

Tropical and temperate freshwater amphidromy: a comparison between life history characteristics of Sicydiinae, ayu, sculpins and galaxiids

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Abstract Amphidromy is a distinctive form of diadromy, but differences in the life histories of tropical and temperate amphidromous fishes suggest that there are two types of freshwater amphidromy. The life histories of Sicydiinae gobies, ayu (*Plecoglossus altivelis*), Japanese sculpins (*Cottus*) and galaxiids (Galaxiidae), suggest that the Sicydiinae are representatives of tropical freshwater amphidromy, whereas ayu, sculpins and galaxiids are representatives of temperate freshwater amphidromy. The Sicydiine larval stage may be required to occur in the ocean for all species, but ayu, sculpins and galaxiids have landlocked or fluvial forms with larvae that do not need to enter the ocean for larval feeding and growth. This suggests that Sicydiine larvae have a high oceanic dependency whereas ayu, sculpins and galaxiid larvae have a low oceanic dependency. Freshwater amphidromous fish in tropical and temperate zones appear to have developed two different strategies in

the evolution of their life histories. It is likely that the evolutionary direction of the larval stage of tropical amphidromy is to remain in the sea and that of temperate amphidromy is towards having the ability to remain in freshwater if needed. Tropical and temperate amphidromy appear to be biologically informative categories and evaluations of this hypothesis will facilitate better understanding of the various forms of amphidromy in the future.

Keywords Amphidromous species · Sicydiine species · Landlocked form · Fluvial form · Oceanic dependency

Introduction

Myers (1949) defined three categories of diadromy, which are anadromy, catadromy and amphidromy. He introduced the new term, 'amphidromy', from the Greek words meaning 'running' and 'around', or 'on both sides'. McDowall (1988) also proposed that amphidromy occurs in two distinct forms: freshwater amphidromy (Fig. 1a), in which spawning is in freshwater and the larvae are temporarily marine before returning to freshwater to grow and mature, and marine amphidromy (Fig. 1b), in which spawning is marine and the larvae/juveniles are temporarily in freshwater before returning to the sea to grow to maturity. However, there has been considerable confusion about the nature of amphidromy and the

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distinctiveness of freshwater amphidromy compared to anadromy (McDowall 2007a). The term amphidromy has sometimes been ignored by North American and European biologists and ichthyologists, whereas anadromy and catadromy have long been used (McDowall 2007a). Some researchers do not distinguish between anadromous and amphidromous fishes and simply describe them as diadromous. On the other hand, this term has become well-established by the majority of researchers who work on temperate and cool temperate islands such as Japan and New Zealand and tropical and subtropical Indo-Pacific insular systems such as Réunion Island, the Hawaiian Islands and French Polynesia, because their studies refer to the species inhabiting these environments as being amphidromous.

There are major differences between anadromous and freshwater amphidromous species that are biologically significant. McDowall (2009) simply and clearly explained the difference in both as follows. In anadromy, reproduction and most somatic growth take place in the different biomes of freshwater and the sea and the return migration to the spawning biome of freshwater is undertaken by mature, adult fish. They do little or no feeding and growing after initiating the return migration, which can therefore be described as a reproductive migration. In contrast, most somatic growth and reproduction in freshwater amphidromous fishes is in freshwater, and the return migration to the spawning biome is undertaken by small juveniles. They return to freshwater to feed and grow for many months or sometimes years before maturation and reproduction occurs in freshwater. This life cycle is also functionally and strategically different from

anadromy in which large mature adults return to freshwater for reproduction, but not for feeding. In amphidromous species, migrations to and from the sea do not involve reproduction and are rather ‘trophic’ migrations (Myers 1949; McDowall 2007a, 2009), so simply considering amphidromous life histories as a special category of anadromy seems to be an oversimplification that is not particularly scientifically useful.

McDowall (1987) reported that amphidromous fishes are present in both northern and southern temperate regions from analysis of data on the geographic distribution of diadromy. In the temperate regions, there are many freshwater amphidromous species such as galaxiid fishes of the genera *Aplochiton*, *Galaxias* and *Neochanna* (McDowall 1988, 1990), retropinnids of the genus *Prototroctes* (McDowall 1988, 1990), some fishes in the family Cottidae (Goto 1990; Yokoyama and Goto 2002), the pinguipedid *Cheimarrichthys fosteri* (McDowall 1990, 2000), the ayu, *Plecoglossus altivelis*, of the family Plecoglossidae (Azuma 1981; Tsujimura and Taniguchi 1995; Iguchi et al. 1999; Iguchi and Nishida 2000), some species in the Eleotridae (McDowall 1990) and in the Gobioidae of the genus *Rhinogobius* (Akihito and Yoshino 1984). Numerous research efforts have been made to study the taxonomy, biology and ecology of these diverse fishes.

McDowall (1987) was dubious about the geographic distribution of amphidromy being mostly in the temperate regions and suspected that a different picture of its latitudinal occurrence would emerge, particularly when gobioid taxonomy and life histories in the tropical zone would be elucidated. Over the past

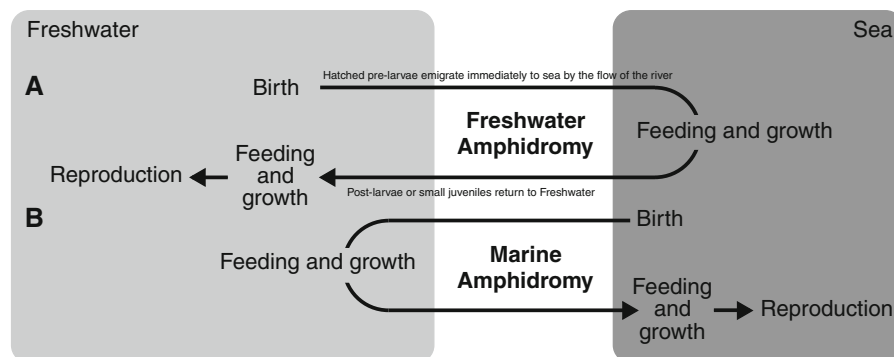


Fig. 1 The different types of amphidromy that are freshwater amphidromy (A) and marine amphidromy (B) as classified by McDowall (1988)

few decades a considerable number of studies have been made on gobioid taxonomy and life histories, especially for the subfamily Sicydiinae (Gobioidei). This subfamily comprises nine described genera and nearly 120 species (Froese and Pauly 2013, FishBase, World Wide Web electronic publication. www.fishbase.org, version 04/2013), which include the genera *Akihito*, *Cotylopus*, *Lentipes*, *Sicydium*, *Sicyopterus*, *Sicyopus*, *Smilosicyopus*, *Stiphodon* and *Parasicydium* (Keith and Lord 2011; Keith et al. 2011). The species in these genera mostly occur on tropical and subtropical islands in the Indo-Pacific, West Africa, Central America and the Caribbean region (McDowall 2007a; Keith and Lord 2011) although *Sicyopterus japonicus* is distributed from Taiwan to Fukushima, Japan and has the northernmost geographic distribution among the Sicydiinae (Iida et al. 2009, 2013). Myers (1949) stated that the amphidromous prototype is the goby genus *Sicydium* and its close allies, which are common in tropical freshwaters around the world. McDowall has recently published six review papers (McDowall 2003, 2004, 2007a, b, 2009, 2010) about freshwater amphidromy that were especially focused on Sicydiine species rather than other freshwater amphidromous species. He suggested that if any tropical and subtropical freshwater fish group could be regarded as 'iconic', it would be these gobies (McDowall 2007a). Over the past few decades a considerable number of studies have been conducted on the taxonomy, biology and ecology of the Sicydiinae (see Keith 2003; McDowall 2007a) and so far it has been found that all species of the Sicydiinae have freshwater amphidromous life histories (Keith and Lord 2011).

To facilitate understanding the freshwater amphidromous fishes in the tropics and subtropics as well as those in the temperate zone, the objectives of this paper are (1) to characterise the life histories of Sicydiinae gobies, ayu (*Plecoglossus altivelis*), Japanese sculpins (*Cottus*) and the Galaxiidae, (2) to compare the life history characters between the Sicydiinae, as a representative of amphidromous species in the tropical zone, and ayu, sculpins and galaxiids as representative species in the temperate zone, and (3) to hypothesise that freshwater amphidromous fishes in tropical and temperate regions have two different strategies in their life histories, which can be categorised as tropical and temperate freshwater amphidromy. Examination of this hypothesis may lead to a better understanding of this particular type of diadromy.

Life history characteristics of the Sicydiinae

All Sicydiine species mainly inhabit tropical and subtropical islands. However, among sicydiine species only *S. japonicus* lives at temperate latitudes (Iida et al. 2013), and various studies have been made on the ecology of this species recently. The juveniles and adults of Sicydiinae gobies grow, feed and reproduce in rivers after their larvae grow in the marine environment. They have high fecundity (50,000 to 70,000 ova in *S. lagocephalus*, Delacroix 1987; Keith et al. 1999, 225,000 in *S. japonicus*, Dôtu and Mito 1955, 1,000 to 10,000 in *Stiphodon percnopterygionus*, Yamasaki and Tachihara, 2006), small eggs (0.49 to 0.58 mm in *S. percnopterygionus*, Yamasaki and Tachihara 2006), and their newly hatched larvae are small in size (1.1 mm in *S. lagocephalus* to 1.8 mm in *S. stimpsoni* and *Lentipes concolor*, Manacop 1953; Lindstrom 1999). After hatching the larvae drift downstream towards the sea where they spend a variable amount of time feeding and growing, ranging from 2 to 9 months (63 to 106 days in *Lentipes concolor*, Radtke et al. 2001, 66 to 164 days in *Cotylopus acutipinnis*, Teichert et al. 2012, 133 to 256 days in *S. lagocephalus*, Hoareau et al. 2007b). They have among the longest marine larval phases of any tropical fish species (Radtke et al. 2001). After this marine stage, the post-larvae come back to rivers at sizes of 13 to 33 mm depending on the species (12.7 to 13.6 mm in *S. percnopterygionus*, Yamasaki et al. 2007, 17 to 23 mm in *C. acutipinnis*, Teichert et al. 2012, 21 to 33 mm in *S. lagocephalus*, Manacop 1953). Soon after entering freshwater as post-larvae, they undergo several changes in body color and fin shape and metamorphose from a planktonic to a benthic feeding mode that is mainly herbivorous (Erdman 1961; Tate 1997; Nishimoto and Kuamo'o 1997; Radtke et al. 2001; Shen and Tzeng 2002; Keith et al. 2008; Taillebois et al. 2011). This is the recruitment phase when they migrate upstream into rivers and start their juvenile growth phase.

Compared to the tropical species of Sicydiinae gobies, *S. japonicus* is different because its spawning and recruitment seasons in the northern region of its range appear to be strictly in summer, apparently because of the clear seasonal changes of factors such as temperature there (Iida et al. 2009). Sicydiine species in tropical and subtropical regions may not experience major seasonal changes in environmental

conditions such as temperature, so their spawning and recruitment seasons appear to be longer than those of *S. japonicus*, but they may experience wet and dry seasons without drastic seasonal water temperature change in temperate latitudes. Possibly as a result of these seasonal changes, the species in tropical and subtropical regions have well-defined peaks in their spawning and recruitment seasons. For example, the breeding season of *Sicydium plumieri* from Puerto Rico begins in early September and finishes in January at the end of the rainy season (Erdman 1961; Lim et al. 2002). Similar phenomena may occur in tropical anguillid eels, where the tropical species apparently spawn and recruit throughout much of the year (Arai et al. 2001; Kuroki et al. 2006) or during the rainy season (Wouthuyzen et al. 2009), while temperate species spawn and recruit during a more limited seasonal period (Tsukamoto 1990).

Sicydiinae gobies all seem to share several life history characteristics such as large clutch sizes with many small eggs that hatch into very small larvae. Their newly hatched undeveloped pre-larvae exhibit continuous upward swimming and sinking as they drift downstream (Bell et al. 1995; Iida et al. 2010) because they are negatively buoyant in freshwater (Bell and Brown 1995; Iida et al. 2010; Ellien et al. 2011). These larvae appear to be physiologically more adapted to brackish water and seawater than to freshwater (Valade et al. 2009; Iida et al. 2010; Ellien et al. 2011) and their subsequent larval stage uses only marine habitats. Iida et al. (2010) reported that the survival rate of newly hatched larvae was significantly higher in 1/3 seawater or seawater than in freshwater. Larvae of *Sicydium punctatum* clearly had a physiological requirement for residing in brackish water in laboratory experiments (Bell and Brown 1995), as did *S. japonicus* larvae (Iida et al. 2010), because they could not complete their larval development in freshwater (Valade et al. 2009; Iida et al. 2010; Ellien et al. 2011). Because of this and the lack of reports of any land-locked or fluvial forms in Sicydiinae, it appears that their larval stage needs to occur in the ocean. Although this should be confirmed for all species, it seems likely that these may be fundamental characteristics of the life history of this subfamily and that Sicydiine larvae have a high oceanic dependency (Fig. 2; Iida et al. 2009).

Within the Sicydiinae there are two species with exceptionally long marine larval phases and some

regional variation in their life histories. The oceanic larval duration (OLD) from hatching to entering freshwater in both *S. japonicus* and *S. lagocephalus* is longer than in other Sicydiine species. The OLD variation of *S. japonicus* was 130 to 198 days in subtropical Taiwan (mean 163 days: Shen and Tzeng 2008) and 173 to 253 days in temperate Wakayama, Japan (mean 208 days: Iida et al. 2008), which were similar to *S. lagocephalus* with an OLD mean of 199 days in Réunion Island (Hoareau et al. 2007b) and a mean of 131 days in New Caledonia and Vanuatu (Lord et al. 2010). Although the longer OLD in *S. japonicus* could be linked to the fact that *S. japonicus* larvae recruit only in spring in order to avoid the low temperatures in the rivers during the winter time in the temperate zone, it may be a general trait of the species. The long OLD in the tropical *S. lagocephalus* is probably not linked to seasonal variations, so its reasons for having a longer OLD are probably similar to those of *S. japonicus* in the southern part of their distribution area. For example, the peak recruitment season of *S. japonicus* from Taiwan was in May (Shen and Tzeng 2008), but recruitment into the estuary occurred almost all year except during summer (July to August). Furthermore, *S. japonicus* spawns almost year-round except in winter in Taiwan, with a major event in autumn (Shen and Tzeng 2008). This spawning season in Taiwan is clearly longer than that of *S. japonicus* in Wakayama, Japan, where the spawning season is only in summer (Iida et al. 2009). This shows that there are differences in the spawning and recruitment seasons between temperate and subtropical areas for the same species. Iida et al. (2009) indicated that the spawning and recruitment seasons of *S. japonicus* in Wakayama, Japan are the shortest known for the Sicydiinae and suggested that the migration strategy of *S. japonicus* in Japan is determined by seasonal changes in the temperate region.

Although there is some life history variation such as that seen in *S. japonicus*, freshwater amphidromous species such as Sicydiinae gobies generally live in a particular type of habitat. Freshwater amphidromous species are mainly found on high oceanic islands (McDowall 2007a, 2010), however, there have been several reports of Sicydiine species distributed on the continents of West Africa (Harrison 1993), Central America (Lyons 2005), southern China (Nip 2010) and a part of northern Australia (Thuesen et al. 2011).

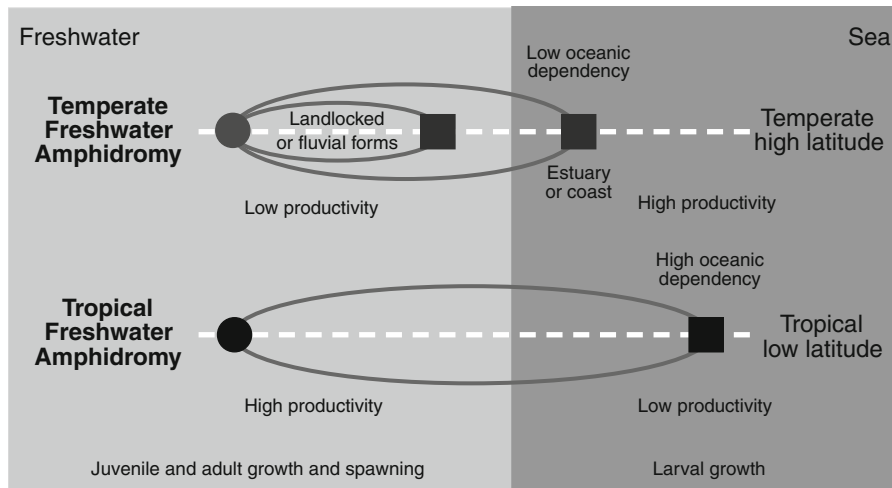


Fig. 2 A diagram representing the proposed categories of temperate and tropical freshwater amphidromy. The larval stages of temperate freshwater amphidromous fishes have the

ability to use freshwater or ocean habitats for growth, and those of tropical freshwater amphidromous fishes can only use ocean habitats for growth

It is likely that one factor affecting the distribution of Sicydiine species is the presence of an altitudinal gradient in the rivers. Small and steep-grade rivers help the downstream migration of Sicydiine larvae, while large and low incline rivers present risks due to exhaustion of larval energy reserves before feeding can begin at sea and due to an extended period of exposure to predation (Tsukamoto 1991; Iguchi and Mizuno 1990; McDowall 2009). Furthermore, there are also mainly true freshwater fishes (non-diadromous) in continental rivers, and this increases the amount of predators and competition for available habitats. For the juveniles and adults, having streams with clear water is also essential to allow the growth of algal and diatom mats for the herbivorous diet of Sicydiinae gobies, except for *Akihito*, *Lentipes*, *Sicyopus* and *Smilosicyopus* species that have a more diversified diet. Lyons (2005) suggested that the pattern of distribution of *Sicydium* gobies in Mexico and Central America is clearly related to the presence of coastal mountain ranges and the width of the coastal plain.

McDowall (2010) showed that freshwater amphidromous fishes are predominantly found on tropical and subtropical islands worldwide, which is clearly true for Sicydiinae gobies. He suggested that this idiosyncratic distribution relates in part to problems in self-recruitment on islands that are often young or volcanic, and because these streams may have ephemeral flows over

relatively short periods of time. Freshwater amphidromy provides the ability to invade new habitats as these become available either on newly emergent (often volcanic) islands, or to re-colonise islands following perturbation such as stream dewatering or the impact of volcanism on older islands. McDowall (2010) also suggested that source/sink population dynamics might be involved with islands 'downstream' in oceanic current systems behaving as sinks, with little or no self-recruitment. However, his suggestions were probably too focused on dispersal rather than retention or self-recruitment, because there are many endemic species of Sicydiinae gobies within oceanic islands; for example, *Cotylopus actipinnis*, *Sicyopterus aiensis* and *S. sarasini* are endemic to the Mascarene Islands (Hoareau et al. 2007b), Vanuatu and New Caledonia (Lord et al. 2010), which could not be maintained if they had a strictly dispersal-based larval strategy. In addition, there are large numbers of post-larvae entering river mouths in many locations where goby fry fisheries occur (Bell 1999) and it is unlikely that these recruiting larvae are mostly from other areas. These high abundances of recruiting larvae support fisheries and often represent examples of self-recruitment in areas such as Réunion Island where there are few other possible sources of larvae (Hoareau et al. 2007a). Furthermore, there are many albinos of *S. japonicus* in local areas of Taiwan but not in other areas (Lin 2007; Watanabe et al. 2010), which suggests

local genetic structure with self-recruitment. It is clear for Sicydiine species that not only dispersal towards other islands can occur, but retention or self-recruitment to local islands also occurs. However, the percentages of occurrences of these two outcomes are not understood yet. Marine dispersal is likely an important ability of the larvae of freshwater amphidromous species, which has led to the geographic expansion of their distributions across wide regions, as opposed to their retention ability, which has probably led to their speciation over evolutionary time scales. Thus it seems likely that some degree of both dispersal and retention are important for these species.

One species among the Sicydiinae that has developed a high dispersal ability is *S. lagocephalus* that inhabits Indo-Pacific island rivers from the Comoros Islands in the Indian Ocean to French Polynesia in the Pacific Ocean and is the most widespread Sicydiine species. Three significantly different genetic groups have been identified within this species using mtDNA cytochrome b sequences (Lord et al. 2012) that include the western Pacific (Okinawa, Guam, Fiji, Samoa, Vanuatu and New Caledonia), Tahiti, and the Indian Ocean (represented by Comoros and Réunion) (Lord et al. 2012), as was also suggested by Keith et al. (2005). This implies that there are limits to larval dispersal among widely separated areas that are likely determined by ocean current patterns (Parenti 1991; McDowall 2010). The population structure may also be related to regional biogeographic history (Lord 2009) or general isolation by distance (Lord et al. 2012). There seems to be a similar pattern of population genetic structure for the tropical freshwater eel, *Anguilla marmorata* (Ishikawa et al. 2004; Minegishi et al. 2008; Watanabe et al. 2008, 2009), which also has a long OLD as a transparent leaf-like larva (leptocephalus) and the widest geographic distribution of all anguillid species.

At the other extreme, some regions are isolated and require local retention of larvae. For example, the small Hawaiian freshwater fish fauna consists of just five species, all of them gobies (Suborder Gobioidei), which are *Awaous guamensis*, *Lentipes concolor*, *Eleotris sandwicensis*, *Sicyopterus stimpsoni*, and *Stenogobius hawaiiensis* (Kinzie 1988; Radtke et al. 1988; Fitzsimons et al. 2002; Fitzsimons and McRae 2007). All but *Awaous guamensis* are Hawaiian endemics (McDowall 2003). However, there are no local-island endemics within these Hawaiian gobies

and no genetic structure has been detected within any of the five species among the different islands (Fitzsimons et al. 1990; Zink et al. 1996; Chubb et al. 1998). Similarly, there has been no genetic structure found in *S. japonicus* either, which is distributed on islands spread out along the path of the Kuroshio Current (Ju 2001; Watanabe et al. 2006). These types of population structures may be determined by the generally long OLD of amphidromous gobies that can result in at least some dispersal occurring among widely separated islands over long time scales. Radtke et al. (1988, 2001) estimated the OLD in three species of Hawaiian gobies as varying from 63 to 106 days in *Lentipes concolor*, 119 to 151 days in *Stenogobius hawaiiensis*, and 150 to 169 days in *Awaous guamensis*. The very widespread non-endemic *Awaous guamensis* that is found in Guam, New Caledonia, Vanuatu and Fiji in the western Pacific (McDowall 2003) has the longest larval life of the Hawaiian gobies and probably is the most recent arrival in the Hawaiian Archipelago (McDowall 2010). However, to recent molecular genetic and morphological analysis of *Awaous guamensis* found that Hawaii and Guam populations of this species consisted of a distinct evolutionary lineage (Lindstrom et al. 2012). The Hawaiian Archipelago is located in the middle of the North Pacific Gyre and constitutes one of the most isolated oceanic island chains on earth, so the lack of population structure within the Hawaiian endemic species indicates that ocean currents or eddies around Hawaii must occasionally transport larvae among the different islands. Therefore, the Hawaiian Islands may illustrate the balance between dispersal and retention in these fish (Murphy and Cowan 2007), because some retention within the island chain is needed and some dispersal among the islands may also be beneficial.

The OLD of the widespread *S. lagocephalus* was compared to those of *Cotylopus acutipinnis*, *S. aiensis* and *S. sarasini*, which had shorter mean OLD values of 101, 79 and 77 days, respectively (Hoareau et al. 2007b; Lord et al. 2010). These OLD are about half that of *S. lagocephalus* (Lord et al. 2010). The mean OLD in other Sicydiine species were generally in the mid-range between the OLD values of *S. lagocephalus* and the endemic species (Bell et al. 1995; Radtke et al. 2001; Yamasaki et al. 2007; see Table 1 in Iida et al. 2009). This suggests that OLD could be one of the factors explaining dispersal and endemism in the

geographic distribution of Sicydiine species (Lord et al. 2010).

Many studies have investigated the relationship between OLD and the geographic distribution of marine organisms. However, the associations between these parameters are variable, because both good correlations (Shanks et al. 2003; Siegel et al. 2003; Rivera et al. 2004; Zatzoff et al. 2004; Kinlan et al. 2005; Lester et al. 2007) and poor or no correlations (Wellington and Victor 1989; Victor and Wellington 2000; Rocha et al. 2002; Nishikawa and Sakai 2005; Severance and Karl 2006; Bowen et al. 2006; Teske et al. 2007) have been found. There are good correlations between OLD and the geographic distribution of *Sicyopterus lagocephalus* and *Cotylopus acutipinnis*, *S. aiensis* or *S. sarasini* (Hoareau et al. 2007b; Lord et al. 2010). But recently, Taillebois et al. (2012) found that the OLD of the widespread species, *Sicyopus zosterophorum* (54.6 ± 5.6 days), was similar to those of the endemic species, *Smilosicyopus chloe* (53.6 ± 5.7 days) and *Akihito vanuatu* (55.4 ± 7.5 days). There are probably many other factors that may have some influence on this association, such as larval specific gravities and behaviours at sea and geography of currents (Stobutzki and Bellwood 1994, 1997, 1998; Leis et al. 1996; Leis and Carson-Ewart 1997; Stobutzki 1997, 1998). Species distributions may also be influenced by factors such as the substrate preferences of adults and juveniles in freshwater habitats (Taillebois et al. 2012).

Life history characteristics of ayu, sculpins and galaxiids

The freshwater faunas of New Zealand in the southwestern temperate Pacific Ocean, and Japan and Taiwan in the subtropical to temperate northwestern Pacific, are major islands or archipelagos where there are a variety amphidromous fishes (McDowall 1988, 2007a, 2009). McDowall (2009) discussed why amphidromy is such a rare phenomenon in longer continental rivers (McDowall 2007a) and why the Sicydiine gobies in particular, are so prevalent on small islands (see Keith 2003) and suggested that this is related to the rapid downstream transport of larvae to the sea that can happen in island streams that are necessarily short, and often steep and swift-flowing. Japan and New Zealand appear to have more species of amphidromous fish

species compared to areas of similar latitudes, and there have been many studies on the ecology of amphidromous fishes in these large temperate islands (McDowall 2010). The ayu *Plecoglossus altivelis* is an amphidromous osmeroid fish with a life span of only 1 year that lives in Japan, Korea, Taiwan and China. Ayu spawn adhesive eggs in gravel along the lower reaches of rivers. The newly hatched larvae (6 mm) drift downstream to the sea in autumn and where they spend the winter months (Iwai 1962). The juveniles (about 60 mm) start an upstream migration in spring and grow to a total length of 150 to 300 mm by the end of summer, while feeding on algae adhering to rocks. In autumn, mature fish spawn and then die. This amphidromous-style pattern also exists in landlocked populations in Lake Biwa and several other lakes in Japan, but the larvae use the lakes for growth instead of the sea. In Lake Biwa, the largest lake in Japan (about 670 km²), there are life history variations among populations, with juveniles and adults remaining in the lake either until spawning in autumn or from early spring until midsummer (Tsukamoto et al. 1987). Both types spawn in the same inlet streams, but in different reaches.

The sculpins (Scorpaeniformes, Cottoidea) represent one of the largest and most diverse teleostean groups, with more than 300 species in nine families (e.g. Nelson 1994; Yabe 1985). Most sculpins live in Northern Hemisphere cool-temperate and subarctic marine habitats, and about 100 species live in freshwater habitats, with most having non-diadromous life histories. Excluding the large number of endemic cottoids (Cottoidei) in Lake Baikal, Siberia (33 species in 3 families and 12 genera), the remaining freshwater sculpins are comprised of the genera *Cottus* (64 species), *Mesocottus* (1 species), *Myoxocephalus* (1 species) and *Trachidermus* (1 species) in the Family Cottidae. The freshwater sculpins, especially *Cottus* and related genera, are regarded as a unique group derived from marine sculpins that invaded freshwater habitats (Yokoyama and Goto 2005). *Cottus* includes bottom-dwelling fish that are widely distributed in Northern Hemisphere freshwater habitats of the Pacific slope of North America and eastern Eurasia, including the Japanese Archipelago. The highest species diversity occurs in the coastal areas of the North Pacific, including Japan. In the Japanese Archipelago, the freshwater sculpin genera *Cottus* and *Trachidermus* exhibit various life history styles

that include catadromy and amphidromy, with lacustrine and fluvial species (Kurawaka 1976; Goto 1990; Goto and Nakano 1993; Shimizu et al. 1994; Byeon et al. 1995).

The Galaxiidae is a southern circum-temperate family of the order Osmeriformes that has about 45 species in Australia (including Tasmania), New Caledonia, Lord Howe Island, New Zealand and associated islands, Patagonia (Chile and Argentina) and the Falkland Islands of South America, and southern South Africa (McDowall 1969, 1990, 2003). The life histories of these fish are fairly well known (McDowall 1988, 1990; McDowall and Fulton 1996), and they include species with non-migratory, amphidromous and possibly catadromous life histories. *Galaxias maculatus* is the single marginally catadromous species, but at least, seven amphidromous species are known from Australia (*G. truttaceus*, *G. brevipinnis*, *G. cleaveri*), New Zealand (*G. brevipinnis*, *G. argenteus*, *G. fasciatus*, *G. postvectis*) and South America (*G. platei*) (McDowall 1988). Amphidromous galaxiids spawn in freshwater and after their larvae hatch (<10 mm long) they move immediately to the sea (McDowall 1988, 1990; O'Connor and Koehn 1998). They spend about 3 to 6 months (Fulton 1986; McDowall et al. 1994) before returning to freshwater as juveniles 30–55 mm long. They never return to sea and there are no exclusively marine galaxiids. Diadromy is obligate in some species, but facultative in others that have 'landlocked' populations in lowland to sub-mountain lakes (McDowall 1972, 1990; Fulton 1986; McDowall and Fulton 1996).

Ayu, sculpins and galaxiids all have landlocked or fluvial forms. It is clear that the larvae of landlocked or fluvial forms do not need to use the ocean for larval development and growth. The Japanese sculpin, *Cottus nozawae*, is a fluvial species that produces a few large eggs that hatch into well developed benthic young that are similar in body morphology to fully formed juveniles (Goto 1990). In contrast, the amphidromous sculpin species, *C. amblystomopsis* produces many small eggs from which pelagic larvae hatch (Goto 1990). Similar types of larvae occur in the amphidromous small-egg type and the fluvial large-egg type of the sculpin *C. pollux* (Mizuno and Niwa 1961; Mizuno 1963). The production of large eggs with more yolk through enhanced vitellogenesis (Goto 1987), and the consequent truncation or elimination of the larval period seems to have facilitated the evolution of fluvial

life histories from freshwater amphidromous species (Balon 1984, 1985; Sargent et al. 1987). The increase in vitellogenesis might have occurred as a result of slight modifications of endocrine mechanisms in response to environmental stimuli such as cold riverine water temperatures (Campbell and Idler 1976; Ng and Idler 1978; Matsuda 1987). In ayu, their larvae seem to stay in coastal marine habitats near the river where they were born (Senta and Kinoshita 1985) and there may be some degree of local population structure in this species (Iguchi et al. 2006). It seems likely that the limited or lack of use of the marine environment by the larvae appears to be a fundamental characteristic of the life histories of some forms of the ayu, *Cottus* and galaxiids with their larvae having a low offshore oceanic dependency (Iida et al. 2009) and a high river/coastal water dependency (Fig. 2).

There may be several advantages to having freshwater amphidromous life histories in the temperate zone. Amphidromous fish larvae in the cold temperate regions may move from the river to the sea for a variety of reasons such as higher availability of larval food in the sea compared to freshwater habitats or avoidance of competition for resources with their juveniles and adults (similar to the ecological opportunity hypothesis, Losos 2010). Marine habitats are typically more productive than temperate freshwater streams (Gross 1987; Gross et al. 1988) and would probably be better for larval growth.

Tropical and temperate freshwater amphidromy

The major differences between the life histories of freshwater amphidromous fishes at different latitudes suggest that there may be two general types of freshwater amphidromous fishes. These differences are related to the degree of oceanic dependency in their larval period with tropical species only being able to use the marine environment for larval growth and temperate species also being able to use rivers or lakes for larval growth in the case of landlocked or fluvial forms at high latitudes (Fig. 2). This suggests that freshwater amphidromous fishes such as the tropical Sicydiinae and the temperate ayu, sculpins or galaxiids have developed different strategies in the evolution of their life histories that may be representative of tropical and temperate forms of amphidromy. Ayu, sculpins and galaxiids inhabit long rivers with gradual

slopes in lowland areas such as in New Zealand or Japan that are different from the shorter streams with steep slopes on tropical high oceanic islands.

Availability of food for the larvae may be an important factor for the development of the tropical amphidromous life history strategy. Although there is sufficient algal growth to provide food for juvenile and adult Sicydiinae gobies in small steep-grade rivers on tropical oceanic islands, there may be lower production of small-sized planktonic food resources for their larvae to feed on in those habitats. There are likely more food resources in the marine environment, but it is unknown where the Sicydiine larvae reside at sea and what they feed on. Sorensen and Hobson (2005) used stable isotope analysis to evaluate the sources of nutrients used by Hawaiian freshwater amphidromous gobies (*Awaous guamensis*, *Lentipes concolor* and *Sicyopterus stimpsoni*) caught migrating into and living in a stream in Hawaii. Stable isotope values of recruiting gobies were consistently closer to those of both inshore plankton and freshwater adults than those of offshore plankton, suggesting that the larvae of these species derive much of their nutrition from inshore environments influenced by freshwater. Hobson et al. (2007) provided evidence that the larvae of amphidromous Hawaiian fish spend the majority of their lives in river plumes and subsist on material associated with freshwater food webs. The larvae of amphidromous gobiids may feed near river mouths and wait there for appropriate recruiting conditions (Lord et al. 2010), but it cannot be concluded that the larvae spend their entire larval life near the shore.

In addition to factors related to larval feeding, there may be a variety of factors that have contributed to the differences in the life histories of amphidromous species however. Differences in climatic patterns affecting river flows and the geomorphology of the temperate and tropical areas where these species live might be important. Small islands do not have large stable freshwater habitats, so the species there have not evolved the ability to use only freshwater. Temperate areas have long rivers and large lakes, so the temperate species evolved or retained the ability to use only freshwater. This suggests that a variety of factors including those such as carrying capacity for larvae (limited in small tropical rivers) and predation pressure (high in temperate coastal waters) need to also be considered to understand the development of amphidromy in the two regions.

It appears though that species such as Sicydiinae gobies can be considered to have a life history termed as “tropical freshwater amphidromy” in which their larvae have a high oceanic dependency and that ayu, sculpins or galaxiids can be considered to have life histories termed as “temperate freshwater amphidromy” in which their larvae can use either freshwater or the ocean. In addition, the subfamily Gobionellinae with the genera *Awaous*, *Stenogobius*, *Schismatogobius* and *Rhinogobius*, the genus *Glossogobius* of the subfamily Gobiinae, some species of the Eleotridae and the Rhyacichthyidae might be included in the category of tropical freshwater amphidromy. Several studies suggest that the same characteristics found in the Sicydiinae are found in the genera *Awaous* (Ego 1956; Ha and Kinzie 1996; Yamasaki and Tachihara 2007) and *Eleotris* (Maeda and Tachihara 2004, 2005; Maeda et al. 2007, 2008), but there is no data on the life history characteristics of the Rhyacichthyidae. The Asian freshwater goby genus *Rhinogobius* is also widely distributed on some islands of the western Pacific including Japan, Taiwan, Hainan Island, the Philippines and in continental Asia, i.e. Russia, Korea, China, Vietnam, Laos, Cambodia and Thailand (Kawanabe and Mizuno 1989; Chen and Kottelat 2003). *Rhinogobius* has amphidromous and landlocked or fluvial species not only in the temperate zone, but also in the tropical zone, which is interesting, and further research on this group might provide useful information for comparisons between tropical and temperate freshwater amphidromous species.

Another less-studied issue in diadromous fish research is that only a few attempts have been made so far at comparing marine amphidromy with other categories of diadromy. Marine amphidromy may also occur in some taxa of fishes that move into freshwater after spawning occurs in the sea or estuary, with their larvae or juveniles returning back to the sea for more growth and reproduction. Myers (1949) suggested that marine amphidromy is probably more developed than is suspected, especially among families such as Mugilidae, Megalopidae (*Megalops*) and Chanidae (*Chanos*). McDowall (1988) introduced two white sardines in the genus *Escualosa* as marine amphidromous fishes. Milton (2009) listed a total of 56 species (4 species of *Ambassis*, 10 species of *Ariidae*, 6 species of *Centropomus*, 9 species of *Engraulidae*, 6 species of *Gerreidae*, *Kuhlia sandvicensis*, 9 species of *Mugilidae*, 2 species of *Megalops*, 3 species of *Ilisha*,

3 species of Syngnathidae and 3 species of *Toxotes*) as marine amphidromous fish. However, the distinction between these life histories and catadromous life histories are not clear.

More research is clearly needed on not only freshwater but also marine amphidromous species that have not been studied in detail and on the ecology of the various life history stages of these groups of diadromous fishes. The hypothesis that there are two life history categories termed as tropical and temperate freshwater amphidromy can hopefully facilitate understanding of the different types of amphidromy. Although these categories may be too general in some cases, they may be useful starting points for future studies.

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