The relationship of spawning mode to conservation of North American minnows (Cyprinidae)

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Synopsis

Approximately 20% of North American minnows are considered imperiled. The factors responsible for imperilment in this group are complex, but the relationship of spawning mode to conservation of North American minnows has not been explored. 1 provide a summary of the spawning modes of imperiled North American minnows, discuss patterns between these modes and conservation status, and predict the spawning modes for several poorly-known imperiled species. Of the 46 species of North American minnows that are imperiled, spawning modes are known for only 13 species. All spawning modes are represented in the imperiled group of minnows except mound-building and egg-clustering, and with the exception of crevice-spawners and pit-ridge-builders, the percentage of imperiled minnows in each category of spawning mode is roughly proportional to the percentage of minnows in that category overall. Species with complex spawning modes, such as mound-building, pit-building and egg-clustering, are among the most common fishes in North American streams. This pattern suggests that there is a relationship between parental care and success (lack of imperilment) in minnows. Spawning mode is an important consideration in the formulation of recovery plans and proactive conservation efforts.

Introduction

As the human population grows, consuming increasing amounts of the earth's resources, habitats of other organisms are increasingly altered or destroyed. As a result, many species have been lost by extinction, and others are imperiled. In some cases, whole communities of organisms are at risk. The discipline of conservation biology has developed in response to this global decline of species. Conservationists strive to understand the processes of imperilment and recovery, and work to protect species and their habitats. Typically, the reasons for a species' decline are complex, and it is difficult to find patterns that apply to all types of organisms. Any conservation effort requires knowledge of ecology, behavior, life history, population dynamics and habitat use. Unfortunately, much of this information is often lacking for imperiled species, in part due to their rarity, but also due to the lack of studies in these areas.

Most conservation efforts have focused on terrestrial, and often tropical, environments and organisms. Although evidence exists to suggest that aquatic diversity is also declining precipitously, aquatic systems have received little attention, and the extent of species loss from these systems is not fully understood (Moyle & Leidy 1992). In the United States, where the fauna is relatively well-studied and data are available, the percentages of imperiled aquatic organisms is much larger than that of terrestrial organisms (36% of crayfishes, 55% of freshwater mussels, and 20% of fishes, as compared to 7% of mammals and 7% of birds; Master 1990). Such high numbers emphasize the need for an understanding of conservation in these and other aquatic groups.

The fish fauna of the United States and Canada includes at least 790 species (Lee et al. 1980, Page & Burr 1991). Of these, minnows, the largest family of fishes in the world, account for approximately 30% of the fauna. Approximately 20% (46/231 species,

subspecies excluded) of minnow species found in the United States are imperiled (Williams et al. 1989). The reasons for this decline are unclear, but are probably the same factors identified as responsible for the decline of fishes in general: (1) physical habitat alteration or loss, (2) pollution, (3) overexploitation, and (4) introduction of nonindigenous species (Warren & Burr 1994, Angermeier 1995).

Investigations must use information from a variety of sources to fully understand the process of imperilment, and eventually to predict and correct the process. On a species-specific scale, conservation studies typically focus on factors such as range size, habitat requirements and life-history. However, this information alone often fails to predict or fully explain imperilment, and investigations must use all available information if we are to fully understand the process. Behavioral ecology is a field that is often overlooked by conservationists, but because the field provides information about the way behavior contributes to survival and reproduction, it is vital to conserving fishes.

Angermeier (1995) examined patterns of extinction among fishes in Virginia using statistical techniques. In general, characteristics (range, habitat, ecology and life history) of extirpated species were not distinguishable from those of nonextirpated species, although some patterns in the data were revealed. Statistical tests of this nature are difficult due to the coarseness of ecological data currently available. This is especially true of data on spawning modes. Angermeier's (1995) study did suggest that knowledge of the ecology of species may help predict imperilment and provide a basis for proactive conservation.

Knowledge about the reproductive biology of imperiled North American cyprinids and its possible application to reversing trends in decline can be found in the useful series on 'Threatened fishes of the world' that have appeared in previous issues of Environmental Biology of Fishes (e.g., Gard 1997, Vinyard 1997, Eisenhour & Strange 1998, Warren & Burr 1998).

The objective of this paper is to explore the relationship between spawning mode and conservation status of North American minnows. First, is there a relationship between spawning mode and imperilment? Second, can spawning mode be predicted for poorly-known, imperiled species? Finally, the importance of including this information when formulating protection plans will be discussed.

Spawning modes of North American minnows

Spawning behavior has been documented for 107 (46%) species of North American minnows; however, thorough studies are available for very few of these species and, as a whole, reproductive behaviors of minnows are poorly understood. The spawning modes of North American minnows can be grouped into eight functional categories: broadcasting (primarily nonguarders, open substratum egg scatters of Balon 1975, 1990), crevice-spawning, pit-building, pit-ridge-building, saucer-building, mound-building (primarily nonguarders, brood hiders of Balon 1975, 1990), egg-clumping and egg-clustering (both guarders, nesters of Balon 1975, 1990) (Johnston & Page 1992). Balon (1975, 1990) classified reproductive modes of fishes, including minnows, into reproductive guilds based primarily on type of spawning substrate used, morphology of early respiratory organs, type of respiratory pigment, and behavior of embryos and larvae. Most of this information is unavailable, for North American minnows. The categories used here are based on spawning behavior only, information that is available for many North American minnows. These categories do not necessarily imply that the behaviors within categories are homologous. Broadcasting is the primitive behavior; others are derived. Some well-studied species with derived behaviors (e.g., *Cyprinella lutrensis, C. formosa, Luxilus cornutus*) are known to have flexible spawning modes, and can revert to broadcasting (Raney 1940a, Vives 1993). Although there are exceptions, including genera with species that have plastic spawning modes, most species within genera of North American minnows share the same spawning mode (Johnston & Page 1992).

Broadcasting refers to the release and abandonment of eggs and sperm over an unprepared substrate. It is the primitive spawning mode in minnows, as it is among fishes in general (Johnston & Page 1992). Over 60% of North American minnows have this spawning mode. Included in this category are minnows such as species of *Gila* that aggregate in large schools during spawning and most likely show no territoriality and limited, if any, mate choice (Moyle 1976, Jonez & Summer 1954, Vanicek & Kramer 1969). There are also species of broadcasters that show territoriality, and in which mate choice is probable (e.g., *Rhinichthys).* Most nest associates, species that spawn in the nests of other species (e.g., species of the *Notropis* subgenus *Hydrophlox, Clinostomus,* and some species of

Phoxinus and *Luxilus),* are alsa included in this category; The spawning behaviors of broadcasters are the least studied among minnows, and when more details are known, it may, be possible to distinguish several spawning modes now included in this broad category.

Crevice-spawning refers to the style of laying eggs in crevices within the substrate or submerged structure. Species of *Cyprinella* and *Hesperoleucus* utilize this mode (Johnston & Page 1992). As in broadcasting, no parental care is displayed by these species. In species of *Cyprinella,* males are territorialand temporarily defend crevices as spawning sites. Males display to females by passing along and in front of crevices. Males are aggressive towards conspecific males, and this aggression takes the form of chases, lateral displays and circle swims (Stout 1975, Rabito & Heins 1985). Additional cues used by males during aggressive encounters may include acoustical signals that are probably produced by all species of *Cyprinella* (Stout 1975, Johnston unpublished).

Saucer building is known for only one species, *Agosia chrysogaster.* These fish spawn in saucer-shaped depressions constructed in the substrate and provide no additional parental care (Minckley & Barber 1971, Minckley 1973).

Spawning pits are constructed by some species of *Luxilus* and *Campostoma* (Johnston & Page 1992). Males dig into the gravel with their snouts or mouths and remove small pieces of substrate, usually gravel (Raney 1940a, Miller 1962). Mating occurs in the pits and eggs are abandoned. Aggression among males of both genera is high and territories are vigorously defended. Both genera of fishes are known to spawn in the nests of *Nocomis* and *Semotilus,* and with each other as nest associates. Some species of *Luxilus* have the largest distributions of any North American minnows: where found they can be abundant (e.g., *Luxilus chrysocephalus).* These species have flexible spawning behaviors and have been reported to spawn as pit-builders (either alone or in association with other species) and as broadcasters (Raney 1940a). This plasticity is found at the generic level as well, e.g., some species of *Luxilus* (pit-builders) are only known to broadcast their eggs (Johnston & Page 1992). However, this difference in spawning mode may be due to a lack of study of the less widespread species.

Pit-ridge nests are constructed only by males of the genus *Semotilus* (Johnston & Page 1992). Males excavate pits in the substrate (often gravel) and place the excavated material just upstream of the resulting pit.

Mating occurs in the pit and the male covers the eggs with gravel after spawning (Reighard 1910), thereby providing some parental care to the offspring. Competition among males for nesting sites and females is fierce, and a complex social system exists which includes the occurrence of a satellite males (Ross 1977).

Gravel mound nests are constructed by species of *Nocomis* and *Exoglossum* (Hankinson 1932, Raney 1939, Van Duzer 1939, Reighard 1943). Mating occurs on the gravel mound. In *Nocomis,* parental care is provided by males that cover the eggs with gravel. As in *Semotilus,* males compete for nests and a complex social system exists.

Egg-clumping refers to the style of placing clumps of eggs in cavities under rocks, where they are guarded by the male (Vives & Minckley *1990). Rhinichthys cobitis* (formerly in the genus *Tiaroga*) is the only cyprinid species known to employ this style (Johnston & Page 1992).

Egg-clustering is similar to egg-clumping, but the eggs are laid in a single layer on the cavity ceiling, rather than in a clump (Johnston & Page 1992). This pattern is found in *Pimephales* (McMillan & Smith 1974), *Codoma* (Minckley & Vives 1990) and *Opsopoeodus* (Page & Johnston 1990). Egg-clusterers and egg-clumpers are the only species of North American minnows known to engage in post-fertilization parental care. In both behaviors, it is the males that guard the eggs until hatching.

A very widespread spawning symbiosis, termed nest association, is found among North American minnows and occurs when one species spawns in the nest of another. The style is known for 36 species, or 34% of species for which spawning behavior has been described. Although most species of nest associates are broadcasters, as discussedabove, many species are also capable of building their own nests but they choose to spawn with other species. Nest associates benefit from the parental care of the host in these situations and in some situations hosts also benefit from the symbiosis by reduced brood predation; dilution of their brood with that of associates offers protection (Johnston 1994b).

Patterns of imperilment

Forty-six species of North American minnows are imperiled (Table 1), and placed in the categories endangered, threatened or special concern (Williams et al. 1989). Unfortunately, spawning modes are known only

Table 1. Species of North American minnows recognized as imperiled (Williams et al. 1989), and the spawning mode of each species (where known).

Species	Spawning mode	Reference
Campostoma ornatum	pit-building	McNatt 1974
Cyprinella caerulea	crevice-spawning	Johnston & Shute 1997
C. callitaenia	crevice-spawning	Wallace & Ramsey 1981
C. formosa	crevice-spawning*	Vives 1993
C. monacha	crevice-spawning	Jenkins & Burkhead 1984
C. proserpina	unknown	
Dionda diaboli	unknown	
Eremichthys acros	unknown	
Gila alvordensis	unknown	
G. boraxobius	unknown	
G. cypha	unknown	
G. ditaenia	unknown	
G. elegans	broadcasting	Jonez & Sumner 1954
G. intermedia	unknown	
G. nigrescens	unknown	
G. purpurea	unknown	
Hemitremia flammea	unknown	
Hybognathus amarus	unknown	
Erimystax cahni	unknown	
Macrhybopsis gelida	unknown	
M. meeki	unknown	
Iotichthys phlegethontis	unknown	
Lepidomeda albivallis	unknown	
L. vittata	broadcasting	Minckley 1973
Lythrurus snelsoni	unknown	
Meda fulgida	broadcasting	Barber et al. 1970
Moapa coriacea	unknown	
Notropis albizonatus	unknown	
N. buccula	unknown	
N. cahabae	unknown	
N. jemezanus	unknown	
N. mekistocholas	unknown	
N. melanostomus	unknown	
N. oxyrhynchus	unknown	
N. perpallidus	unknown	
N. semperasper	unknown	
Oregonichthys crameri	unknown	
Phenacobius teretulus	unknown	
Phoxinus cumberlandensis	broadcasting**	Starnes & Starnes 1981
P. tennesseensis	broadcasting**	Jenkins & Burkhead 1994
Plagopterus argentissimus	unknown	
Pogonichthys macrolepidotus	unknown	
Ptychocheilus lucius	broadcasting	Vanicek & Kramer 1969
Relictus solitarius	unknown	
Rhinichthys cobitis	egg-clumping	Vives & Minckley 1990
Semotilus lumbee	pit-ridge-building	Maurakis & Loos 1984

* Also known to spawn as a broadcaster.
** Denotes nest associates.

for 28% of these fishes, emphasizing both the critical need for information on these species and the need for studies on reproduction in minnows in general.

All spawning modes are represented in the imperiled group of minnows (Table 1) except mound-building and egg-clustering, which are found in 7% and 5% of minnows, respectively. With -the exception of *Rhinichthys cobitis,* an imperiled species that is the only known egg-clumper, the percentage of imperiled minnows in each category of spawning mode is roughly proportional to the percentage of minnows in that category overall (broadcasting, 60% overall, 46% among imperiled species; crevice-spawning, 16% overall, 31% imperiled species; pit-building, 7% overall, 8% imperiled species; pit-ridge-building, 4% overall, 8% imperiled species). The exceptions are crevice-spawners, (represented among imperiled minnows by species of *Cyprinella),* and pit-ridge builders (represented by *Semotilus lumbee),* which have a higher percentage of imperiled species than would be expected.

With the exception of *Hesperoleucas symmetricus,* crevice-spawning is unique to species of *Cyprinella.* Several species of *Cyprinella* are also known to spawn as broadcasters (Vives 1993). With only one other species for comparison, it is difficult to draw conclusions about the susceptibility of crevice-spawners to imperilment. However, it is possible that this spawning mode contributes to low brood survivorship under some circumstances, such as habitat degradation. Crevice-spawning species rely on substrate for egg deposition and clean, flowing water to prevent the eggs, which are hidden in the crevice, from dying. Mortality of eggs could occur due to low oxygen conditions, which can be exacerbated by silt. Since the eggs are deposited deep into crevices (Wallace & Ramsey 1981) there is no opportunity for post-fertilization parental care, which might include fanning the eggs to increase oxygenation and remove silt. It is possible that the reproductive success of these species is reduced in habitats with altered flow patterns, increased siltation, and reduced structure such as woody debris.

Another factor that may lead to lower reproductive success in *Cyprinella* is hybridization. Although only one of the imperiled species of *Cyprinella* is currently threatened by introduced species (e.g., *C. callitaenia* by *C. lutrensis;* J. DeVivo personal communication), the hybrid swarms that have been formed by congeners indicate that this is a potential threat to the integrity of all species of *Cyprinella.* Several factors may contribute to the formation of hybrid swarms that occur

when *C. lutrensis* contacts other species (e.g., C. *callitaenia, C. venusta, C. spiloptera, C. whipplei, C. camura)* (Hubbs & Strawn 1956, Page & Smith 1970, Smith 1979, Johnston personal observation, DeVivo personal communication), most of which are correlated with habitat degradation (e.g., loss of habitat segregation, lack of visual cues). It is possible that the sounds (calls) produced by most species of *Cyprinella* (Delco 1960, Stout 197.5, Johnston unpublished) during spawning act as pre-mating isolating mechanisms. Hybrids may be formed if individuals of *C. lutrensis* are attracted to the calls of all species and spawn with congenerics. Also, the physical properties of the calls may be altered in degraded habitats if the preferred spawning habitat is unavailable (Forrest & Miller 1993), and a breakdown of this pre-mating isolating mechanism may occur.

The percentage of pit-ridge-builders in the imperiled category is also higher than the representation of species with this spawning mode among minnows overall (8% vs. 4%). This may be an artifact of the small number of pit-ridge-builders in general, or may be a valid correlation. *Semotilus lumbee,* the imperiled species of pit-ridge-builder, is restricted to the coastal plain of North and South Carolina and occupies a relatively small range (Snelson & Suttkus 1978). Although the primary cause of imperilment for this species is small range size, it is possible that other factors may contribute to the species' rarity. The sand substrate of the habitat of this species may only be suitable for the pit-ridge-building spawning mode, which involves covering the eggs for incubation when water quality is high and silt is uncommon. *Semotilus atromaculatus* and *S. corporalis* inhabit streams with a variety of substrate types, but are common in gravel-bottomed streams (Page & Burr 1991), where water could easily flow over eggs, removing silt and providing oxygen for developing embryos. Like *S. lumbee, S. thoreauianus* most commonly inhabits streams with sand substrate and also has a relatively small range. It is possible that, due to the pit-ridge spawning mode, this species may be especially sensitive to habitat degradation. The status of this species should be carefully monitored.

Predicting spawning mode from phylogeny

One method for gaining insight into the spawning behavior of poorly known species is to examine the behavior of close relatives. With the aid of a phylogenetic hypothesis, the probable spawning modes can

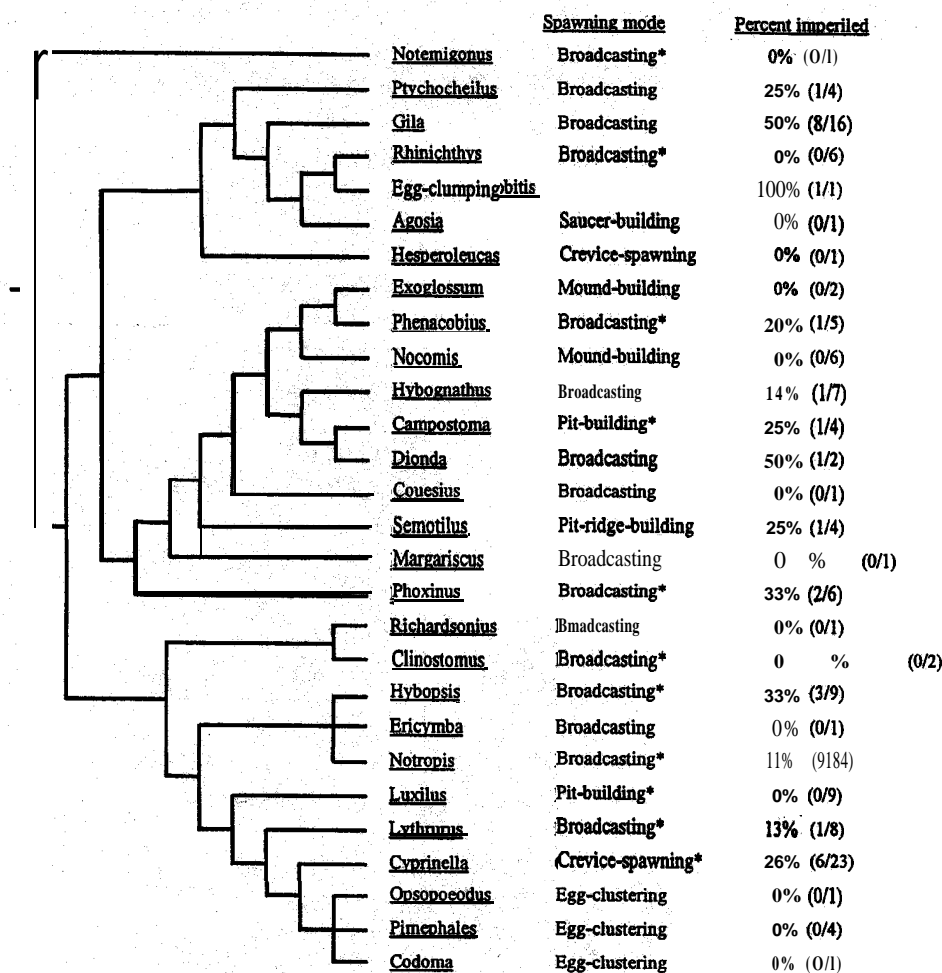|	Spawning mode	Percent imperiled
Notemigonus	Broadcasting*	0% (0/1)
Ptychocheilus	Broadcasting	25% (1/4)
Gila	Broadcasting	50% (8/16)
Rhinichthys	Broadcasting*	0% (0/6)
Egg-clumping*bitis		100% (1/1)
Agosia	Saucer-building	0% (0/1)
Hesperoleucas	Crevice-spawning	0% (0/1)
Exoglossum	Mound-building	0% (0/2)
Phenacobius	Broadcasting*	20% (1/5)
Nocomis	Mound-building	0% (0/6)
Hybognathus	Broadcasting	14% (1/7)
Campostoma	Pit-building*	25% (1/4)
Dionda	Broadcasting	50% (1/2)
Couesius	Broadcasting	0% (0/1)
Semotilus	Pit-ridge-building	25% (1/4)
Margariscus	Broadcasting	0 % (0/1)
Phoxinus	Broadcasting*	33% (2/6)
Richardsonius	Broadcasting	0% (0/1)
Clinostomus	Broadcasting*	0 % (0/2)
Hybopsis	Broadcasting*	33% (3/9)
Ericymba	Broadcasting	0% (0/1)
Notropis	Broadcasting*	11% (9184)
Luxilus	Pit-building*	0% (0/9)
Lythrurus	Broadcasting*	13% (1/8)
Cyprinella	Crevice-spawning*	26% (6/23)
Opsopoeodus	Egg-clustering	0% (0/1)
Pimephales	Egg-clustering	0% (0/4)
Codoma	Egg-clustering	0% (0/1)

Figure 1. Hypothesized phylogenetic relationships among North American minnows based on morphology (adapted from Johnston & Page 1992 based on Coburn & Cavender 1992). Genera not included in figure are *Eremichthys, Hemitremia, Iotichthys, Lepidomeda, Meda, Moapa, Mylocheilus, Oregonichthys, Orthodon, Plagopterus, Pogonichthys* and *Relictus:* The relationships of these excluded genera are unresolved and/or the spawning mode has not been determined. *Hybopsis* includes species often included in *Erimystax* and *Macrhybopsis (e.g.,* Page & Burr 1991). Nest associates are identified with an asterisk.

be predicted by examining character states in well-studied relatives (Brooks et al. 1992). With few exceptions (e.g., **Rhinichthys, Luxilus** and **Cyprinella),** all spawning modes are consistent within genera of North American minnows (Johnston & Page 1992). Consequently, it is likely that all species of *Gila* are broadcasters (Figure 1). Spawning behavior has been described for six species in this genus, including the imperiled *Gila elegans*; all are known to broadcast their eggs. Other groups in the *Gila* clade that broadcast their eggs include species of **Ptychocheilus** and species of **Rhinichthys,** except **R. cobitis** (Johnston & Page 1992). A less parsimonious alternative is that some species of *Gila* have the crevice-spawning mode, found in the sister group **Hesperoleucas.**

Because some species of **Dionda, Lythrurus, Hybopsis** (including **Macrhybopsis)** *Hybognathus, Erimystax, Meda, Notropis* and **Phenacobius** are broadcasters, it is probable that all species in these genera are broadcasters. It is also probable that all species of **Cyprinella** have the potential to spawn in crevices. The phylogenetic relationships of the genera **Iotichthys, Eremichthys, Moapa, Oregonichthys, Plagopterus, Pogonichthys,** and *Relictus* (not included in Figure 1) are not fully resolved, and their spawning modes are unknown. Because the majority of minnows

have the broadcasting style, the safest prediction would be that these fishes also are broadcasters.

The spawning mode of *Hemitremia,* the proposed sister species to *Semotilus* (Coburn & Cavender 1992) (not shown in Figure 1), is not easily predicted. Although most species in this clade are broadcasters, *Semotilus* species are pit-ridge-builders. It is possible that pit-ridge-building also *occurs in Hemitremia.*

If it is assumed that many of the imperiled species for which spawning mode is unknown are broadcasters (all in Table *1* except *Cyprinella proserpina* and *Hemitremia flammea*), then the percentage of imperiled species with the broadcasting spawning mode increases to 80%. Although this seems higher than expected (over 60% of minnows with known spawning modes are broadcasters), if we assume that all species of minnows for which spawning modes are undescribed (except species of *Cyprinella* with unknown spawning modes) are broadcasters, the percentage in all minnows also goes up to 80%. So although it seems as though species with the broadcasting spawning mode may be especially susceptible to imperilment, they are actually represented as often as would be expected in this group. This is also true if the genera with high numbers of imperiled species with the broadcasting spawning mode are compared to those with low numbers or no imperiled species.

A relationship does however exist between spawning mode and a lack of imperiled species. No species of egg-clusterer or mound builder is imperiled, nor are any species of *Luxilus,* one of the two pit-building genera, imperiled (Figure 1). *Agosia chrysogaster,* the only species which builds saucer nests, is also not imperiled, nor are most species of pit-ridge-builders *(Semotilus)* or pit-builders in the genus *Campostoma.* In fact, many of these species are the most abundant fishes in streams throughout eastern North America (Page &Burr 1991). This pattern suggests that there is a relationship between parental care and success (lack of imperilment) in minnows. The exception is *Rhinichthys cobitis,* which has parental care and is imperiled.

Berkman & Rabeni (1987) found no correlation between the numbers of fishes with parental care and silt loads in streams, although broadcasting species were negatively affected by high silt loads. The authors attributed post-fertilization parental care, such as fanning and mouthing eggs, which would tend to remove silt, to this finding. Among North American minnows, this type of parental care is found only in egg-clusterers. (It is not known if the species of egg-clumper cares for eggs in this way.) Fishes with pre-fertilization parental care (e.g., mound-builders, pit-builders, pit-ridge-builders, saucer-builders) manipulate the substrate and may create a better environment for the development of the brood. Mound and pit-ridge builders also cover eggs after spawning, which reduces predation (Johnston 1994a). These behaviors contribute to high reproductive success and could be one of the reasons these fishes are so successful.

The relevance of spawning mode to conservation efforts

Small range size, which can lead conservationists to classify a fish as imperiled, is either a historical condition or the result of more recent range loss. Many imperiled North American minnows, especially monotypic species, have historically small ranges and often inhabit springs, a notoriously endangered habitat *(e.g., Eremichthys acros, Hemitremia flammea, Iotichthys phlegethontis, Lepidomeda albivallis, Moapa coriacea, Relictus solitarius).* Although information on spawning behavior is useful for protecting these species, it does little to predict imperilment, since range restriction is the overwhelming cause of endangerment. However, for some species *(e.g., Cyprinella),* spawning mode, coupled with phylogenetic information (genus-level), may be used to predict imperilment. Knowledge of spawning modes can also be used in recovery plans, particularly of species whose range size is declining.

Physical habitat loss or degradation is almost certainly responsible for the extirpation of many fishes, and often the habitat may have become unsuitable because of a fish's spawning requirements. For example, many species that broadcast their eggs aggregate in large numbers to spawn over suitable substrate (Johnston & Page 1992). Alteration of habitat may reduce the size of spawning areas or fragment populations so that the formation of large spawning aggregations is difficult. Dams are responsible for fragmenting populations of riverine fishes, and are a major cause of decline for some species (Moyle & Williams 1990).

Dams also alter flow patterns in rivers, and may therefore be responsible for loss of breeding habitat for some fishes. Eddy habitat may be critical for successful breeding of *Gila cypha* (Karp & Tyus 1990; see also Gorman & Stone 1999 this issue). Reproduction in sturgeons, which also broadcast eggs, is directly

related to flow regimes in large rivers. Low flows affect spawning habitat availability and may allow silt to settle over eggs (Veshchev & Novikova 1983, see also Noakes et al. 1999 this issue).

Species that require clean substrate for spawning, such as broadcasters, are negatively affected by siltation in streams (Berkman & Rabeni 1987). Siltation may cause egg or brood mortality in a number of ways (Cordone & Kelley 1961, Smith 1971). Loss of range by species *such* as *Erimystax cahni* that require clean gravel areas for spawning can be attributed to increased siltation (Jenkins & Burkhead 1994).

Information on spawning structure used by fishes with various spawning modes, such as the egg-clumper and crevice-spawners, is important for protection efforts. Crevice-spawning fishes use habitat structure (crevices) as spawning substrates. Although the crevices used vary, it is obvious that'habitat structure is important to these species. Some species, such as the blue shiner, *Cyprinella caerulea,* are known to make microhabitat shifts during the spawning season to utilize crevices (Johnston & Shute 1997). Any conservation effort aimed at habitat protection must ensure that both the spawning and typical habitat are included in the plans.

Vives (1993) has suggested that spawning substrate use and even spawning mode may be plastic for some species, but few thorough studies of spawning behavior in minnows exist. Our understanding of flexibility in spawning mode and brood survival under different conditions is therefore minimal. It is probable that some species have a greater degree of flexibility in spawning characteristics than others. As discussed earlier, some species are capable of reverting to more primitive spawning modes (e.g., some species of crevice-spawners or pit-builders).

For some species, however, both spawning mode and substrate may be obligatory. For example, it has been suggested that some species of nest associates will spawn only with hosts (Wallin 1992). While this is certainly not true for all species of nest associates (e.g., *Luxilus* and *Campostoma* spp.), it may be true for others (e.g., *Hydrophlox* subgenus of *Notropis*; *Lythrurus).* Such complex ecological relationships should be taken into account when developing protection plans for different species.

For nest associates, conservation plans must focus on the fish community as a whole, and not just the species of concern. The hosts of nest associates, such as species of *Nocomis* (gravel-mound-builders), are considered keystone species in many stream communities (Vives 1990). Nest associates benefit from the parental care of hosts, which improves brood survivorship (Johnston 1994a). It is not known if nest associates would spawn in the absence of hosts, and whether brood survivorship would be sufficient to maintain populations under these circumstances. In some situations hosts benefit from nesting associations as well, which also emphasizes the importance of maintaining community structure as a conservation measure (Johnston 1994b). Some species, such as bluenose shiners, *Pteronotropis welaka,* will spawn as nest associates of sunfish, and probably also broadcast eggs in vegetation (Knight & Johnston unpublished). Conservation efforts for bluenose shiners, which are thought to be declining throughout their range, must take into account the importance of other species in the fish community, as well as the importance of vegetation to this species.

Introduced fishes may cause the decline of native species due to competition or predation (Moyle & Leidy 1992). The introduction of non-indigenous species may also affect the reproductive success of native fishes via hybridization. In addition to the hybrid swarms formed by C. *Zutrensis* discussed above, hybrid minnows are often formed by nest associate species under natural circumstances (Raney 1940b). When species of nest associates are introduced into new drainages and contact native species, hybrids are also formed (Johnston et al. 1995). The frequency of formation of these hybrids may be greater when closely related species come into contact, and the effect on the. population of native- species must be carefully monitored.

In cases where populations of fishes are critically imperiled, captive breeding programs have been established so that field populations can be supplemented with laboratory-raised animals. Knowledge of the spawning modes of these species is necessary to the success of these programs (Rakes et al. 1999 this issue). Not only can information on spawning modes be used to successfully breed fishes in the laboratory, but information on related species can be used to predict the spawning requirements of species when that information is lacking.

An understanding of the spawning modes of species not only identifies habitat structure important to the spawning process but also highlights the importance of complex ecological relationships of fishes. This understanding assists in conservation efforts in the field,

and is also critical to captive propagation, when necessary. Information on spawning behavior should be used in conjunction with information on ecology, habitat requirements and life history to predict and prevent the imperilment of more species of minnows as well as other fishes. The lack of information for most species of imperiled minnows should highlight the need for more research on the basic biology of these species if we wish to prevent their extinctions.

Acknowledgements

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