Micronesica 30(1): 3–14, 1997

Is There Such a Thing as Amphidromy?[1]

R. M. McDowall

National Institute of Water and Atmospheric Research,
P.O. Box 8602, Christchurch, New Zealand

Abstract—Anadromy and amphidromy are different migratory/life history strategies. However, few North American ichthyologists and fisheries biologists use the term amphidromy, and usually describe amphidromous fishes as anadromous. By contrast those who study fishes of the fresh waters of tropical islands, as well as Japan, New Zealand and Australia, routinely use the term amphidromy. This difference in practice is attributed to the general lack of amphidromous fishes in continental North America.

Amphidromy is used to describe migratory fish that return from the sea to fresh waters at a juvenile stage; they do most of their feeding and growing in fresh water and eventually reproduce there. By contrast, in anadromous fishes, the return migration from the sea to fresh water is of adult fish approaching sexual maturity. Most or all feeding and growth of anadromous fishes takes place in the sea; they usually undertake little or no feeding in fresh water, though they reproduce there.

Introduction

The term *diadromous* was introduced by George Myers (1949) to describe *truly migratory fishes that migrate between the sea and fresh water.* Old and long-used sub-categories of diadromy include *anadromous* and *catadromous.* In addition, Myers (1949) introduced a third new sub-category, *amphidromous.* These three terms are defined as follows (after McDowall 1992, and adapted from Myers' usage):

- Anadromous: Diadromous fishes which spend most of their lives in the sea, and which migrate into fresh waters to breed;
- Catadromous: Diadromous fishes which spend most of their lives in fresh water, and which migrate to sea to breed;
- Amphidromous: Diadromous fishes in which migration between fresh water and the sea is not for the purpose of breeding, but occurs at some other stage of the life cycle.

[1]ASIH symposium on freshwater gobies. Email:Bob@ Chch.NIWA.CRI.NZ

To this last definition may be added the condition that amphidromous fishes undertake most of their feeding and growing in the same biome as they reproduce in, i.e., in fresh water. By contrast, anadromous fishes feed and grow primarily in a different biome from that in which they reproduce (the sea and fresh water, respectively).

Both anadromy and catadromy have long had wide acceptance throughout the world of ichthyology and fisheries biology (see McDowall 1988), though their usage has not always been consistent with Myers' (1949) definitions. The abstracting journal *Aquatic Sciences and Fisheries Abstracts,* for instance, uses anadromy for any upstream migration and catadromy for any downstream migration; as a result species are often listed there as both anadromous and catadromous depending on the direction in which the life stage under discussion is migrating. This usage, which was proposed decades ago by Meek (1916) but has long been rejected, most explicitly by Myers (1949), clearly equates closely with upstream/downstream and contranatant/denatant, and Myers' terms then have little distinctive meaning or advantage. However, such blatant misusage is rare and, in general, when applied the terms mean much what Myers intended.

Usage of Amphidromy

Amphidromy, the third of Myers' (1949) terms, is little used by biologists in continental North America. Perhaps typical is Moyle & Cech (1993), who explicitly state that there are two types of diadromous fishes: "**anadromous** species that migrate from salt water to spawn in fresh water and **catadromous** species that migrate from fresh water to spawn in the ocean". Nelson (1994) defined these two forms of diadromy in terms of where species spawn, with those spawning in fresh water being called anadromous while those that spawn in the sea are described as catadromous. As a result, Nelson (1994) labeled as anadromous some diadromous galaxiids that seem to me, clearly, to fit within Myers' definition of amphidromy, and which are routinely described that way by some ichthyologists (McDowall 1988, and see below). Lagler et al. (1977) did recognize the occurrence of amphidromy, but defined it as "completely free movement between fresh and marine water, not for the purpose of breeding". As so defined amphidromous is little different from euryhaline; this definition is much broader than Myers' (1949) and does not even fall within Myers' (1949) definition of diadromy. It is an inappropriate use of the term. However, it is not only in North America that amphidromy seems to be largely ignored or rejected. Howes & Sanford (1987) described the Japanese osmeroid, *Plecoglossus altivelis,* as anadromous, whereas the Japanese regard it as amphidromous (Iguchi & Ito 1994, Tsujimura & Taniguchi 1995), and it is according to Myers' (1949) definitions. Some workers seem to just avoid the issues of distinguishing fish as anadromous or amphidromous by describing them as diadromous (Fulton 1986, Maciolek & Ford 1987, Humphries 1990).

In contrast with most of their continental North American colleagues, however, ichthyologists and fisheries biologists particularly in Hawai'i, Japan, Australia and New Zealand, but also elsewhere, routinely use the additional term

amphidromous. Fish families that contain species so-described, include Galaxiidae, Aplochitonidae, Prototroctidae (Australia, New Zealand, South America), Plecoglossidae (Japan), Pinguipedidae (New Zealand), Cottidae (Japan), and Eleotridae and Gobiidae (New Zealand, Hawai'i, Japan and many tropical Atlantic and Pacific islands) (McDowall 1988, Kido et al. 1983, Nishimoto & Fitzsimons 1986, Goto 1990, Radtke & Kinzie 1991, 1996, Kinzie 1993, Fitzsimons & Nishimoto 1995, Iguchi & Mizuno 1990, 1991, Iguchi & Ito 1994, Tsujimura & Taniguchi 1995). Some mainland North American ichthyologists, especially those who have studied tropical gobies, have applied the term (Erdman 1961, 1986, Parenti & Maciolek 1993).

Perhaps most North American biologists do not use the term amphidromy simply because there are scarcely any species in continental North America that might be classed as amphidromous, though possibly occasional cottids and gobies are amphidromous, e.g. *Leptocottus armatus* along the Pacific coast of North America, and *Dormitator latifrons* and *Awaous tajasica* from the Gulf of Mexico. Certainly, according to Myers' (1949) definitions, there are amphidromous sicydiine gobies in the Caribbean (Clark 1905, Erdman 1961, 1986, McDowall 1988), and many amphidromous species in New Zealand, Australia, and Japan; the entire freshwater fish fauna of Hawai'i is amphidromous (Radtke & Kinzie 1991, 1996).

Unlike most of his North American colleagues, Stearley (1992) applied the term amphidromy to the salmonid genera *Hucho* and *Salvelinus,* as well as to some species of *Salmo* and *Oncorhynchus,* though other authors have hitherto described them as anadromous.

While it is important not to become pedantic about the meaning and definitions of technical terminology in any field of science, it is also important that there be some measure of consistency so that statements are unambiguous and not subject to misunderstanding. There clearly seems to be inconsistency, and therefore misunderstanding, about the various forms of diadromy, amphidromy in particular. It is the purpose of this note to address and clarify that question.

Purposes of Migration and the Characteristics of Amphidromy and Anadromy

Northcote (1979) identified several "purposes" for fish migrations generally (in a discussion not concerned with anadromy and amphidromy). He recognized *feeding migrations, spawning migrations* and *wintering migrations.* All three are undertaken by diadromous fishes, though feeding and spawning are the most usual. In relation to these categories of Northcote (1979) and in terms of strict definitions of subcategories of diadromy (Myers 1949, McDowall 1992), there are basic differences between anadromy and amphidromy.

The issue that I wish to explore here is whether these differences in the life history patterns in fish that fit Myers' (1949) definitions of anadromy and amphidromy are sufficiently distinct to make it worthwhile to retain both terms. In essence: Is the migration of small juvenile fishes into freshwater to feed and grow for some months to years before spawning there, sufficiently different from the mi-

gration of large, mature, and often non-trophic adults into fresh water to spawn, for these differences to be recognized as different categories of diadromy? Or, are these just the extremes of a continuum or not really different, at all?

Fishes conforming to Myers' (1949) definitions, and described as amphidromous (by the numerous authors listed earlier as applying the term) have the following combination of characteristics:

- The initial movement to sea is of newly hatched embryos that do not feed until reaching the sea (this is not a distinctive feature of amphidromy, being true of many species that are anadromous according to Myers' (1949) definitions);
- The life stage that leaves the sea to return to fresh water is a juvenile, some might say a larval or post-larval fish, usually transparent, and usually without many of the defining morphological characters of the respective adults into which they will grow;
- Movement from the sea involves an ontogenetic habitat shift from a marine pelagic/planktonic to a freshwater benthic existence;
- The fish changes distinctly in appearance following entry to fresh water, growing and developing the defining adult characters (including becoming pigmented);
- There is a prolonged period of feeding and growing in fresh water—most growth that these amphidromous species undergo takes place in fresh water;
- Only rudiments of gonads are present at migration from the sea, and there are no signs of any secondary sexual characteristics.
- Reproduction is typically at least 6 months away, may be as much as 18 or 30 months away, and takes place in fresh water.

In the various amphidromous eleotrids and gobies, the return migrant to fresh water, though up to several months old (Radtke & Kinzie 1991), may be only 15 mm long (about half the length of a salmonid at hatch); in galaxiids they are a little larger, typically 30–55 mm long and up to about six months old (McDowall et al. 1994). In terms of the various salmonid life stages (alevin, parr, smolt, juvenile, adult), the returning migratory stage of amphidromous fishes compares best with the smolt, being the harbinger of a migratory shift of osmoregulatory environment, a stage at which a major change of behavior is undertaken, and the beginning of the stage at which most growth takes place. A major difference, though, is that the direction of the migration is reversed as salmonid smolts migrations are from fresh water to the sea. In Northcote's (1979) terms, then, the amphidromous migration when the fish return to fresh water is essentially a feeding one.

Anadromous species have the following characteristics:

- They go to sea at larval to juvenile stages soon after hatching, or after a period of weeks to months (or occasionally even years) feeding and growing in fresh water;
- However, in spite of any feeding and growth in fresh water, most growth takes place at sea, in a different biome from that where reproduction takes place;

- They undertake their return migrations to fresh water as adults, usually at or close to adult size; silvery coloration at sea may be replaced by strongly marked and darker color patterns following movement into fresh water;
- Many (perhaps most) do not feed at all following departure from the sea and even if they do feed in fresh water, in most anadromous species there is little growth after migration;
- There is not the same marked shift in habit from pelagic/planktonic to benthic;
- Secondary sexual characteristics have often started to develop at the time of migration, though typically will become much more strongly accentuated during further residence in fresh water;
- Gonads vary in maturity from occasionally rudimentary to usually well-developed to mature or close to ovulation;
- The focus of migration is impending reproduction.

In Northcote's (1979) terminology, then, anadromous fish undertake what is primarily a spawning migration.

Is There an Amphidromy-Anadromy Continuum?

Problems in the application of Myers' terminology arise partly because there is something of a continuum between amphidromy and anadromy. In the most strict expression of anadromy, the only activities undertaken after leaving the sea relate explicitly to reaching the spawning grounds and actually reproducing. Though it may take some time for gonads to mature and ovulate and for reproduction to take place, the fish leave the sea energetically and physiologically fully-equipped to reproduce, and no or little feeding or somatic growth take place. Some species may mature and spawn within a few days or weeks of leaving the sea and usually at no great distance up stream (as in pink salmon, *Oncorhynchus gorbuscha*—Heard 1991); in others it may be weeks or months before breeding takes place (as in other Pacific salmons of the genus *Oncorhynchus*). An extreme is the southern pouched lamprey, *Geotria australis* (f. Geotriidae), in which there is an entirely non-trophic, freshwater phase that may last for 18 months, during which time energy is transferred from the soma to the reproductive organs, as the latter develop from rudimentary at migration to mature at spawning (Glova 1995).

In addition to the varying duration of the period between migration from the sea and spawning, there are some diadromous species that feed in fresh water for weeks or even months before reproducing, though there appears to be little somatic growth (some *Salvelinus*—f. Salmonidae); energy is obtained and presumably is transferred from the food to the growing/maturing gonads or is used to sustain the fish while gonadal growth and maturation take place, with subsequent spawning in fresh water. Rarely, there are species in which behavior is highly flexible: in New Zealand's *Retropinna retropinna* (f. Retropinnidae) some fish return as mature adults and soon spawn (i.e. anadromy), but others return as sub-adults

and may feed for several weeks to months before spawning (perhaps amphidromy) (McDowall 1990).

Stearley (1992) considered some salmonids, such as charrs of the genus *Salvelinus,* to be amphidromous presumably because they migrate seasonally, between rivers and the sea once to several times, before there is a spawning migration from the sea to fresh water. These early migrations are for feeding and/or wintering and so could be described as amphidromous (as Stearley 1992 indicates)—though they do not involve migration into fresh water of very small juveniles as is the case with amphidromous eleotrids, gobies and galaxiids, etc. The later, specifically spawning, migrations of these charrs equate to anadromy. Following their first (anadromous) spawning migration, the fish may stay in fresh water to feed and spawn once or more often; or there may be further annual/seasonal movements to the sea to feed and recover and then back to fresh water to spawn; or there may even be a return to feeding migrations to and from the sea, once or more often, before another spawning migration takes place. Different individuals of a species may have different life-time migratory behaviors. It is these species that Stearley (1992) has regarded as amphidromous. Classifying these species/migrations is difficult, though in my view, since they undergo most of their pre-spawning growth at sea, they are best regarded as anadromous, according to Myers' (1949) definitions.

The extent to which species conform strictly to Myers' definitions thus varies and is partly the source of our problems. Some fish conform closely to his anadromous, such as Pacific salmons, various other salmonids, lampreys, most osmerids, salangids and clupeids. Some groups seem less strictly anadromous, such as sturgeons, further salmonids and clupeids, and others—they are known to feed following migration from the sea and while they move upstream to the spawning grounds, during which time their gonads undergo final development, though there is little if any somatic growth. Similarly, some conform closely to amphidromous, such as sicydiine gobies, some eleotrids, galaxiids, and others.

Whether the term amphidromy has any value, as distinct from anadromy, depends partly on where within the life cycles attention is focused. If it is focused on where reproduction takes place, there is no essential difference between anadromy and most amphidromy—reproduction occurs in fresh water—as Nelson (1994) concludes. If, however, attention is focused on the species' essential life history structure, on what the purpose of the migration is, e.g. in terms of Northcote's (1979) feeding and spawning migrations, then it seems to me that amphidromy and anadromy are quite different forms of diadromy, and that there is value in using different terminologies.

The value of the terms also depends partly on the nature of the evident continuum between extremes of anadromy and amphidromy—on whether this continuum has only one frequency mode or has more than one distinct mode of species at different locations along the continuum. There is a distinct concentration of species that have very clearly amphidromous life cycles, probably over 60 species, mostly in the families Galaxiidae, Eleotridae and Gobiidae (McDowall 1988)—and a great many more if Parenti & Maciolek's (1993) conclusion that sicydiine

gobies are mostly amphidromous, proves to be correct. There are also many fish that clearly and unequivocally can be described as anadromous (sensu Myers 1949), including lampreys, sturgeons, most salmonids, salangids, osmerids, clupeids, and a variety of other families (ca. 110 species—McDowall 1988).

But, certainly, there are some species in which there is variation and/or confusion in the patterns/purposes of migration that involve both trophic and/or reproductive purposes, and in which classification as anadromous and/or amphidromous is not as clear—such as those salmonids that Stearley (1992) calls amphidromous. However, this lack of clarity seldom, if ever, involves uncertainty as to whether the life history strategy most resembles, and is a variant of:

- Amphidromy as seen in galaxiids or gobies, rather than
- Anadromy as in salmonids or osmerids.

As it happens, these problematical variants are always closely related to strictly anadromous species but show some amphidromous-like characteristics, rather than being related to amphidromous species and showing some anadromous-like features. Thus, in terms of modes of species abundance along an hypothetical amphidromous-anadromous continuum, there seems to me to be a very obvious mode at the amphidromous end, another at the anadromous end, with the anadromy mode skewed with a tail in the distribution that extends towards the amphidromous extreme that is formed by a small number of species in which there are multiple and/or multi-purpose migrations to and from the sea. They seem to be few and in my view are not frequent enough to seriously consider abandoning the distinction between anadromy and amphidromy.

It might, perhaps, be argued that the lack of explicit and exclusive definitions for these terms mitigates against their acceptance. However the same sorts of arguments would apply to descriptions of fish as herbivorous or carnivorous, and benthic or pelagic, etc. yet most would argue that these terms are useful and heuristic. Anadromous and amphidromous are no less useful terms. Some species will probably always be equivocal and defy easy placement in one or other of anadromy and amphidromy, but this seems no reason to abandon the term amphidromy. Classification of species as anadromous or amphidromous, or even as diadromous or not, must be seen as an attempt to categorize somewhat variable life history strategies; none of these categories of migration can be described as a "natural phenomenon", but rather together they comprise "similar, often convergent behaviors" seen in various fish (McDowall 1993).

In my view, then, there is such a thing as amphidromy, and the term has utility and is heuristic. It is a useful collective term for a distinctive life history strategy in diadromous fishes (and also some crustaceans and molluscs)—more clear cut, in fact, than anadromy. However, perhaps there is a need to amend its definition to increase attention on the extent to which amphidromous fishes undertake feeding, growth and maturation in fresh water before reproducing there.

Thus I suggest the following amended definitions:

Anadromy is a strategy in which most feeding and growth take place at sea, prior to a migration of fully-grown, mature, adult fish into fresh water to repro-

duce; there is either no subsequent feeding in fresh water or, if there is, such feeding is accompanied by little somatic growth; the principle feeding and growing biome (the sea) differs from the reproductive biome (fresh water).

Amphidromy is a strategy involving migration of small post-larval to juvenile fish from the sea into fresh water, where there is prolonged feeding, during which most somatic growth from juvenile to adult stages takes place, as well as the attainment of sexual maturity, and where spawning also occurs; the principle feeding and growing biome (fresh water) is the same as the reproductive biome.

The Evolution of Different Forms of Diadromy and the Place of Amphidromy

Gross (1987) examined the evolution of diadromous life styles and argued that amphidromy is an intermediate, transition stage in the evolution of exclusively freshwater species from marine species and vica versa. He envisaged marine species evolving into euryhaline wanderers, then becoming amphidromous, catadromous and finally freshwater species, particularly in the tropics, while freshwater species become euryhaline wanderers, then amphidromous, anadromous, and finally entirely marine, particularly at temperate latitudes. There are examples of species of apparently marine derivation becoming amphidromous, as with New Zealand's torrentfish (*Cheimarrichthys fosteri*—f. Pinguipedidae), or catadromous, as with New Zealand's black flounder (*Rhombosolea retiaria*—f. Pleuronectidae). But there is little empirical evidence to support the scenario presented by Gross (1987). In fact, most common is the evolution of entirely freshwater species from ancestries interpreted as either anadromous or amphidromous (McDowall 1988, 1990). Rarely do species of apparently marine ancestry evolve to spawn in fresh water, or the reverse, and there seems a strong, traditional attachment at the family level or even above, to spawning in one medium, e.g., of about 60 diadromous salmoniform species in the families Salmonidae, Osmeridae, Salangidae, Galaxiidae, Aplochitonidae, Retropinnidae and Prototroctidae, only about 3 (osmerids) spawn in the sea.

Gross (1987) argued his case, in part, on the basis that he perceived the freshwater fish faunas of Hawaii, Australia and New Zealand to have marine origins, though there is little evidence to support this rather old, and altogether too-widespread misconception that has become increasingly accepted and authoritative with the passage of time; it lacks any compelling documentation (McDowall 1993).

Balon & Bruton (1994) also viewed amphidromy as a transition phase in a shift of species from the ocean to fresh water. They discussed this in the context of the amphidromous sicydiine goby, *Sicyopterus lagocephalus,* from the Comoro Islands in the western Indian Ocean. *S. lagocephalus* is one of many similar sicydiine gobies throughout the tropics that are amphidromous (McDowall 1988, Parenti & Maciolek 1993). Balon & Bruton (1994) described it as a species at "an early evolutionary state of freshwater invasion" and argued that the very small amount of yolk in its eggs prevents it "from spending its entire life in fresh

water. . . . Given time and environmental constancy the altricial, indirectly developing forms with small eggs and high fecundity (such as *S. lagocephalus*) will change into more precocial forms, and ultimately direct developing forms with large eggs and low fecundity, from a life spent at least partly in the sea to one spent entirely in fresh water". This trend can certainly be seen in some amphidromous fishes (McDowall 1988, 1990), but just as often there is a shift from an oceanic larval trophic stage to a lacustrine freshwater trophic stage, with no change in the allocation of yolk to eggs, or in egg size itself, i.e., the species may remain altricial in Balon & Bruton's (1994) terminology, in spite of a shift away from amphidromy to wholly freshwater life in lakes. Furthermore, *S. lagocephalus* is but one of many, perhaps more than 90, amphidromous sicydiine gobies spread throughout the tropics with the same life cycle (Parenti & Maciolek 1993), and it is difficult to see why any or even all such species should be described as "invading fresh water". Moreover, there seems no reason to assume that processes envisaged by Balon & Bruton (1994) are either inevitable or necessarily beneficial to the species' survival. Balon & Bruton (1994) conclude by asserting that "freshwater amphidromy is 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". However, they do not recognize that in at least two critical respects amphidromy, as seen in *S. lagocephalus,* is quite distinct from anadromy, i.e. that in anadromous fishes most feeding and growth take place in a biome different from that in which reproduction takes place, and the return migration to fresh water is essentially a spawning one, whereas in the amphidromous *S. lagocephalus* and numerous other sicydiine gobies, the return migration to fresh water is essentially a trophic one, and most feeding and growth take place there, as does reproduction.

Conclusion

Amphidromy, as envisaged by Myers (1949), seems to be a quite ancient, widespread, successful, and evolutionarily stable life history strategy that has evolved in many fish groups (at least 10 families and perhaps more than once in some of these). It is characteristic of groups that need not be regarded as having either marine or freshwater derivations during their recent phylogenetic history (McDowall 1993). Although it would be highly desirable if the presence/absence of amphidromy could be placed in a specific phylogenetic context, unfortunately, at present, there are no cladograms of the groups in which amphidromy is common to permit this. It is my view that amphidromy is an ancient phenomenon in galaxiid fishes (McDowall 1970, 1993). It also appears to be a primitive characteristic in the New Zealand/Australian genus *Gobiomorphus* (Eleotridae). Parenti & Maciolek (1993) treat it as a general phenomenon in the sicydiine gobies, and this conclusion is widely supported where life histories of these generally little-understood fishes are known (see numerous citations in McDowall 1988). Amphidromy is, like anadromy, a strategy that gives rise through processes like landlocking to entirely freshwater stocks and species. But there seems no reason to

regard it as a transitory phase that will inevitably lead to either an anadromous or entirely freshwater life style. Sometimes it may; but sometimes it may not!

Acknowledgments

I am grateful to R. A. Kinzie III, J. S. Nelson and P. J. Miller for discussions and comments that contributed to clarity of this discussion.

References

Balon, E. K. & M. N. Bruton. 1994. Fishes of the Tatinga River, Comoros, with comments on freshwater amphidromy in the goby *Sicyopterus lagocephalus.* Ichthyological Exploration of Freshwaters 5: 25–40.

Clark, A. H. 1905. Habits of West Indian whitebait. American Naturalist 39: 335–337.

Erdman D. S. 1961. Notes on the biology of the gobiid fish *Sicydium plumieri* in Puerto Rico. Bulletin of Marine Science, Gulf and Caribbean 11: 448–456.

Erdman D. S. 1986. The green stream goby, *Sicydium plumieri,* in Puerto Rico. Tropical Fish Hobbyist 34(6): 70–74.

Fitzsimons, J. M. & R. T. Nishimoto. 1995. Use of fish behavior in assessing the effects of hurricane Iniki on the Hawaiian island of Kaua'i. Environmental Biology of Fishes 43: 39–50.

Fulton, W. 1986. The Tasmanian mudfish, *Galaxias cleaveri.* Fishes of Sahul 4: 150–151.

Glova, G. J. 1995. The secret life of the lamprey. Water and Atmosphere (N.Z.) 3(2): 20–21.

Goto, A. 1990. Alternative life-history styles of Japanese sculpins revisited. Environmental Biology of Fishes 28: 101–112.

Gross, M. R. 1987. The evolution of diadromy in fishes. American Fisheries Society Symposium 1: 14–25.

Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In:* C. Groot & L. Margolis (eds.). Pacific Salmon Life Histories, pp. 119–230. University of British Columbia, Vancouver.

Howes, G. J. & C. P. J. Sanford. 1987. The phylogenetic position of the Plecoglossidae (Teleostei, Salmoniformes) with comments on the Osmeridae and Osmeroidei. *In* Proceedings of the Congress of European Ichthyologists, 1985, pp. 17–30. Department of Vertebrate Zoology, Swedish Museum of Natural History, Stockholm.

Humphries, P. A. 1990. Morphological variation in diadromous and landlocked populations of the spotted galaxias, *Galaxias truttaceus,* in Tasmania, south-eastern Australia. Environmental Biology of Fishes 27: 97–105.

Iguchi, K. & F. Ito. 1994. Occurrence of cross-mating in ayu: amphidromous x land-locked forms and diploid x triploid. Fisheries Science 60: 653–656.

Iguchi, K. & N. Mizuno. 1990. Diel changes in larval drift among amphidromous gobies in Japan, especially *Rhinogobius brunneus.* Journal of Fish Biology 37: 255–264.

Iguchi, K. & N. Mizuno. 1991. Mechanisms of embryonic drift in the amphidromous goby, *Rhinogobius brunneus*. Environmental Biology of Fishes 31: 295–300.

Kido, M. H., P. Ha & R. A. Kinzie. 1983. Insect introductions and diet changes in an endemic Hawaiian amphidromous goby, *Awaous stamineus* (Pisces: Gobiidae). Pacific Science 47: 43–50.

Kinzie, R. A. 1993. Reproductive biology of an endemic, amphidromous goby *Lentipes concolor* in Hawaiian streams. Environmental Biology of Fishes 37: 257–268.

Lagler K. F., J. E. Bardach, R. R. Miller & D. R. M. Passino. 1977. Ichthyology. New York, Wiley. 506 pp.

McDowall, R. M. 1970. The galaxiid fishes of New Zealand. Bulletin of the Museum of Comparative Zoology, Harvard University 139: 341–431.

McDowall, R. M. 1988. Diadromy in Fishes: Migrations between Freshwater and Marine Environments. Croom Helm, London. 308 pp.

McDowall, R. M. 1990. New Zealand Freshwater Fishes: a Natural History and Guide. Heinemann Reed, Auckland. 553 pp.

McDowall, R. M. 1992. Diadromy: origins and definitions of terminology. Copeia 1992: 248–251.

McDowall, R. M. 1993. A marine ancestry for diadromous fishes? Sometimes yes, but mostly no. Environmental Biology of Fishes 37: 329–335.

McDowall, R. M., C. P. Mitchell & E. B. Brothers. 1994. Age at migration from the sea of juvenile *Galaxias* in New Zealand (Pisces: Galaxiidae). Bulletin of Marine Science 54: 385–402.

Maciolek, J. A. & J. I. Ford. 1987. Macrofauna and environment of the Nanpil-Kiepw River, Ponape, Eastern Caroline Islands. Bulletin of Marine Science 41: 623–632.

Meek, A. 1916. The Migrations of Fishes. Arnold, London. 427 pp.

Moyle P. B. & J. J. Cech. 1981. Fishes: An Introduction to Ichthyology. Prentice-Hall, Englewood Cliffs. 593 pp.

Myers, G. S. 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. Copeia 1949: 89–97.

Nelson, J. S. 1994. Fishes of the World. Wiley, New York. 600 pp.

Nishimoto, R. T. & J. M. Fitzsimons. 1986. Courtship, territoriality, and coloration in the endemic Hawaiian freshwater goby, *Lentipes concolor*. Indo-Pacific Fish Biology: Proceedings of the 2nd International Conference on Indo-Pacific Fishes, pp. 811–817.

Northcote, T. G. 1979. Migratory strategies and production in freshwater fishes. *In:* S. D. Gerking (ed.). Ecology of Freshwater Fish Production, pp. 326–359. Blackwell, Oxford.

Parenti, L. R. & J. A. Maciolek. 1993. New sicydiine gobies from Ponape and Palau, Micronesia, with comments on the systematics of the subfamily Sicydiinae (Teleostei: Gobiidae). Bulletin of Marine Science 53: 945–972.

Radtke, R. L., & R. A. Kinzie. 1991. Hawaiian amphidromous gobies: perspectives on recruitment processes and life history events. *In* New Directions in

Research, Management and Conservation of Hawaiian Freshwater Stream Ecosystems: Proceedings of the 1990 Symposium on Freshwater Stream Biology and Fisheries Management, pp. 125–141. Division of Aquatic Resources, Department of Land and Natural Resources, Honolulu.

Radtke R. L. & R. A. Kinzie. 1996. Evidence of a marine larval stage in endemic Hawaiian stream gobies from isolated high-elevation locations. Transactions of the American Fisheries Society 125: 613–621.

Stearley, R. L. 1992. Historical ecology of Salmoninae, with special reference to *Oncorhynchus. In:* R. L. Mayden (ed.). Systematics, Historical Ecology and North American Freshwater Fishes, pp. 622–758. Stanford University Press, Stanford.

Tsujimura, A. & N. Taniguchi. 1995. Genetic differences in some reproductive characters found between landlocked and amphidromous forms of ayu, *Plecoglossus altivelis altivelis.* Nippon Suisan Gakkaishi 61: 165–170.