photoperiod in controlling reproduction in mosquitofishes is also unclear. Medlen (1951) concluded that temperature was of primary significance in controlling reproduction in _G. affinis_, with photoperiod playing only a minor role. However, several authors have noted that this species ceases field reproduction in the winter in springs with constant water temperatures high enough to support reproduction (Brown and Fox 1966; Davis 1978), implicating a strong photoperiod response. Yet, Bennett and Goodyear (1978) and Meffe (unpubl. data) found that mosquitofish in a thermal pond reproduce year-round. _G. geiseri_, a species presumed to have evolved in constant-temperature (20-23 C) springs, appears to reproduce throughout the winter in Texas (Davis 1978). Likewise, _P. occidentalis_ reproduces throughout the year in a constant-temperature (28 C) spring but ceases reproduction in winter in variable temperature habitats (Schoenherr 1977).

In more tropical environments where photoperiod and temperatures are more constant, significant reproduction may occur year-round (e.g., Turner 1938). However, small differences in photoperiod may have a subtle effect even in the tropics. For example, Burns (1985) examined reproduction of *Poeciliopsis gracilis* and P. *sphenops* at photoperiods representing the extremes experienced by these fish in El Salvador (11.3 and 12.9 hours of light); females on the longer photoperiods had higher fecundities and males had higher gonadosomatic indices. There is obviously a great deal to be learned about the effect of photoperiod and its interaction with temperature in the control of poeciliid reproduction.

Energetics

Because of its importance in mosquito control, there has been a considerable amount of interest in the efficiency and energetics of *G. affinis.* Shakuntala and Reddy (1977) maintained mosquitofish on restricted and ad lib rations of Tubifex worms. Fish on the restricted diet grew slowly, food intake (food consumed per weight of fish per day) varied between 64.7 and 79.5 mg/g/day over the 30 day experiment, and conversion efficiency varied between 7-8%. Fish on the ad lib diet grew quickly and took in more food, especially at smaller sizes, but consumption declined sharply with increasing fish size; conversion efficiencies were between 13-14%.

Shakuntala and Reddy (1979) showed that temperature and salinity interacted to control the food intake of mosquitofish. Consumption increased and conversion efficiency decreased with temperature at each of five salinity levels from 0-7 ppt.

Maximum growth rate was at 25 C and 5 ppt; maximum conversion efficiency was at 3 ppt and 20 C.

Wurtsbaugh and Cech (1983) fed Tubifex worms to mosquitofish to investigate the effects of temperature and ration on growth patterns. On an ad lib diet, consumption ranged from 7% of dry body weight/day at 10 C to 83% at 35 . There was no growth at 10 C and a peak in growth of 21% dry body weight/day at 30 C. Conversion efficiencies increased from 0% at 10 C to a maximum of 28% at 30 C. On a reduced ration, the temperature of peak growth was reduced from 30 to 25 C.

Cech et al. (1985) evaluated the respiratory metabolic rates of mosquitofish at various temperatures and dissolved oxygen tensions. Rates generally increased with temperature but were significantly depressed at 30 and 35 C under severe hypoxic conditions. At 20 C the metabolic rate of the mosquitofish (0.09 mg O_2/hr) is about 30% lower than that of a guppy but is generally in line with other fish of the same size. Based on metabolic rate and energy content of various sized mosquito larvae, Cech et al. (1980) calculated the food demands of mosquitofish in terms of numbers of mosquito larvae per day. A 0.5 g fish under normoxic conditions would eat about 80 "small" larvae per day at 10 C and that number would increase to about 475 per day at 35 C.

Little is known about the metabolism and energy demands of other poeciliids. The guppy has a higher growth rate and conversion efficiency than the mosquitofish on diets varying from 100% mosquito larvae to 100% Tubifex worms (Reddy and Shakuntala 19XX). Since the guppy also has a higher metabolic rate, this result probably could have been anticipated. Most other published information on energetics in poeciliids relates to the costs of reproduction and viviparity. These subjects are reviewed elsewhere in this volume.

POPULATION REGULATION

A poorly understood topic in poeciliid ecology is basic aspects of population size and regulation. Although several authors have evaluated relative abundance of poeciliids in different habitats (e.g., Snelson 1980; Meffe 1984b; Hughes 1985; Botsford et al. 1987), we are not aware of any research that attempts to make reasonable estimates of population size or density. The reasons for this void are fairly obvious. First, poeciliids are quite small and hard to mark or tag by conventional means (Heugel et al. 1977). Although some mass-marking techniques have been developed for poeciliids (Vondracek et al. 1980), they have not yet been applied in any significant way to basic ecological questions. Secondly, poeciliid populations tend to be large and, in many cases, temporally variable, which makes it necessary to tag large numbers of individuals to reasonably estimate population parameters. Both the practical difficulty of tagging and the necessity of marking large numbers of animals render mark-recapture methods for estimating population size difficult to employ. Finally, many poeciliids occupy highly variable, even temporally ephemeral, habitats. For example, small streams occupied by species of <u>Poeciliopsis</u> vary from stagnant disconnected pools to flooded torrents, often over very short periods of time (Thibault 1974a;

Meffe 1984b). Likewise, tropical and subtropical marshs that are home to many poeciliids undergo dramatic fluctuations in depth and extent of water coverage during annual or even daily hydrologic cycles (Kushlan 1980). The concentration/dilution effects produced by changes in habitat availability greatly complicate density or even relative abundance estimates and may confound or mask many basic ecological processes.

The best studied case of population dynamics in a poeciliid involves mosquitofish stocked into California rice fields for the purpose of mosquito control. In general, mosquitofish populations increase during the rice-growing season. However, the details are highly variable from case to case. The timing and rate of population increase differ among fields. In many, populations do not appear to reach "carrying capacity" and final population numbers may differ among fields by an order of magnitude or more (Reed and Bryant 1975; Norland and Bowman 1976; Farley and Younce 1977). Botsford et al. (1987) found that some of the variability in population development is associated with ecological conditions (rice plant height) at the time of stocking. Some of the variation is also explained by synchronized parturition resulting in pulses of recruitment. Rather than a smooth increase in population, growth curves exhibited at least two well-defined peaks, with an intervening period of population stability or decline. In most cases, the second peak was approximately the same magnitude as the first, suggesting that a maximum had been reached. The factors controlling populations during the period of declining numbers were not identified but were assumed to be increased mortality due either to predation or habitat (food) limitations.

These mosquitofish experiments were terminated at the end of the rice-growing season, so we do not know how populations would have varied over time. However, we suspect that such experiments closely approximate the conditions in many natural poeciliid populations. There is ample circumstantial evidence suggesting that most poeciliid populations are temporally variable, probably growing and declining erratically during the year under the influence of both biotic and abiotic "regulatory" agents (Schoenherr 1977). Such populations probably never reach a plateau or steady-state before they are reduced by some seasonal or unpredictable abiotic event.

Abiotic Factors

Abiotic factors may play a dominant role in controlling the size of many poeciliid populations. However, this is difficult to evaluate directly because most poeciliids are naturally short-lived, the vast majority probably not surviving more than 15-18 months in the wild. Heavy mortality has been associated with periods of environmental stress, such as cold temperatures (Krumholz 1948; Hughes 1985), low-water conditions (Kushlan 1980; Wetherington 1982), or floods (Collins et al. 1981; Meffe 1984b).

Biotic Factors

As noted above and elsewhere is this volume (Snelson chapter), predation can have a dramatic effect on both the evolution and phenotypic variability of many morphological, behavioral, and life history traits in poeciliids. This is nowhere better illustrated than in the excellent series of articles by Haskins, Seghers, Endler, and Reznick demonstrating the impact of predation on the evolution and ecology of the guppy. In these and other studies, predation has been shown to impact behavior, coloration, size at maturity, courtship, reproductive effort, sex ratio, and habitat selection. However, none of these studies make it clear that predation is a dominant influence in limiting or controlling population size. Predation by introduced mosquitofish on native Sonoran topminnows *occidentalis)* in the American southwest is a noteworthy exception. In this case, mosquitofish predation is so severe that it is responsible for complete elimination of the topminnow in many habitats (Meffe 1985b). This subject is further discussed elsewhere in this volume (Courtenay and Meffe)

Population Self-Regulation

Breder and Coates (1932) were the first authors to suggest that laboratory populations of the guppy were self-regulating, stabilizing at nine individuals per 5.5 1 tank regardless of original stocking density. This seminal work has been followed by a number of other studies evaluating regulation in laboratory populations of guppies (Shoemaker 1944; Silliman 1948, 1968; Rose 1959; Warren 1973a, b & c; Yamagishi 1976a & b; Dahlgren 1979). The results and explanations coming from these studies have varied. Some authors have confirmed long-term population stability (Silliman 1948, 1968; Warren 1973a) whereas others have found that populations cycle (Shoemaker 1944) or gradually decline over long periods of time (Yamagishi 1976a).

Factors considered important in "regulating" laboratory populations at high densities are depressed reproduction due to increased aggression and/or reduced courtship (Warren 1973b, 1973c), reduced fecundity (Dahlgren 1979), increased cannibalism (Shoemaker 1944; Rose 1959; Yamagishi 1976a & b; Meffe 1984a), and the buildup of unknown metabolites or pheromones in the tank water (Warren 1973b). The relevance of any of these laboratory results to regulation of natural populations remains unknown.

COMMUNITY ECOLOGY

Of all the poorly-known aspects of poeciliid ecology, community-level information is most lacking. Poeciliids have rarely been the specific or even incidental subjects of community ecologists. Most information on poeciliids as part of larger communities derives from species lists. From this information, and simple observation, a few general comments can be made.

Within native environments, poeciliids range from members of extremely simple to complex communities. In headwater desert arroyos or springs, one poeciliid species (Poeciliopsis spp. or Gambusia spp.) may constitute the entire fish "community" (Peden 1973; Vrijenhoek 1979; Meffe et al. 1983), or be present with only a few other species (Hubbs 1957). In some small rivers in Trinidad, P. reticulata occurs with few other species (Reznick and Endler 1982). In contrast, poeciliids in many lotic and lentic habitats in southeastern United States (e.g., Hunt 1953; Harrington and Harrington 1961) and many areas in Central and South America (e.g., Zaret and Rand 1971) are members of diverse communities of many families .

Where introduced, poeciliids often become much more abundant than within their native ranges, in some cases excluding resident species. Community changes as a result of **poeciliid** introductions are especially evident in the American southwest, where G. affinis is prevalent and often swarms new habitats (Meffe 1985b; Courtenay and Meffe, this volume). Great success of introduced poeciliids is often correlated with species-poor habitats, particularly those with few predaceous fishes. These habitats also tend to be disturbed by man, making them less fit for native fishes.

In simple, two-species poeciliid communities in Arizona, Meffe (1984b) studied effects of flash flooding on community structure. The native P. occidentalis was being replaced through much of its native range through predation by introduced mosquitofish (Meffe 1985b). In a natural spring-seep ecosystem, replacement was slowed or stopped by periodic flooding that removed a disproportionate number of mosquitofish due to their inappropriate behavioral responses to flooding. In stabilized habitats free of natural floods, mosquitofish typically extirpate the native fish.

Obviously, the role of **poeciliids** in community ecology is virtually unknown and is an area worthy of future pursuit. Much can be learned from **poeciliids** about energy flow, (as both predators and prey), competitive and niche relationships, and physiological ecology as related to community concepts.

CONCLUSIONS

In this chapter we have summarized selected aspects of **poeciliid** ecology. Considering the economic importance of these fishes (aquarist trade, biological control, conservation, medical research) and the vast amount of literature accumulated, the gaps in our understanding are striking. As should be obvious, most of what is known is based on only a few species, notably Gambusia affinis and Poecilia reticulata; we know nothing about the ecology of the vast majority of livebearers. Furthermore, much of what we have learned is based upon "tank ecology". Only a handful of species has been extensively studied in the field and the majority of such studies have been conducted in the United States, at the northern periphery of the familial range.

While we do not dispute the importance of laboratory experimental studies in unraveling complex ecological questions, we are impressed that there remains a great need for basic natural history research in this group, especially on Central and South American, and Caribbean species. The genus Xiphophorus is a telling example: the genetics of this genus is probably as well known as any comparable-sized group of teleost fishes, but basic aspects of ecology and natural history are completely undocumented. We need more information about how and where diverse poeciliid species live before we can hope to make synthetic statements about the ecology of the family.

We also need to promote a fruitful interchange between the results of field and laboratory studies. For example, population self-regulation in the guppy was identified, and has been extensively studied in the laboratory. Is it an artifact of the laboratory setting or does the phenomenon have relevance in natural populations? Likewise, is cannibalism largely a laboratory artifact or is it of real importance in the trophic and reproductive ecologies of some species in the wild? Flow of ideas in the reverse direction is also needed. Field studies have repeatedly shown that many poeciliids are successful, even dominant, in stressful habitats that are at best marginal for most other fishes. What are the adaptations that allow poeciliids to thrive is such habitats? We are intrigued by the fact that the mosquitofish seems to have a daily cycle of temperature tolerance. How widespread might this and similar phenomena be? Laboratory investigations into the physiology and behavior of species that range across a diversity of habitats would appear to be wide open and potentially fruitful. Here again, we note that what little is known is based on only a few species. We have no idea whether or not they are "typical" of the family as a whole.

The livebearing habit has evolved in many other groups of fishes but none have been as successful as the Poeciliidae (Wourms 1981). The related family Goodeidae, for example, also exhibits specialized viviparity, but has fewer than 1/5 the number of species and is zoogeographically restricted to the Mexican plateau. This suggests that the success of poeciliids, whether defined in terms of diversity, zoogeographic range, or ecological adaptability, must be attributable to something more than their mode of reproduction. Additional ecological studies are necessary to clearly define what those generalized adaptations might be.

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