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Hawaiian Stream Fishes: the Role of Amphidromy in History, Ecology, and Conservation Biology

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Abstract

Amphidromy, a pattern of migrations between fresh water and the ocean, known among some fish groups and especially the gobioids, is universal to all Hawaiian stream fishes and also to some gastropod molluscs and decapod crustaceans. A clear understanding of this pattern of migrations is profoundly important to diverse aspects of the biogeography, ecology, and conservation of the Hawaiian fauna, as it is for the faunas of islands widely across the tropics, subtropics, and extending into the northern and southern cool temperate zones.

Introduction

The small Hawaiian freshwater fish fauna, with only 5 gobioid species, represents a far eastern, oceanic outpost of the fauna of the Indo-West Pacific (Springer, 1982; Nishimoto & Kuamoʻo, 1991, 1997; Fitzsimons & Nishimoto, 1995; Fitzsimons *et al.*, 2002). The fauna comprises four endemic species: *Lentipes concolor, Sicyopterus stimpsoni,* and *Stenogobius hawaiiensis* in the family Gobiidae and *Eleotris sandwicensis* in the related Eleotridae. In addition *Awaous guamensis* is a non-endemic Hawaiian gobiid that is found also in Guam in the Mariana Islands, New Caledonia, Vanuatu, and Fiji. All of these gobioid species are amphidromous (Ego, 1956; Tomihama, 1972; Maciolek, 1977; Radtke & Kinzie, 1991, 1996; Kinzie, 1993a, b; Ha & Kinzie, 1996). The stream fish fauna of Hawaiʻi resembles other aspects of the biota of Hawaiʻi in having an external dispersal origin (Wagner & Funk, 1995; Price & Wagner, 2004).

The nature and place of amphidromy

The presence of amphidromy in every one of these species is the core, fundamental driver of a whole series of biogeographical and ecological characteristics of the fauna, such that an understanding of amphidromy is crucial for understanding, managing, and conserving the fauna. Amphidromy is a specialised migratory behaviour that is widely present in the fish faunas of the islands of the globe, especially in the tropics and subtropics of the central and western Pacific, southeast Asia, and the Indian Ocean as far west as the Seychelles, Reunion, and the Comoro Islands (McDowall, 1988; Balon & Bruton, 1994). There are also amphidromous gobioids widely in the Caribbean islands and in Central America (Lyons & Schneider, 1990; Pringle, 1997; Fievet & Guennec, 1998). Amphidromous species are rarely found on continents.

Amphidromy involves reproduction in fresh water, an immediate migration of the newly hatched larvae to sea, a period of a few weeks to a few months feeding and growing at sea, and a return migration of small juveniles to fresh water—where subsequent feeding and growth to maturity take place, and so the life cycle is completed (Myers, 1949; McDowall, 1988, 1997a).

Implications of diadromy for Hawaiian streams

In the rest of this paper I outline the role of amphidromy in the historical biogeography, proximate ecology, and conservation biology of the fauna at a series of spatial and temporal scales.

***1) A dispersal fauna*:** Clearly, the presence of amphidromy in all members of the Hawaiian freshwater fish fauna reflects the role of life at sea in allowing freshwater fish to reach these remote and relatively youthful Hawaiian Islands in the first place (Polhemus, 1996; Kroenke, 1996; McDowall, 2003). Were there not amphidromous species elsewhere in the eastern/central Pacific (McDowall, 1988; Marquet & Laboute, 1992; Watson, 1992, 1995; Watson & Kottelat, 1994; Watson & Chen, 1998; Marquet *et al.*, 1996; Serét, 1997) it is possible that the Hawaiian Islands would have no freshwater fish at all. There is no hint that its fish fauna is derived from marine fishes in the seas around the islands (amphidromous gobioid species are not derivatives from local marine taxa across their range – McDowall, 1997b). And since five different genera, each known widely across the Indo-West Pacific, are represented in the fauna, there has plainly been rare, but repeated, dispersal of invading propagules, logically from the west, where other, and routinely amphidromous, species in all of these genera are to be found. The wider distribution of the only nonendemic Hawaiian freshwater fish, *A. guamensis* (Watson, 1992), implies that such eastward dispersions may still be going on, and there is no reason to think that it is not.

2) The absence of local island endemics: There are no local-island endemics in the Hawaiian freshwater fish fauna [unlike the widespread presence of local-island endemics on various Hawaiian islands in other biotic groups (Wagner & Funk, 1995)]; all five species are widespread across the Hawaiian archipelago, and this implies that either the range of each of the five species is relatively young in Hawai‘i or, more likely, that there is continued dispersion by the five species across the archipelago. It seems likely that the amphidromous freshwater fish species are naturally spreading from older islands to younger islands, as the latter emerge, become ecologically stable, and acquire freshwater biotas [as is true of other biotic groups (Wagner & Funk, 1995)].

3) A lack of genetic structuring: Studies of genetic diversification using DNA sequencing show that there has been no local island diversification or structuring among the various Hawaiian Island populations of any of these gobioids, and this is consistent with the view that there is continuing dispersion of these gobies across the islands (Zink, 1991; Zink *et al.*, 1996; Fitzsimons *et al.*, 1990; Chubb *et al.*, 1998).

4) Recruitment into island stream fish populations: The fact that larvae of Hawaii’s amphidromous gobioids spend part of their lives in the sea means that Hawaiian streams are continually subject to invasion of propagules from the sea (Ego, 1956). As a result, invasive juveniles are the mechanism for recruitment of new cohorts into the populations. An outcome of this is that ecological processes that take place at sea, beyond the streams of Hawai‘i, affect recruitment processes. Amphidromy is therefore of crucial importance in determining the basic age structure and recruitment dynamics of freshwater fish populations in the islands’ streams.

5) The role of marine ecological processes: Marine processes in the ecology and behaviour of these amphidromous species may be of crucial importance for recruitment success and population recovery of the faunas of steep islands—where there is a high likelihood of ‘flash’ floods sweeping newly hatched larvae out of the streams, and to sea.

6) Recruitment dynamics: Population structure and community dynamics are, to some extent, controlled by the processes of juvenile invasion into Hawaiian streams from the sea. Because all fish populations are governed by the continual immigration of juvenile gobioids, the fish communities present in Hawaiian streams result from differences among the species in their patterns and processes of invasion.

7) Differing patterns of invasion: It can be predicted that for some species, which invade only short distances up stream, all of the community ecological processes take place in the lower reaches of streams and make them vulnerable to anthropogenic impacts *(S. hawaiiensis and E. sandwicensis*). For longer-distance migrators, it will be primarily the juveniles that are found in the lower reaches of streams and will be affected by such impacts.

8) Changing species richness: Because of differences in the distances that the various species penetrate upstream, there will be a downstream-upstream shift in species richness driven by invasion processes and dynamics.

9) Changing species composition: Parallel to that shift in species richness will be a change in species composition, in a downstream-upstream direction in streams, as one species after another drops out of the communities (McDowall, 1998) (This statement is applicable to the extent that young fish migrating upstream from the ocean and through the lower reaches of the streams, are counted along with resident adults).

10) Changing age and size structure of the populations: It is predictable that there will tend to be a shift in the age structure of the populations, with fewer small juveniles being found in the inland/upstream habitats (McDowall, 1988, 1990).

11) Changing trophic structures**:** Some Hawaiian gobioids are herbivorous and feed on periphyton taken from the substrate (Tomihama, 1972; Kido, 1996a, b; Fitzsimons *et al.*, 2003). There seems to be a downstream-upstream shift among species from carnivory to herbivory, probably parallel to a downstream-upstream increase in size/age that is associated with the duration of immigration. It is interesting that the species that penetrate least distances inland tend to be the predators (Fitzsimons & Nishimoto, 1995), and it is predictable that their prey may at times include the immigrating juveniles of other gobioids.

12) Climbing falls and finding food on the way: Some Hawaiian gobies are astonishing climbers of falls, with *Lentipes concolor* being a superb climber (Fitzsimons & Nishimoto, 1995; Englund & Filbert, 1997). It would be interesting to know whether this species is able to climb these heights, in part, as a result of its herbivory. This might give it an ability to feed and restore muscle energy by consuming algae (diatoms are algae) on the surfaces of the falls as it climbs. This would, in turn, mean that there is less urgency in getting to the tops of falls, compared with the energy constraints on climbing by carnivorous species for which food may be less easily available.

13) High risk island habitats**:** Freshwater habitats on small islands are likely to be ephemeral owing to the small size of stream catchments and because rainfall can be unreliable, especially on the leeward sides of islands. Moreover, some of the Hawaiian Islands are still active volcanoes. These various factors are likely to result in possibly repeated local extirpation of stream faunas, including their freshwater fishes.

14) Amphidromy and demography: Clearly, amphidromous migrations confer both risks and advantages on the populations, and these are presumably reflected in life history strategies. Amphidromous species run risks of dispersion and expatriation while at sea and, with that, difficulties in returning to freshwater habitats. These may be compensated for by small eggs, high fecundity, and the trophic advantages of life in the oceanic plankton where small food organisms may abound. Comparisons across the five Hawaiian species of fecundity, egg size, distribution, and duration of life at sea, and age and size at return to freshwater, would be of interest in clarifying demography.

15) Amphidromy and faunal restoration: Amphidromy provides a mechanism that facilitates the repopulation of streams that are affected by perturbations such as unreliable rainfall, or when streams are recovering their biotas after the impacts of active volcanism, or as new streams form once volcanic activity has settled down.

16) Amphidromy and the implications of habitat perturbation: Anthropogenic perturbation of the flows and biotas of Hawaiian streams is likely to have widespread impacts on fish communities, e.g.:

i) if stream mouths are blocked, as a result of flow fluctuations and water abstraction, entry into streams by juveniles from the sea will be prevented and effects on stream fish species profound;

ii) if stream reaches further inland are dewatered by water abstraction, even though entry to streams may still be possible, the immigrating larvae will be hindered in reaching suitable habitats further upstream, especially for those species that migrate long distances upstream. In addition to obstructing their upstream movement, hindrances to migration will make them more vulnerable to predation;

iii) if there are point-source polluting discharges into streams, a number of effects may ensue, including prevention of migration upstream past the discharge points and mortalities for resident fish populations downstream from the discharge point;

iv) and introduced species will rapidly discover the concentrated upstream migrations of juvenile gobioids as a rich source of food.

A broader perspective

What is discussed above for the freshwater fish fauna of Hawai'i needs to be seen in a broader context. Amphidromous gobies are important components of fish faunas of islands across the Indo-West Pacific, as well as widely in the Caribbean. Very similar issues to those in the Hawaiian fauna apply also to our understanding of the ecology and conservation of fish faunas broadly across the tropics and subtropics, where amphidromous gobies are widespread, although in few countries is the fauna so dominated by this group.

Conclusions: an overview of the role of amphidromy

Amphidromous migrations need to be seen as crucial elements in the ecology of Hawaiian streams:

- in facilitating overall distribution to and colonisation of the islands;
- of dispersal among the islands;
- in maintaining the species' community balance in the fish faunas;
- contributing to the nature (lack of) genetic structuring across the islands;
- juvenile recruitment into populations;
- the establishment of community structure;
- for restoration of fish communities following perturbation.

Thus amphidromy is of fundamental importance to the history and ecology of all indigenous freshwater fishes in Hawaiian streams, at a wide range of temporal and spatial scales, and should be viewed as a giant homeostatic mechanism that facilitates long term equilibrium in a fauna subject to the effects of geographical isolation and natural and anthropogenic perturbation (Fitzsimons & Nishimoto, 1995). The managers of Hawaiian waterways and those responsible for the conservation of their biotas need to be cognisant of:

— the patterns of fish migrations into streams from the sea;

— the importance of these migrations for maintaining the fish communities;

— the potential for diverse impacts both within and beyond the islands' streams to disrupt these communities.

I have focussed here only on fishes. There are decapod crustaceans and gastropod molluscs that are also amphidromous in the streams of Hawai'i and again more widely across the Indo-West Pacific (Ford & Kinzie, 1982; Schneider & Frost, 1986; Kano & Kase, 2003), and similar principles apply to how their ecologies can be affected by stream management practices. It is easy enough to imagine shrimps migrating into streams from the sea (Fievet *et al.*, 2001); migrating gastropod molluscs need a bit more imagination, but they, too, do migrate upstream into Hawaiian fresh waters from the sea.

Finally, what is described above for Hawaiian Islands applies equally to the freshwater biotas of islands throughout the tropics and subtropics, extending north to Japan and south to New Zealand, where there are similarly amphidromous fishes, decapod crustaceans, and gastropod molluscs. Across this broader spatial range the stream faunas are generally rather more diverse, and include other fish groups with alternative life history strategies.

Thus what is important for the conservation and management of the entire freshwater fauna of Hawaiian streams is almost equally important for island streams across a wide span of the globe.

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