

Evolution and Life History Patterns in Freshwater Gobies¹

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Abstract—Gobioid fishes have invaded freshwater systems from the tropics to warm temperate regions. This move has brought about many changes in the biology of the fishes that have made the transition. However, the basic reproductive biology of most freshwater gobioids appears to be similar to that seen in near-shore marine species. Many freshwater gobioids retain a link to the sea through their amphidromous life cycle, but several genera have produced landlocked forms with no diadromy. Egg size, and the inversely related fecundity, change markedly when landlocking results in the production of non-planktonic young. Where it has been determined, the planktonic phase in the amphidromous species is quite long relative to typical shallow water marine gobies and is particularly long in the genus *Awaous*, which has other atypical features in its reproductive biology. Patterns of endemism in freshwater gobioids may be explained only in part by the length of planktonic larval life.

Introduction

This paper, like the others appearing in this issue of *Micronesica*, summarizes a talk presented at the “freshwater section” of the “goby” symposium held in conjunction with the 76th annual meeting of the American Society of Ichthyologists and Herpetologists in New Orleans in June 1996. My paper there introduced the topics in the session. I took advantage of the occasion to point out areas that I felt might develop into particularly interesting or fruitful avenues for future research. Because of this, my paper is idiosyncratic, reflecting my own bias as to where we might usefully direct our research into the biology of freshwater gobies.

The gobioid fishes (including families Eleotrididae (=Eleotridae), Gobiidae, Rhyacichthyidae and others) comprise one of the most speciose groups of fishes on Earth (Hoese 1984). The papers presented at the New Orleans symposium testify to that fact, as well as the extensive radiation that has led to the diverse ecological roles played by these fishes. This paper, along with the others in this issue, focuses on one particular aspect of this radiation, the move from the sea into freshwater habitats. Whereas the separation of teleost fishes into the main freshwater

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and marine lines lies far back in the history of this group, it is generally accepted that the modern gobioid fishes are firmly marine and that the move to freshwater is a trait derived, possibly several times, from the main gobioid stock. Of the fish that have made this move, many retain a marine component in their life history (McDowall 1987, 1988, 1997). Others, as will be discussed below, spend their entire lives in freshwater.

The basic questions we have been asking relate to the fact that, physiologically and ecologically, the move to freshwater would seem to have necessitated fundamental changes in many aspects biology of the fishes that made this transition. Specifically I address the question—how might these changes have affected the population biology of the freshwater gobioids? We can look for patterns that either:

- 1) unite the freshwater gobioids in some way: that is, a suite of life history patterns that are characteristic of all the freshwater forms, or;
- 2) separate them in some way from the bulk of the gobioid species that live their entire lives in the sea.

The first question that needs an answer is what subset of the gobioid fishes are we dealing with, and in what regions and habitats has this transition taken place? Of the 2000 or so gobioid species, 100 or more have moved into freshwater (McDowall 1988). What sorts of species have done this? In an earlier paper I pointed out that the eleotridids are the dominant gobioids in freshwaters of the southern hemisphere, while freshwater systems in the northern hemisphere are characterized by gobiids, and freshwaters in the tropics are characterized by gobies in the subfamily Sicydiinae (Kinzie 1991). This could perhaps be a biased view because the sicydiines are typically the dominant freshwater gobioids in island streams and many of these island groups are spread out across the tropics (Parenti & Maciolek 1993). Thus, part of the pattern might simply reflect the availability of islands with suitable streams as much as the biogeography of the fish themselves.

In the patterns that I address in this paper, I look for consistencies or inconsistencies in the biology of the freshwater gobioids when they are compared with marine forms. In accordance with the choices outlined in the preceding paragraph we might find that:

- 1) The move to freshwater, while it may have been made many times from disparate stocks within the gobioid fishes, has led through subsequent evolutionary events to convergence on a fairly distinct "freshwater profile".
- 2) The ancestors of the forms that moved to freshwater may have already shared a set of characteristics that promoted success in the new habitat. These characteristics may have been shared for phylogenetic reasons (i.e. the groups were related); for ecological reasons (the forms occurred in similar habitats in the sea); or both. If this second scenario is true, the forms that gave rise to the freshwater gobioids would probably not represent a typical cross section of all the forms available.
- 3) Finally, there may be no clear pattern.

Where might we look for such patterns? Any aspect of the biology of these fishes might contain examples that could be used in searching for such similarities, e.g. trophic status, habitat use, morphology or behavior. Several papers in the symposium and in this issue address these topics. The particular topic I address here is that of reproductive biology and life history patterns. Specifically, I will address the features of the life history of the freshwater gobioids termed "tokeology" by Miller (1984).

Basic Reproductive Biology of Freshwater Gobies

NESTING

The first point I wish to make is that there are, in fact, few reports on the reproductive biology of freshwater gobioids, especially in natural situations. Thus, any conclusions drawn here are certainly subject to revision as more species are studied. Nevertheless, the species that have been studied come from a wide and fairly representative set of the habitats used by these fishes which makes the similarities to be outlined below more striking (for examples see Dotu & Mito 1955, Mizuno, 1960, Lugli et al. 1992, Daoulas et al. 1993, Auty 1978, McDowall 1965, Hidaka & Takahashi 1987, Foster & Fuiman 1987, Kim & Han 1989, Kinzie 1993, Fitzsimons et al. 1993).

These studies show that, in essentially all the freshwater gobioids that have been studied, eggs are laid demersally, often on the underside of objects, but sometimes on or in vegetation. Females typically leave or are driven away from the nests immediately after spawning, and it is the males that carry out all egg tending and nest guarding activities. This breeding scheme should be very familiar to students of marine gobies where this pattern is also typical (for example see Thresher 1984, Gibson 1970, Cole 1981, Lindström & Wennström 1994). Thus, my first point is that this "standard" gobioid mating habit seems to have transferred to freshwater with little change.

MATING SYSTEMS

Here the lack of information is an even greater problem. Nevertheless, for the few non-sicydiine species for which we have data on mating systems, the pattern appears to be polygyny with males procuring and guarding nests comprised of batches of eggs from more than one female (Lugli et al. 1992, Daoulas et al. 1993). The freshwater cottids that have been studied also exhibit simultaneous polygyny as will be discussed below. The apparent monogamous system of *Chaenogobius isaza* may be a result of constraints imposed by water temperature and interspecific competition, rather than an intrinsic feature of the reproductive biology of this species (Hidaka & Takahashi 1987). Polygyny is also typical of many marine gobioids. There is even less information on mating systems of sicydiine gobies. In aquarium studies they do not appear to be polygynous (Kinzie 1993), but the artificial nature of such conditions makes field verification necessary to answer this question.

SEXUALITY

Again we are faced with a lack of appropriate observational information, but a tentative suggestion, based mostly on the lack of data to the contrary, is that in the sicydiines, and possibly other freshwater gobioids there is no hermaphroditism, no sex change and no alternative mating strategies. Against this is a note that *Stiphodon astilbos* may undergo sex reversal, but this was based only on observations of external morphology (Ryan 1986). Another report by Watson (1991) describes two morphologically distinct male phases of *Stenogobius caudimaculosus*, but he adds that this is the only instance of male dimorphism he observed. Given that sex change, hermaphroditism, alternative mating strategies etc., are so prominent among marine gobioids (Magnhagen 1994, Cole & Shapiro 1990) it seems that this feature is characteristic of gobioids and so would repay more intensive searching among the freshwater species.

Landlocking in Freshwater Gobies

The second point I wish to make here is that, in spite of the apparently conservative reproductive biology of the freshwater gobioids, some forms have undergone a major life history transformation—completion of the entire life cycle in freshwater—and even more strikingly, may have made this great ecological transition in an exceedingly short span of evolutionary time (Mizuno 1960).

Many freshwater gobioids, along with numerous species from many marine groups that have made the transition to freshwater, have made the shift while retaining a part of the life history in the marine realm. Diadromy is a very common life history feature in many species (McDowall 1988). Whereas the ultimate causes of this habitat shift are not known for certain (Gross 1987, Gross et al. 1988), there are three general sorts of patterns that are typical; anadromy, catadromy and, as found in most diadromous gobioids, amphidromy—the diadromous pattern where the move from one habitat to the other is not directly linked to a breeding migration (McDowall 1988, 1997). As species with marine ancestors, the diadromous gobioids display what is termed freshwater amphidromy, where the adults mature and breed in freshwater and where the newly hatched fry are carried to estuaries or the open ocean where they complete their larval life.

Landlocking might be viewed as the next step in this pattern of invasion of freshwaters, the condition where the requisite larval period in the ocean is eliminated and the entire life is spent in freshwater. The evolutionary pathway that has led to landlocking is not unique to gobioids, occurring in the ecologically very similar sculpins (Goto & Andoh 1990) and analogously in several salmonid clades. An interesting variation on this evolutionary trend is seen in those landlocked species where the migratory phase to and from the adult stream habitat is retained but the larval habitat is a lake rather than a marine situation (Takahashi 1988, Hidaka & Takahashi 1987).

Landlocking has apparently involved a major shift in the reproductive biology of the fishes. Reproductive effort shifts from the production of many small eggs that give rise to altricial hatchlings after a short incubation period to production of

a few large eggs that hatch into precocial young (Mizuno 1960, Kishi 1979, Katoh & Nishida 1994). Where the planktonic larval stages are retained as in limnetic species, egg size remains similar to that found in the amphidromous forms (Mizuno 1960). There is little information available on the mating systems or sexuality of landlocked gobioids (but see Hidaka & Takahashi 1987). This is another area that would provide many important insights.

Whereas we know little about what effects landlocking has had on the reproductive biology of these fishes, there is some very informative work by Japanese workers on the evolutionary biology involved. The *Rhynogobius* complex, which is found throughout the length of Japan, consists of numerous color morphs (Mizuno et al. 1982, 1979, Hayashi 1984, Masuda et al. 1989). These types were, for the most part, originally assigned to the species *R. brunnius*. Within the eight color types that occur in western Japan, Masuda et al. (1989), using electrophoretic methods, discerned four species in this complex, as well as four types which might, together, represent a fifth species. Perhaps even more impressive is the study of the genetics of four Okinawan *Rhinogobius* morphs by Katoh & Nishida (1994), who showed that the closest relative of one of the amphidromous Okinawan forms was the landlocked form. This species pair had a Nei's genetic similarity of more than 0.97. This result suggests that this major shift in life history pattern, from amphidromous to landlocked, which presumably entailed the shift in bestowal, has occurred either very abruptly or that it has occurred with very little alteration in other parts of the genome. Chen & Shao (1996) describe a similar situation in Taiwan where eight species are described in the *R. brunnius* complex, including an endemic landlocked species, *R. rubomaculatus*. The genus *Chaenogobius*, which also appears to be taxonomically complex, has landlocked representatives as well as fully marine and amphidromous species (Kikuchi & Sawara 1994, Aizawa et al. 1994). A very similar situation has been described by Goto for the cottids in Northern Japan, where speciation within the landlocked sister taxon of an amphidromous cottid appears to be occurring (Andoh & Goto 1988, Goto & Andoh 1990).

Landlocking of any sicydiine goby has not yet been reported. This could simply be due to lack of sufficient work, however, it may also be that such a transition is not likely to have long-term success in island situations, where sicydiines are most common. One reason might be that the permanent loss of the marine phase would commit a line to an island stream system—a fairly ephemeral habitat in evolutionary time. Another bit of evidence why landlocking may not occur in sicydiine species is discussed below.

Life History Trends in Amphidromous Gobioids

Thus far I have been emphasizing similarities in the life history features of the amphidromous gobioid fishes; the typical breeding system with more or less strongly expressed male territoriality at least during breeding, the demersal nesting habit and the egg tending behaviors. As noted above many of these habits and behaviors are commonly seen in marine gobioids as well. One striking difference

that has occurred in at least some of the amphidromous species is the very long life of the marine larvae. Larval life of most coral reef fishes, including the few gobies that have been studied averages about 40 days, slightly longer than one lunar month (Brothers et al. 1985, Victor 1986, but see Sponaugle & Cowen 1994 for an exception). The sicydiines studied by Bell et al. (1995) and Radtke & Kinzie (1996) have larval lives more than twice as long. The two non-sicydiine Hawaiian species that have been studied appear to have even longer larval lives (Radtke et al. 1988). Because we lack data for length of larval life for amphidromous gobioids from large island systems such as Japan, Taiwan, the Philippines, etc., or from continental streams, we cannot safely speculate whether this condition is related to the isolation of oceanic islands, or whether it is common to amphidromous gobioid fishes wherever they occur. This too would be a very fruitful area of study. The work by Bell and Radtke and their colleagues also suggests that the larval period, while long, may be rather strongly constrained, implying that the time spent in the plankton may be under some form of fairly stringent control.

One view of the life history of freshwater gobies might then be that there are two extremes expressed—the very long larval life of the amphidromous forms and the abbreviated precocial development of the landlocked forms. Whether there is a spectrum of intermediates or whether evolution has followed a bimodal path needs elucidation.

The Genus *Awaous* and Bestowal Patterns of Freshwater Gobies

The third point I wish to raise concerns the genus *Awaous*. This genus, which has just been revised by Watson (1992), presents several exceptions to the generalizations pointed out above, as well as other features that would well repay further study. *Awaous* is one of the largest gobies, reaching more than 30 cm in length (Ego 1956). Whereas some eleotridids approach such sizes, the gobies, both marine and freshwater are generally smaller. Secondly, while most of the freshwater gobies have either an Indo-Pacific or an East Pacific-Atlantic distribution (Akihito & Meguro 1979, Birdsong et al. 1988), *Awaous* is circumtropical. Further, as mentioned by Birdsong et al., wherever fishes in this genus occur, they appear to be remarkably similar in appearance. While the differences described by Watson (1992) clearly separate the species, the overall picture is one of general morphological homogeneity. The longest planktonic larval life reported for any gobioid, and for that matter almost any shallow, tropical, benthic fish, is over 150 days for *Awaous guamensis* from Hawai'i (Radtke et al. 1988). Thus we have a genus that differs from the pattern described above for amphidromous gobies in that very large fish with exceptionally long lived larvae occur in the tropics around the globe. Are there any features of the life history of this fish that might serve to tie these observations together?

A study of the reproductive biology of *Awaous guamensis* in Hawai'i (Ha & Kinzie 1996) suggests some possible lines of inquiry. Females of this species lay very large (up to 1,500,000 eggs) clutches of quite small eggs (dia. ~0.43mm) (Ego 1956). The fry that hatch from these eggs are in a very altricial stage (D.

Lindstrom Pers. Comm.). In Hawai'i, the species was believed to require downstream breeding migrations to spawning sites, commonly located at the first riffle upstream of the stream mouth, where aggregations of nesting individuals occurred (Ego 1956, Kido & Heacock 1992). The fact that fishermen often found many dead individuals of both sexes washing downstream from these spawning sites gave rise to the idea that all individuals died after spawning. (Ego 1956). Although more recent study has shown that post-spawning mortality is not universal (Ego 1956, Kido & Heacock 1992, Ha & Kinzie 1996), and that some individuals may breed in more upstream locations (D. Lindstrom Pers. Comm.), the general pattern of dense breeding aggregations at downstream sites with high mortality for the participants seems to be typical of this species in Hawai'i. This spawning pattern is in great need of verification in other places where *Awaous* occurs. It is worth noting that some Japanese amphidromous cottids apparently also have downstream migrations as part of their breeding biology (Goto 1987, 1988, 1989).

There has been extensive theoretical work on the tradeoffs between production of a few large eggs vs. many small ones (Winemiller & Rose 1993). Some disadvantages for small egg size, such as reduction in the size of the target for fertilization (Podolsky & Strathmann 1996), do not appear applicable for demersally spawning fishes such as the gobioids. While common sense would suggest that smaller larvae must spend longer in the planktonic stage and might recruit at smaller sizes, experimental work with invertebrates suggests that if this difference does exist, it is not great (Hart 1995). Modeling approaches to the egg size trade-off suggest that the advantage in fecundity resulting from production of the maximum number of the smallest possible eggs is lost when prey for the larvae are sparse or strongly clumped, but high fecundity is an advantage when food resources are abundant (Winemiller & Rose 1993). Application of these results to actual conditions is complicated by the fact that larval fish in different taxa appear to have distinct food preferences which are in turn influenced by the nature of the water mass (Rissik & Suthers 1996). The general consensus is that unless there is ample food, the smaller larvae resulting from small eggs will be poorer feeders in the plankton thus extending the time they must spend there and so increasing the chances of starvation or predation. However, other factors might also set a lower limit on egg size, such as the absolute amount of maternal hormone per offspring which might have important implications in subsequent developmental processes (Tagawa et al. 1990, Lam 1994).

A further divergence of *Awaous* from the gobioid norm is suggested by the observation that *Awaous guamensis* nests in Hawai'i are guarded by females and the possibly polygynous males oversee a larger area containing several nests, each one guarded by the female which laid the eggs therein (Ha & Kinzie 1996). It could be hypothesized that in this fish there has been a trend to maximization of the number of young produced. This would be achieved by the combination of large body size, high fecundity made possible because of the small maternal investment per individual egg and maximization of the proportion of females that can simultaneously breed. The costs incurred in this breeding mode, the small size of the individual fry, might be offset by moving the nesting site as close to the

ocean as possible to ensure that the fry arrive at the potentially more productive larval habitat (Gross et al. 1988) in as short a time as possible. The second cost, the long time required to reach settlement size, would then be reflected in the very long larval life of this fish. This scenario is, in most aspects, highly speculative, but like many of the other points raised in this paper, it indicates an array of useful research questions.

Evolution and Speciation in Freshwater Gobioid Fishes

The final topic I would like to suggest as an important avenue of future study is the nature of speciation in the freshwater gobioid fishes. Not only would this expand our understanding of what has occurred in the taxa that have made the move to freshwater, but it is also of general interest to the study of evolutionary biology. Do we see any patterns of speciation in the freshwater gobioids that might shed light on the mechanisms of evolution, particularly of invading species? Specifically what patterns of endemism do we see in these fishes?

In genera such as *Rhinogobius* and *Chaenogobius*, it appears that there is extensive and probably rapid speciation occurring within regions. Not only are there numerous, more or less distinct, morphological forms that show varying degrees of genetic relationship, but the life histories of species within these radiating complexes include both amphidromous and landlocked species. Within the landlocked forms some retain small egg size and have a planktonic larval stage in deep lakes, while others have switched to a reduced number of large eggs. Species in these groups also occur in brackish and fully marine habitats. These two genera occur in most drainages of East Asia and island groups including Japan, Taiwan, and the Philippines (Chen & Shao 1996).

The Sicydiinae present a different pattern. While sicydiine gobies occur in the same regions as the two genera discussed above, they do not appear to exhibit extensive within island radiations. Rather fishes in this subfamily have been described as showing "island-group endemism" (Parenti & Maciolek 1993). Island-group endemism refers to situations where species are endemic to particular islands or archipelagos, with different island groups harboring different, but related, species. There is usually no radiation within an island group. For example, Hawai'i the most isolated archipelago on earth, exhibits island endemism in the freshwater gobioids, with four of the five species occurring only there, but there is no evidence of any radiation. In fact each of the Hawaiian gobioids is in a separate genus which prompted the suggestion that the only successful invaders (the progenitors on the modern Hawaiian species) were those that were sufficiently different ecologically that they could establish themselves (Kinzie 1988). There may be within-island radiations in some non-sicydiine gobies. Watson (1991) suggests that the genus *Stenogobius* shows evidence of within-island group radiation in New Guinea—a large continental Island but also in the oceanic and isolated Marquesas.

How can we account for these differences? Most explanations relate in some way to the length of time that the larvae spend in the sea. Parenti & Maciolek (1993) suggested that the short larval life of the sicydiine gobies is correlated with

high island-group endemism. However, the existing information indicates that amphidromous gobioids have long, rather than short larval lives (Radtke et al. 1988, Bell et al. 1995, Radtke & Kinzie 1996). In fact, it may be the long larval lives of the island species that prevent within archipelago radiations (Fitzsimons et al. 1990). If this suggestion finds support as an explanation for the lack of radiation in the sicydiine species, it will still leave unanswered questions about the radiations in other groups. It has frequently been suggested that larval gobioids may not go far beyond the stream mouth, and that maturation takes place in estuarine regions and not off shore. If this is the case for some species, it could account for radiations in regions where river systems have estuarine systems that are large and productive enough for the larval forms to complete their entire life therein. If the length of larval life in these forms was reduced, either intrinsically, or because of the highly productive conditions, isolation to separate stream systems would be enhanced, and speciation might be promoted. What the situation is in the Marquesas, where Watson (1991) has described several endemic species in the genus *Stenogobius* is unclear. This is of particular interest since in Hawai'i the species in this genus has a very long larval life (Radtke et al. 1988).

Against these gobioid radiations, either within islands or between island systems, the monotypic nature of *Rhyacichthys aspro*, and the cosmopolitan nature of the genus *Awaous* stand in marked contrast. There is certainly enough here to keep evolutionary biologists engaged for years to come.

Summary

The 1996 goby symposium, and the papers collected in this issue, show how far we have come in our understanding of this complex, diverse and important group of fishes, as well as how much more there is to do. In subsequent papers in this issue, specific research results show how and where researchers are pursuing these goals. The purpose of this paper was to illustrate some avenues that might be particularly rewarding. These include:

- 1) What are the mating systems of freshwater gobioid fishes; landlocked and amphidromous, sicydiine and non-sicydiine?
- 2) Do any fresh water gobioids exhibit sex change, hermaphroditism or alternate mating systems, particularly of the form where male morphologies are dimorphic?
- 3) Is the long larval life reported for sicydiine species in Hawai'i and Dominica typical of sicydiine gobies no matter where they occur?
- 4) Do non-sicydiine amphidromous gobioids on oceanic islands typically have even longer larval lives?
- 5) What is the length of larval live of amphidromous gobioids on large islands (e.g. Japan, Taiwan) and on continents?
- 6) What is the evolutionary and biogeographical history of fishes in the genus *Awaous*?

- 7) Is the suggested life history put forward here for *Awaous* valid, and if so is this trend seen in any other amphidromous gobioids?
- 8) What has driven the different modes of speciation and endemism in the freshwater gobioid fishes?

Clearly this research program can carry us well into the next century, Diverse and speciose as the gobies are, the result will likely be, even more interesting questions—perhaps the best excuse for studying this fascinating group.

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