

The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis

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Abstract

Diadromy is a term used to describe migrations of fishes between fresh waters and the sea; these migrations are regular, physiologically mediated movements which occur at predictable life history phases in each diadromous species, they involve most members of a species' populations, and they are usually obligatory. Around 250 fish species are regarded as diadromous. A review of the life history strategies amongst families of fishes that include diadromous species provides little support for a suggested scenario for their evolution that involves: (1) evolution of anadromy via amphidromy from fishes of marine origins, and (2) evolution of catadromy through amphidromy from fishes of freshwater origins, even though these scenarios seem intuitively reasonable. The various forms of diadromy appear to have had multiple independent origins amongst diverse fish groups. There is increasing confidence that behavioural characteristics of animals are heuristic in generating and interpreting phylogenies. However, examination of fishes shows wide variability of diadromous life histories within closely related families and genera, within species, and there is even ontogenetic variation in patterns of behaviour by individual fish. In addition, there is multiple loss of diadromy in many diadromous fish species in which the life history becomes restricted to fresh waters. This variation suggests that diadromy is a behavioural character of dubious worth in determining phylogenetic relationships. Moreover, it appears to have been an ancestral condition in some fish

families, such as Anguillidae, Salmonidae, Galaxiidae, Osmeridae, and others, and perhaps in the whole salmonoid/osmeroid/galaxioid complex of families. This, too, makes diadromy of dubious worth in phylogenetic analysis.

Introduction

Biologists are increasingly using behavioural characters to help in understanding the evolutionary history of life. With the rapidly growing application of cladistic techniques – for determining monophyletic groups of species and understanding their relationships (Hennig, 1966; Wiley, 1981) – has come greater emphasis on the utility of behavioural attributes. McLennan *et al.* (1988) pointed out that Tinbergen (1959, 1964) had long ago asserted that behavioural characters were no different from morphological characters in their heuristic value in determining phylogenetic relationships, though there are persistent concerns that they may be more labile, more prone to homoplasy (convergence or parallel evolution) and even reversal, more troublesome in determining homologies, and more difficult to quantify than morphological characters. However, Dobson (1985), McLennan *et al.* (1988), de Queiroz and Wimberger (1993) and McLennan (1994) all had little doubt that behavioural characters could be subjected to rigorous phylogenetic analysis. de Queiroz and Wimberger (1993) found “no justification for discriminating against behavioural characters as indicators of phylogenetic relationship”, and considered that arguments for “evolutionary lability of behaviour [were] based on unsubstantiated empirical claims and/or questionable theoretical justification”. Paterson *et al.* (1995) mapped behavioural characters onto a phylogeny of several families of sea birds and concluded that they “contained as much phylogenetic signal as DNA sequences and isozyme data”. They thought that “behavioural characters should be used when available”. McLennan (1994), in particular, has championed the use of behavioural characters in reconstructing fish phylogenies, stressing that “the advent of a rigorous method for determining genealogical relationships (Hennig, 1966) has nudged behavioural research onto the ascending scale of the cycle” of fluctuating interest in phylogenetic approaches to the evolution of animal behaviour.

On the other hand, information on phylogenetic relationships is crucial to rigorous interpretation of the adaptive significance of differing character states, including behaviour. Again, McLennan (1991) has emphasized this, arguing that “it is impossible to establish a character transformation sequence independent of the phylogenetic relationships of the organisms displaying the characters”. Studies of behaviour and phylogeny thus have interacting, mutual benefits although there is a real danger of circularity.

Behavioural characters ought to be capable of phylogenetic analysis insofar as they result from evolutionary/selective processes and have a genetic rather than phenotypic basis, and as long as they comply with the constraints that apply to morphological characters in phylogenetic analysis (see Wiley, 1981 and Mayden and Wiley, 1992 for a general discussion of the principles of phylogenetic analysis). The constraints are that:

- Relationships need to be interpreted in terms of primitive (plesiomorphic) and derived (apomorphic) characters;
- Switching between alternative character states and reversal of evolutionary events should be regarded as unlikely;

- Outgroup analysis should be used to determine polarities of primitive/advanced character states;
- Character should be consistent within a clade/species, without significant variation among its members;
- Characters compared between clades regarded as similar should be similar because of common ancestry rather than owing to homoplasy.

McLennan *et al.* (1988) showed that behavioural characters could be used to produce a rigorous phylogeny of the sticklebacks (Gasterosteidae). It is interesting that sticklebacks were chosen for these analyses, because this family is amongst the most intensively studied of all fishes – behaviourally, morphologically and taxonomically. Some of Tinbergen's (1953) foundation behavioural studies were on sticklebacks, and literature on diverse aspects of the biology of this small group of fishes is extensive (Wootton, 1976, 1984). They are a prime example of what can be achieved using behaviour in phylogenetic studies, but also are atypical owing to the vast amount of work that has been done in comparison with other fish families. However, there are other intensively studied groups, such as the Salmonidae. What has been achieved needs to be seen as a model to aspire to, rather than a standard to be set, for other groups.

Diadromy: a distinctive behavioural character

One behavioural character complex amongst fishes is diadromy: a term introduced by Myers (1949) to describe distinctive migrations of aquatic organisms between fresh water and the sea. Most diadromous species are fishes (McDowall, 1988), although there are also diadromous molluscs and crustaceans (Williams and Smith, 1979; Resh *et al.*, 1990; Schneider and Lyons, 1993).

Little is recorded about the likely evolutionary pathways leading to the existence of diadromy in diverse families of fishes, and some understanding of this subject, including the evolutionary relationships (if any) between different forms of diadromy, is fundamental to the use of diadromy as a character in phylogenetic analysis. Gross (1987) examined this topic and hypothesized that diadromy, in its various forms, has dual origins/pathways of derivation. That paper has been widely cited (Kinzie, 1991; Radtke and Kinzie, 1991; Northcote, 1992; Svenning *et al.*, 1992) and the ideas, while intuitively logical, seem to be largely without empirical or analytical foundation and have been subjected to no subsequent testing or evaluation. Others have applied Gross's scenario in studies of the evolution and interrelationships of fishes, primarily though not exclusively salmonids (Stearley, 1992; McLennan, 1994).

Stearley (1992) drew from Gross's (1987) scenario for the evolution of the different forms of diadromy in salmonids using, amongst characters that establish salmonid relationships, different forms of diadromy that he considered to be represented in the family. McLennan (1994), in turn, drew from Stearley's (1992) analysis of salmonid phylogeny in exploring the value of behavioural characters for reconstructing phylogenetic relationships. As the edifice sustained by Gross's (1987) analysis grows larger and increasingly remote from his discussion, the frailties of his analysis become obscured, and the assurance with which dependent proposals are presented becomes

stronger – perhaps with little justification. So much hinges on Gross's (1987) scenario that its validity becomes more profoundly important.

In this discussion paper, I initially return to Gross's (1987) analysis of the evolution of diadromy, and reconsider the processes that Gross viewed as fundamental to it.

- I examine whether the theory/scenario presented by Gross (1987) is coherent; and
- I examine whether it has any empirical or interpretative support from amongst diadromous fishes and their close relatives.
- Having done that, I explore the implications of my conclusions for the discussions of Stearley (1992) and McLennan (1994).

In doing so, in terms of the constraints on using diadromy (a behavioural character) in phylogenetic analysis, a number of points must be recognized. Diadromy in each of its forms (see below) has clearly evolved multiple times within fishes (as well as in crustaceans and molluscs). There is thus clear multiple homoplasy in diadromy amongst fishes. And, although patterns of behaviour in diverse groups may be similar, without careful analysis of phylogenetic relationships based on other characters, homology of behaviour cannot be assumed.

What is diadromy?

Myers (1949) coined the term **diadromy** to describe true migrations between fresh water and the sea. Essential, defining features of diadromous migrations are that:

- They are regular, physiologically mediated movements between the two biomes;
- They occur at predictable times and at characteristic life history phases in each species;
- They involve a majority of the members of a species' populations and are usually obligatory;
- Because they are part of a species' cycle, they necessarily involve two reciprocal migrations, one from fresh water to the sea, and the other in the opposite direction.

According to Myers (1949), diadromy comes in three subcategories; with growing understanding of the phenomenon, problems have arisen in Myers' original definitions, resulting in the following (adapted from McDowall, 1997) (Fig. 1).

- **Anadromy:** Diadromous fishes in which most feeding and growth are at sea prior to migration of fully grown, adult fish into fresh water to reproduce; either there is no subsequent feeding in fresh water, or any feeding is accompanied by little somatic growth; the principal feeding and growing biome (the sea) differs from the reproductive biome (fresh water).
- **Catadromy:** Diadromous fishes in which most feeding and growth are in fresh water prior to migration of fully grown, adult fish to sea to reproduce; there is either no subsequent feeding at sea, or any feeding is accompanied by little somatic growth; the principal feeding and growing biome (fresh water) differs from the reproductive biome (the sea).

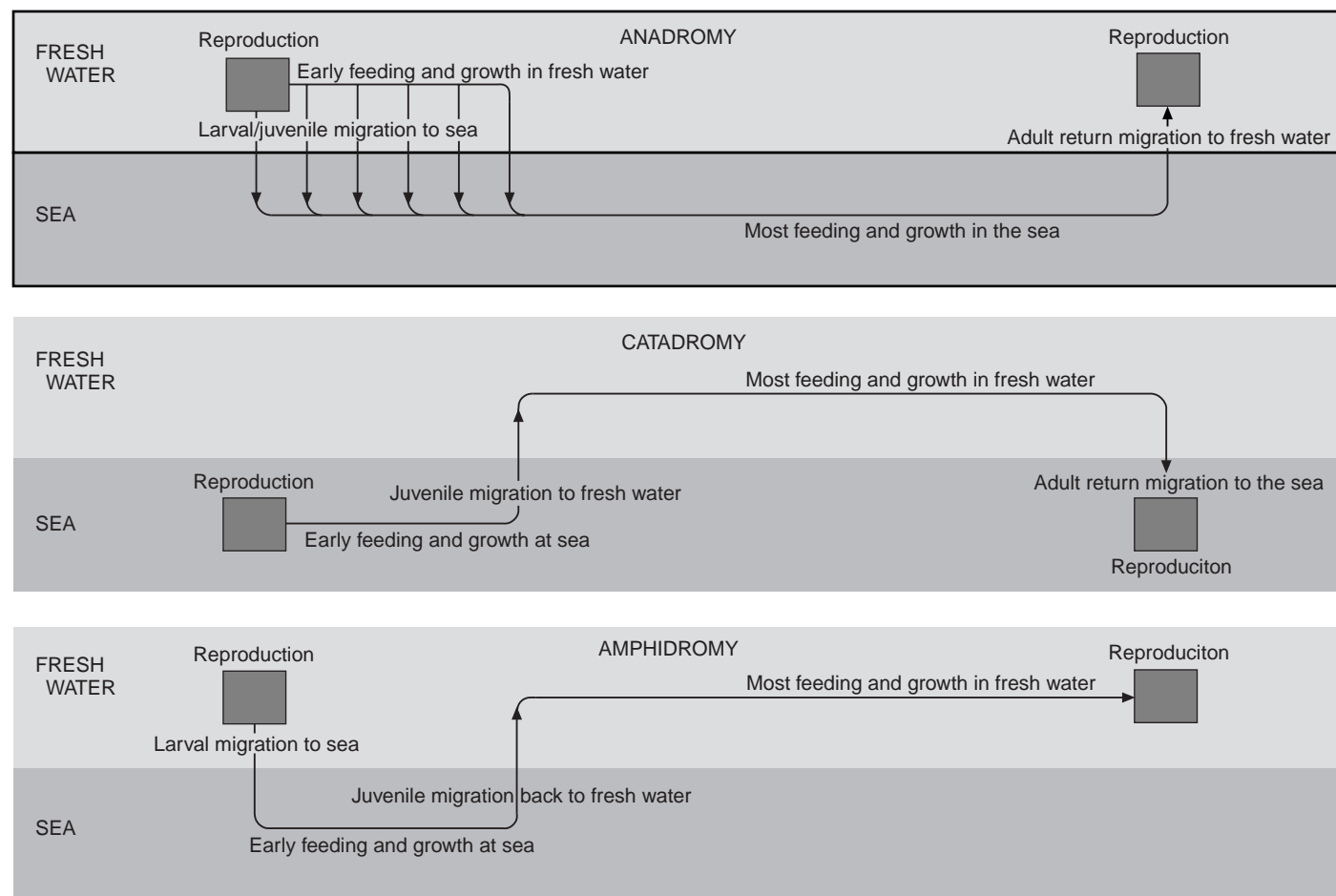


Fig. 1. Migration patterns between fresh waters and the sea in the three different types of diadromy.

- **Amphidromy:** Diadromous fishes in which there is migration of larval fish to sea soon after hatching, followed by early feeding and growth at sea, and then a migration of small postlarval to juvenile fish from the sea back into fresh water; there is further, prolonged feeding in fresh water during which most somatic growth from juvenile to adult stages occurs, as well as sexual maturation and reproduction; the principal feeding biome is the same as the reproductive biome (fresh water).

Both anadromy and catadromy have long had wide acceptance in ichthyology and fisheries biology (McDowall, 1988), although their usage has not always been consistent with Myers's (1949) definitions. Amphidromy has been more controversial, being well accepted in lands where amphidromous species are common (Japan, Hawaii, Australia, New Zealand), but less recognized elsewhere (McDowall, 1997).

Diadromy was listed as occurring in 227 species of fish (McDowall, 1988), in addition to which there is an undocumented number of crustaceans (atyid and palaemonid shrimps – families Atyidae and Palaemonidae) and gastropod molluscs (family Neritidae) (Williams and Smith, 1979; Resh *et al.*, 1990; Schneider and Lyons, 1993; Hughes *et al.*, 1995; Kakimoto and Hayashi, 1995). Amongst the listed fish species, about 110 are anadromous (48%), 56 catadromous (25%) and 61 amphidromous (27%) (McDowall, 1988). Myers (1949) speculated that the number of amphidromous species recognized was then probably an underestimate, and this prediction has proved correct. Although a considerable number of species has, since 1949, been added to the list, the number of amphidromous species recognized is still probably an underestimate. This is partly because there is a perception that amphidromy is a life history strategy not distinct from anadromy or catadromy (Balon and Bruton, 1994; McDowall, 1997) and partly because the life histories of amphidromous species are often poorly elucidated. This latter is true because many putative amphidromous species are found on remote tropical islands and are little studied. In total, the number of diadromous species is likely to reach around 250.

One question that Gross (1987) raised was whether diadromous fishes are a “real (biological) category, or an artificial category based on perceived needs to group and pigeonhole fishes”. He compared demographic characteristics of confamilial diadromous and non-diadromous species, and found no significant or consistent differences. However, more detailed analysis may have produced a different result, especially if attention had been given to comparing diadromous/non-diadromous species pairs on carefully structured phylogenetic basis. I do not accept Gross's (1987) footnote comment that “Comparing species within the same families largely controls for complications of phylogeny”, because within-family, between-species variation in characters such as egg diameter, age at maturity, maximum size and fecundity may be greater than within-species variation between diadromous and non-diadromous stocks of that species, or between diadromous and non-diadromous sister species. Size at maturity, egg size, fecundity and spawning season differ between diadromous/non-diadromous pairs of populations, or between closely related species (McDowall, 1988, 1990). It is emerging also that there is more variation within some diadromous salmonid populations than has hitherto been evident, e.g. as shown by Quinn *et al.* (1995) in a study of egg size variation in Alaskan sockeye salmon, *Oncorhynchus nerka*. Furthermore, Gross (1987) made comparisons between species only in single characters, but because characters such as size at maturity, egg size and fecundity

covary (e.g. larger individuals usually have more and sometimes larger eggs), comparisons are valid only when they take into account such covariation. Quinn *et al.* (1995) argued for trade-offs between different aspects of fecundity and egg size in anadromous sockeye salmon, and this might suggest that a search for simple differences between anadromous and non-anadromous fishes would be unsuccessful, unless other influences are considered at the same time.

Gross (1987) concluded, perhaps not surprisingly, that diadromous fishes are a “group of species [that] have been artificially (versus biologically) classified based largely on their habit of migrating between the sea and fresh water . . . classification of fishes as being either diadromous or nondiadromous is thus based on convenience rather than on biology”. To the extent that this is true, ‘diadromous fishes’ as a category are no different from ‘carnivorous fishes’, ‘semelparous fishes’, ‘pelagic fishes’ or any number of other ‘groupings’ or guilds of fishes based on ecological, behavioural or other criteria (Balon, 1975, 1981; Arthington, 1992). They are species grouped by a comparable (and not necessarily homologous) characteristic that does not necessarily (and almost certainly does not), have a common ancestry across all diadromous species. However, diadromy may have a common ancestry within some large groups in which diadromy is a common phenomenon, as in the salmonoid/osmeroid/galaxioid fishes, perhaps also in the lampreys, the sturgeons, and the sicydiine gobies (McDowall, 1993; Johnson and Patterson, 1996).

Gross (1987) developed an ecological/evolutionary model based on the evolutionary principle (which can probably be regarded as a truism) that diadromy would evolve if this provided selective advantages, i.e. that if diadromy results in a parent leaving more progeny than non-diadromy, then diadromy would be selectively favoured. He factored characteristics such as growth rates, survival, fecundity and the costs of migration into his model. There is nothing controversial about this, either in the modelling approach or the result. He presented his conceptual overview of the evolution of anadromy and catadromy and their relationship to amphidromy (Fig. 2). He viewed all forms of diadromy evolving in species from their initial development of “occasional excursions to feed” in the biome not their major habitat, i.e. facultative wandering of freshwater fishes into the sea, and of marine fishes into fresh water. This seems logical – that the development of ability to osmoregulate in a different-salinity environment will be beneficial in preceding development of regular migrations between the sea and fresh water. In practice, although there are many primarily marine species in diverse families that wander into the lower reaches of rivers to feed or for other purposes, there seem to be few freshwater species that facultatively wander into the sea.

The ability to osmoregulate across a broad spectrum of salinities intuitively seems a likely prerequisite for the evolution of diadromy, and it is often assumed that diadromous fish are euryhaline. However, it is appropriate here to note the distinction drawn by Fontaine (1975) between *euryhaline* species, which can freely move between different salinities, and *amphihaline* species, which can do so only at certain growth stages. Some diadromous species are highly restricted in the timing of their migrations if they are to avoid osmoregulatory-induced mortalities. Their ability to move across salinity gradients results from carefully timed and physiologically mediated changes, such as at smolting in some salmon species. This restriction on movement may have evolved after diadromy developed and could be a mechanism for ensuring that the timing of movement optimizes migrant survival and growth. We

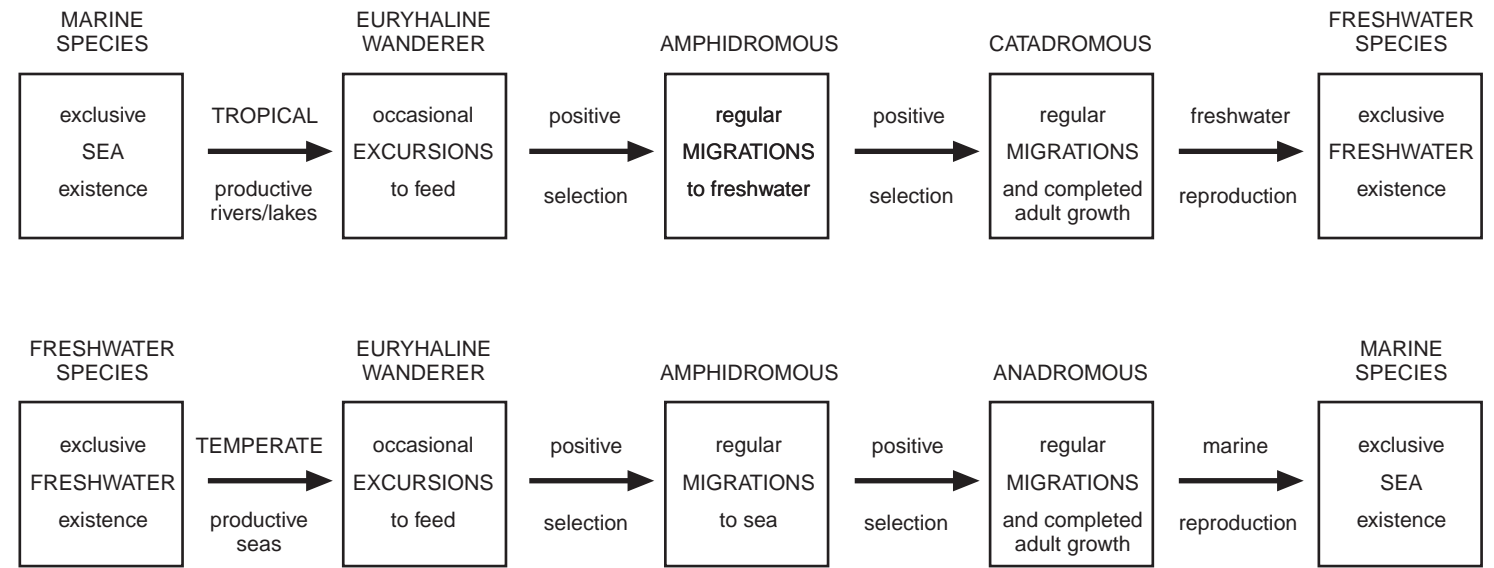


Fig. 2. Patterns of evolution of the different forms of diadromy as hypothesized by Gross (1987) (redrawn from Gross, 1987).

cannot determine whether this is so, and must be content to recognize that not all diadromous fishes are euryhaline, if this means freedom to move at any time between varying salinities.

Gross considered the logical extension of facultative wandering to be the development of amphidromy, i.e. regularizing of facultative wandering into a more clearly defined habit that became regular in time, life stage, and direction. This offers no obvious conceptual problems. However, he further envisaged amphidromy to be the intermediate stage in the evolution of both anadromy and catadromy, with anadromy evolving from freshwater-spawning amphidromous species and catadromy evolving from marine-spawning amphidromous species. These changes, again, are intuitively logical, involving lengthening of the larval–juvenile trophic stage to incorporate all growth and maturation in the non-breeding biome (fresh water in catadromous fishes and the sea in anadromous fishes). This avoids a shift of reproductive biome and thus conforms to a perception that the gametes of fishes are amongst the most sensitive to changes in salinity (Tchernavin, 1939; Foster, 1969). This sensitivity probably also extends through larval and early juvenile life (Tchernavin, 1939; Hoar, 1976). Thus, Gross's (1987) scenario treats reproduction as perhaps the last life stage/behaviour to shift from one biome to the other.

Examination of families that include more than a few diadromous species reveals few, clear, within-family examples of the adoption of different diadromous migratory strategies. With the dubious exception of some salmonids that Stearley (1992) classified as amphidromous (see below), all diadromous Salmonidae, Osmeridae (except *Plecoglossus*), Retropinnidae, Petromyzontidae (and other lampreys), Acipenseridae and Salangidae are anadromous. All diadromous Anguillidae and Mugilidae are catadromous. Diadromous Prototroctidae, Eleotridae and the sicydiine gobies (Gobiidae) are all amphidromous. There are exceptions, such as some catadromous gobies, not apparently closely related to sicydiine gobies, and Clupeidae which can be anadromous (most), catadromous (few) and amphidromous (occasional) although there is consistent behaviour within genera. One species of Galaxiidae, the inanga, *Galaxias maculatus*, is often listed as 'catadromous' while other diadromous galaxiids are amphidromous. However, this 'catadromous' species undertakes a downstream spawning migration only as far as river estuaries and it does not move to sea to spawn. Spawning in this species appears to be in fresh water, just upstream of the salt wedge that develops in river estuaries at high tide (Mitchell, 1994; Taylor, 1996). This species is therefore, at best, only "marginally catadromous" (McDowall, 1988). Gross (1987) cites Morrow (1980) as reporting that the pink salmon, *Oncorhynchus gorbuscha*, spawns in "saline estuaries", and Helle (1970) certainly reported this for a pink salmon population in a stream entering Prince William Sound, Alaska: 70% of the spawning in a population of around 120 000 salmon took place in the intertidal zone in one year and 30% in another. However, Morrow (1980) also stated that pink salmon "eggs and alevins are unable to adapt to salt water (salinity 31.8 parts per thousand)", though "they can withstand exposure to it for a day or more without serious harm". There are thus two apparent instances of at least partial, within-genera shifts of spawning biome and diadromous strategy: inanga, shifting from an amphidromous to a marginally catadromous pattern, and pink salmon, shifting from being anadromous to a pattern that is probably most aptly described as marginally anadromous or even non-diadromous because the shift in biome is almost eliminated. Most pertinent, however, is

that such within-genera shifts in subcategories of diadromy, or shifts in spawning biome amongst diadromous fishes, are rare, as are within-family shifts in many families.

The evolution of anadromy

Gross's (1987) hypothesis that anadromy should have evolved from freshwater species, through the intermediate stage of amphidromy, is not supported by examination of the behaviour and relationships of diadromous fishes. Firstly, there are few instances of freshwater species becoming facultative marine wanderers, so there is little support amongst existing fishes for the initial stage of Gross's hypothesized process on the evolutionary pathway to anadromy. Furthermore, there are both amphidromous and anadromous species of probable marine ancestry that reproduce in fresh water, and in which the persistent marine phase is the larval and early juvenile stages, e.g. the North American gadid tomcod, *Microgadus tomcod*, the New Zealand pinguipedid torrentfish, *Cheimarrichthys fosteri*, perhaps the engraulid *Anchoviella lepidentstole*, the sygnathid *Microphis brachyurus*, percichthyids such as the Australian bass *Macquaria novemaculeata* and the Japanese sea bass *Lateolabrax japonicus*. Further possible examples are all of the sicydiine gobies including genera such as *Sicyopterus*, *Sicydium* and *Sicyopus* (Parenti and Maciolek, 1993), but only if a marine ancestry of gobies is sustained. In a similar category are alosid and other clupeid shads, such as the North Atlantic species of *Alosa* and the Asiatic/Indian Ocean *Hilsa*. Extensive phylogenetic studies of diverse groups are needed to understand relationships properly and to clarify these issues. Some argue that salmonids and their relatives have a freshwater ancestry (Tchernavin, 1939; Hoar, 1976), and this implies that anadromy in salmonids is a secondary development in a group of freshwater origins. This view is taken by Gross (1987). However, Regan (1911) and Thorpe (1982) took a different view, that salmonids are marine fish that are establishing themselves in fresh water, which is contrary to Gross's (1987) scenario. There is probably no universal answer to this question. No doubt some anadromous fishes have marine origins and some freshwater origins. Whether any fishes have evolved through an amphidromous stage to anadromy is unclear.

The evolution of catadromy

Although there are numerous amphidromous species that spawn in fresh water, there are virtually no well-authenticated instances of the reverse series of migrations, i.e. species that spawn at sea, with migration into fresh water for larval and early juvenile life, followed by the return of well-grown juveniles to sea where they feed, grow, mature and spawn. Almost all amphidromous species spawn in fresh water. Thus there is virtually no empirical evidence that amphidromy is a precursor to the evolution of catadromy in formerly marine species. As far as I am aware, there is only one possibly amphidromous species that spawns in the sea and has larvae that then enter fresh water (the cottid *Leptocottus armatus*) (McDowall, 1988). Its amphidromy is uncertain, and this seems to be the only example of amphidromy of the sort that Gross (1987) hypothesizes as an intermediate step on the evolutionary path to catadromy.

The torrentfish is amphidromous and is the only member of its family ever found in fresh water – all of its relatives are marine fishes (family Pinguipedidae, widespread in the Atlantic and Pacific Oceans – Nelson, 1994). It is believed to spawn in fresh water

with its larvae moving to sea on hatching, where they live for several months before returning to rivers as juveniles about 20 mm long (McDowall, 1990, 1994). These grow and mature, probably over 1–2 years, before they spawn in fresh water. According to Gross's scenario, an amphidromous fish of marine ancestry moving into fresh water ought to return to the sea to spawn, but this is not what the torrentfish does. Thus in adopting a diadromous life cycle it has become amphidromous, by shifting from marine (as in other Pinguipedidae) to freshwater spawning.

The evolution of marine species of freshwater ancestry, via anadromy

Gross (1987) envisaged an end point in evolving migratory strategies involving anadromous species becoming entirely marine but there are very few marine fishes that seem likely to have had freshwater/anadromous origins. Three marine Osmeridae (McAllister, 1963; Scott and Crossman, 1973) may be presumed to have had an anadromous ancestry, although phylogenetic studies are needed to determine this. Some sticklebacks that have anadromous populations also have populations that are entirely marine (and entirely freshwater), so the distinctive feature of such fish is more their life history/habitat flexibility rather than their biome/migratory shifts.

The evolution of freshwater species of marine ancestry, via catadromy

Gross (1987) similarly envisaged evolving migratory strategies leading to catadromous species becoming wholly freshwater. Evidence from diadromous fishes and their relatives seems very slim. Grey mullets of the family Mugilidae are amongst the most flexible and variable of catadromous fishes, but all of them, whether catadromous, facultative marine wanderers, or entirely marine, spawn at sea. Freshwater eels of the family Anguillidae also are entirely marine spawners. Examples, therefore, of the scenario that Gross (1987) envisaged seem lacking.

Other patterns of evolution away from diadromous strategies

There are numerous examples of individuals within species, of species, or of closely related groups of species, diverging from a diadromous strategy, some of which are discussed below. The occurrence of such divergence varies greatly, often between closely related species – in some of which diadromy is obligatory while in others it is variably facultative. In almost every instance, these involve anadromous or amphidromous fishes becoming entirely freshwater-living. Divergence takes several forms.

Many anadromous salmonids are polytypic, including within their populations/genotypes some individuals that are non-migratory – although whether or not they are migratory may not be determined genetically. This is well exhibited in the Salmonidae; Rounsefell (1958) classified various North American salmonids as 'optionally', 'adaptively', or 'obligatorily' anadromous. There is a similar gradient from obligatory to facultative occurrence of diadromy in other families such as Osmeridae, Galaxiidae, Eleotridae. Northcote (1967) summarized that: "Temperate freshwater fish, particularly the salmonids, appear to have a high degree of plasticity in their migratory behaviour. It is not uncommon to find in a single species, even in a single population, a certain fraction which is non-migratory, along with the migratory component."

There is latitudinal shift in the prevalence of diadromy in some species; for instance, the brown trout, *Salmo trutta*, tends to be anadromous in cooler, boreal waters, but further south it tends to abandon anadromy and eventually becomes restricted to fresh water. Thorpe (1987) described how fish from a non-migratory population in Poland, 1600 km upstream from the sea, were transplanted to coastal streams, whereupon some individuals smolted and went to sea. Introduced into New Zealand, the species mirrors the variability observed in the native range, being increasingly anadromous in cooler (southern) locations (McDowall, 1990). Nordeng (1983) transplanted fluviatile Arctic charr *Salvelinus alpinus*, into cooler, northern localities in Scandinavia and found that they became anadromous. Kato (1991) reported that the range of anadromous masu salmon, *Oncorhynchus masou*, in Japan does not extend as far south as that of non-anadromous stocks. Sockeye salmon, *O. nerka*, exhibits both anadromous and non-anadromous (kokanee) migratory types in its native range. When anadromous sockeye were introduced to New Zealand in the early 1990s, the result was a non-migratory population (McDowall, 1990). The same happened with anadromous Atlantic salmon, *Salmo salar* (McDowall, 1990). Even chinook salmon, which Rounsefell (1958) classified as 'obligatorily anadromous', established lake-limited, non-anadromous populations (alongside anadromous populations) when introduced into New Zealand lakes (McDowall, 1990).

The New Zealand retropinnid common smelt, *Retropinna retropinna*, exhibits life history variation comparable with that of brown trout. Some populations are unequivocally anadromous – larvae go to sea on hatching and do not return to fresh water until fully mature adults, which spawn and die (McDowall, 1990). But in other populations the fish return to fresh water as juveniles, and remain there to feed and grow for several months before they mature, spawn and die. This life cycle is clearly amphidromous. Furthermore, diadromous and non-diadromous stocks of common smelt may co-occur in New Zealand low-elevation lakes with river outlets. Non-diadromous stocks result from 'capture' of progeny of spawnings within lakes. Sometimes this may be because lakes are temporarily open to sea, allowing occasional immigration by the spawning adults from the sea, followed by lake outlet closure which prevents the emigration of the progeny back to sea, as in Lake Ellesmere on the South Island of New Zealand. But often, there are no impediments to immigration or emigration and it appears that some larvae are retained in the lakes and voluntarily adopt a non-diadromous, entirely lake-dwelling life history strategy, as in lakes of the lower Waikato River on New Zealand's North Island (McDowall, 1979; Northcote and Ward, 1985). These examples represent the very great flexibility in life history strategy exhibited by diadromous fishes, flexibility that is represented in diverse fish families (discussed at length and in detail by McDowall, 1988).

Many anadromous and amphidromous fishes are known to abandon diadromy when the lakes in which they occur become landlocked, preventing migration to and from the sea (discussed at length by McDowall, 1988). Moreover, a long-term consequence of isolation by landlocking is the evolution of distinct daughter species. There are numerous instances in which non-migratory species are regarded as derivatives of diadromous species (Salmonidae, Osmeridae, Galaxiidae, Retropinnidae, Mordaciidae, Petromyzontidae, Acipenseridae, Eleotridae, Clupeidae – review, McDowall, 1988).

Thus, overall, the trend in both amphidromous and anadromous species appears to be for evolution/speciation towards entirely freshwater, rather than towards marine, non-diadromous stocks/species as Gross (1987) predicted.

Implications for the role of diadromy in the phylogeny of Salmonidae

Amongst an innovative analysis of phylogenetic relationships of salmonid fishes, Stearley (1992) included behavioural characteristics, including diadromy. There seem to me to be three issues relating to this study that need to be addressed in the context of the preceding discussion of Gross's (1987) scenario for the evolution of diadromy:

1. The use of amphidromy to describe the migrations of some salmonids;
2. The relation to this usage of Gross's scenarios of the evolution of diadromy; and
3. The relevance of the migratory behaviour of outgroups of the Salmonidae to migration within the family.

Stearley (1992) classified various diadromous salmonids as anadromous or amphidromous. His application of amphidromous to salmonids is novel, as all earlier workers have routinely described diadromous salmonids as anadromous (McDowall, 1988). Stearley's choice of amphidromous seems to relate to a misunderstanding of the nature of the phenomenon. Myers (1949) defined amphidromy as "Diadromous fishes whose migration from fresh water to the sea, or vice versa, is not for the purpose of breeding, but occurs regularly at some other definite stage of the life cycle".

Myers nominated "the goby genus *Sicydium* and its close allies" as the "prototype". To these, I long ago added several Galaxiidae as amphidromous (McDowall, 1968), to which have since been added members of diverse other groups, including the Japanese ayu *Plecoglossus altivelis*, Osmeridae, the southern graylings (*Prototroctes* spp. Retropinnidae) from Australia and New Zealand, various Cottidae and Eleotridae and, as Myers (1949) suggested, many more sicydiine gobies (McDowall, 1988). All of them conform to the regular pattern of emigration of newly hatched larvae to sea, return migration of small juveniles, and most growth, maturation and then reproduction occurring in fresh water. I have progressively amended the definition of amphidromy to try to increase clarity and improve understanding (McDowall, 1988, 1992, 1997), perhaps with limited success!

The habit, as in amphidromous species, of moving to sea immediately on hatching is found in few salmonids, notably in pink salmon (*O. gorbuscha* – Heard, 1991) but also many stocks of chum salmon (*O. keta* – Salo, 1991) and some stocks of chinook and sockeye salmon (*O. tshawytscha* and *O. nerka* – Healey, 1991; Burgner, 1991). However, most salmonids undertake weeks, months, or even years of juvenile feeding and growth before 'smolting' and migrating to sea, and this seems to include species such as cutthroat trout, *Oncorhynchus clarki*, and brook charr, *Salvelinus fontinalis*, that Stearley (1992) classed as amphidromous (early emigration is more routine in other anadromous families such as Osmeridae, Clupeidae, Retropinnidae). At the well-grown, juvenile life stage, these anadromous salmonid smolts are moving seawards. In contrast, the comparably small but well-grown juveniles of the species that Myers (1949) would have labelled amphidromous are returning from the sea to fresh water. The directions of juvenile migrations are thus opposite in anadromous and amphidromous species. And whereas salmonids undergo most of their feeding, growth and maturation at sea before returning to fresh water to spawn, amphidromous species do most of the feeding and growing in fresh water before they mature and spawn there. Thus, partitioning of the various life stages between freshwater and marine habitats is very different (almost

totally reversed) in anadromous and amphidromous species. In my view, amphidromy is therefore not “little more than a special case of anadromy in which the feeding interval at sea is limited to the larva[l] period of the early ontogeny”, as Balon and Bruton (1994) argued. The only common feature of anadromy and amphidromy is that reproduction and egg development occur in fresh water. It could as logically be argued that amphidromy is closest to catadromy. In both, larval and early juvenile life is at sea, and small juveniles migrate into fresh water, which is where most growth and maturation take place. The chief difference is that amphidromous species stay in fresh water to reproduce whereas catadromous species return to sea to reproduce.

Clearly there are problems in classifying some salmonids, as they are extremely flexible in life history strategy (reinforcing Gross's, 1987, belief that diadromy and its various forms are not distinctive phenomena but convenient groupings of similar behaviours). As discussed above for the brown trout, there seems to be almost a continuum from an explicitly anadromous pattern to nothing more definite than a facultative, time- and direction-variable, primarily trophic, wandering between freshwater and marine biomes. Rather than calling this amphidromy, as Stearley (1992) does, it seems to me to be barely diadromous, at all. Similar irregular, partly trophic migrations between fresh water and the sea seem to be characteristic of other salmonids, and Stearley's (1992) classification of diverse salmonids as amphidromous – including species of *Coregonus*, *Salvelinus*, *Salmo* and *Oncorhynchus* – is apparently a recognition of these movements between the two biomes primarily for trophic rather than, or in addition to, reproductive purposes. In my view, the habits of salmonids that Stearley (1992) classified as amphidromous are different from the amphidromy defined by Myers (1949) and as detailed above.

What does this mean for Stearley's (1992) phylogenetic analysis? It calls into question his statement that “Salmonine life histories, when mapped onto their phylogeny, demonstrate a stepped trend, from freshwater to amphidromous to anadromous clades”. I do not believe that they represent Gross's scenario of a shift from amphidromy to anadromy. The trend is better described as from rather erratic, almost facultative, freshwater/marine wandering to more explicit anadromy. However, specifically, the great variability between stocks, between individuals of the same species, and even between year within individuals in species such as brown trout, suggests that the various character states are not clear alternatives, have uncertain polarity, and probably do not meet the criteria needed for their use as character states in phylogenetic analysis.

Furthermore, though Stearley (1992) nominated, amongst several others, the osmerid genera *Spirinchus* and *Thaleichthys* as outgroups for determining the polarity of character states in his phylogeny of the Salmonidae, he does not apply outgroup comparisons when evaluating the various forms of diadromy in salmonids. Both osmerid genera nominated as outgroups are explicitly anadromous (as are most other osmerids) (McAllister, 1963; Scott and Crossman, 1973). That being so, anadromy should be regarded as occurring in a common ancestor of Osmeridae and Salmonidae, and as a plesiomorphic (primitive, ancestral) character in Salmonidae. Any variations from anadromy within the Salmonidae are the apomorphic (derived) character states.

McLennan (1994) used Stearley's (1992) study as one of several examples of the application of behavioural characters to determine phylogenetic relationships (Fig. 3). Predictably, the difficulties just discussed in Stearley (1992) become compounded.

anadromous, as for the proposed outgroup, there are also eight state changes if amphidromy is accepted, or only five state changes with an entirely freshwater life history in *Hucho hucho*, *Salvelinus namaycush*, *O. chrysogaster*, *O. gilae*/*O. apache* and *O. aguabonita*. Given that a shift from diadromy to entirely freshwater life is often observed in many lineages of diadromous fishes (McDowall, 1988), this is clearly both the most parsimonious phylogeny as well as the most likely evolutionarily and biologically.

Summary

Overall, it seems that the intuitively reasonable scenarios presented by Gross (1987) to explain the evolution of diadromy fail to correlate with what is observed of the behaviour, evolution and relationships of diadromous fishes. The patterns of evolution, from biome restricted, to facultative wandering, to amphidromy, and thence to anadromy and catadromy, may have occurred in some instances, but there is little explicit evidence for this. The scenarios observed amongst the diverse diadromous fishes and their relatives cover a much wider range of possibilities than those hypothesized by Gross, to the extent that his scenarios seem to have little compelling and widespread support. They are instead a small possible part of a much broader picture. In particular, species groups that are amphidromous tend not to have sister species/species groups that are either anadromous or catadromous. This does not preclude a common ancestor of extant anadromous or catadromous species from having had such an amphidromous ancestry even within a genus or family, or a monophyletic group of genera or species.

Each of the various forms of diadromy clearly has multiple origins throughout the diversity of fishes, and the migratory patterns that occur have taxonomic group-specific idiosyncrasies. Moreover, it is clear that whether or not to migrate is highly variable at the species level. In some species, individual fish may decide whether or not to migrate, depending perhaps on growth rate, condition, state of maturity and on environmental variables such as freshwater and sea temperatures. So diadromy is in some species determined by the individual state, which is sometimes mediated by environmental conditions meaning that residential non-diadromous progeny can have diadromous parentage, and vice versa (Rounsefell, 1958; Nordeng, 1983; Northcote, 1992). Until there is a better idea of the phylogenetic relationships within this broad span of primitive teleostean fishes, including Salmonidae, the polarity of different forms of diadromy as an indicator of relationships probably cannot be clarified or advanced much further. Moreover, because there is obvious within-species variation, between individuals within reproductive family variation, and even within individual variation in whether or not diadromous migrations are undertaken, the value of diadromy in phylogenetic studies seems to be very limited. The multiple origins of diadromy suggest that only the development of phylogenies at the species or species-group level will allow for valid interpretation of its evolution and significance in phylogenetic analysis. Johnson and Patterson (1996) have addressed the place of diadromy in the phylogeny of the lower euteleostean fishes, including the salmonoids, osmeroids and galaxioids, although they did not do so inconclusively. What is needed are genus- and species-level phylogenies onto which can be mapped different forms of diadromy to enable the identification of changes in strategy within species groups. Even then, phylogenies may be so uncertain that there may be little assurance in interpreting changes. Moreover, the

obvious facultativeness that characterizes diadromy in some species groups, and even within species, suggests that diadromy may have limited value only, even at this level.

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