

Review

Investigating Diadromy in Fishes and Its Loss in an -Omics Era

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SUMMARY

Diadromy, the predictable movements of individuals between marine and freshwater environments, is biogeographically and phylogenetically widespread across fishes. Thus, despite the high energetic and potential fitness costs involved in moving between distinct environments, diadromy appears to be an effective life history strategy. Yet, the origin and molecular mechanisms that underpin this migratory behavior are not fully understood. In this review, we aim first to summarize what is known about diadromy in fishes; this includes the phylogenetic relationship among diadromous species, a description of the main hypotheses regarding its origin, and a discussion of the presence of non-migratory populations within diadromous species. Second, we discuss how recent research based on -omics approaches (chiefly genomics, transcriptomics, and epigenomics) is beginning to provide answers to questions on the genetic bases and origin(s) of diadromy. Finally, we suggest future directions for -omics research that can help tackle questions on the evolution of diadromy.

INTRODUCTION

Diadromy refers to the predictable migration between marine and freshwater environments that certain species undertake during specific periods in their life (McDowall, 2008a). Although diadromy in fishes is rare (present in less than 1% of all fish species), it is widely distributed both phylogenetically and biogeographically, with many diadromous species known for their evolutionary, historical, cultural, or economic value (McDowall, 1999).

The fact that diadromy involves movement between such distinct environments suggests that it requires major physiological and behavioral adaptations. In turn, such movements have important ecological and evolutionary consequences. For instance, diadromy has played a role in the genetic structure of populations (e.g., Chubb et al., 1998; Delgado et al., 2019; Taillebois et al., 2013) and in postglacial colonization (e.g., Reusch et al., 2001; Mateus et al., 2016). Despite this relevant influence on species biology, little is known about the potential selective pressures leading to its origin, the molecular mechanisms underlying the capacity for diadromy, and the effects on species evolution. Why has diadromy evolved? Which genes give diadromous individuals the ability to migrate? And why have some diadromous populations stopped migrating? These are questions not yet adequately answered. Important efforts have, however, been made to improve our understanding of diadromy including the formulation of hypotheses about its origins (e.g., Gross 1987; Tsukamoto et al., 2009) and the search for genes that differentiate diadromous and non-migratory populations (e.g., Perrier et al., 2013; Taugbøl et al., 2014).

The development of otolith and bone tissue microchemistry during the last decade has facilitated the description and classification of diadromous fishes as this method traces the presence of individuals to marine or freshwater environments (e.g., Hale and Swearer 2008; Feutry et al., 2012; Hughes et al., 2014; Warburton et al., 2018; Górski et al., 2018). Additionally, technological advances in sequencing technologies, specifically in -omics (high-throughput sequencing to study large-scale genomes, transcriptomes, epigenomes, etc.), are facilitating significant advances in our understanding of the roles of genetics, the environment, and their interaction in the evolution of life history traits (see reviews on genomics [Orsini et al., 2013], transcriptomics [Alvarez et al., 2015], and epigenomics [Metzger and Schulte, 2016]). Studies based on -omics approaches have been conducted on many diadromous species (see section “-Omics studies in diadromous fishes”), although -omics studies analyzing diadromy as a common trait in taxa across the phylogeny of fishes are lacking.

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Although migratory behavior is present in all major animal taxa from invertebrates to mammals (Merlin and Liedvogel, 2019), the genetic bases and the evolutionary consequences of migratory behavior are not fully understood. The combination of new sequencing technologies and -omics approaches is key for the study of the evolution of life histories including the study of diadromy. Here, we aim to review our knowledge on diadromy across the phylogeny of fishes and how -omics techniques are helping answer questions about the ecology and evolution of diadromous species. We organized this essay in three sections: (1) What is known about diadromy in fishes? Here, we describe the classification, the distribution of diadromy from a phylogenetic and biogeographic perspective, the main hypotheses proposed to explain its origin, and the presence of non-migratory populations in diadromous species. (2) The contribution of -omics research to our understanding of diadromy. In this section, we discuss how research in genomics, transcriptomics, and epigenomics is providing information about the life history of diadromous species, the facultative nature of this migratory behavior, the molecular bases underpinning this trait, and the origin of diadromy. (3) What questions could future research focus on? In this section, we elaborate on broad questions that future -omics research can help address regarding the evolution, genetic mechanisms, and maintenance of diadromy in fishes.

Diadromy in Fishes—What Is Known?

The term “diadromy” was first introduced by Myers to describe “truly” migratory fishes (Myers, 1949), with “truly” referring to the movement between marine and freshwater environments (McDowall, 1993). McDowall (1997) expanded the definition and proposed specific characteristics that all diadromous species must fulfill. These include: migration must be mediated through physiological changes, it must occur at predicted times, and it should involve reciprocal migrations (McDowall, 1997). Although most diadromous species are known to be euryhaline, some are amphihaline, meaning that they can only adapt to a different salinity at a particular life stage (McDowall, 2009).

Diadromous species include fishes, gastropod mollusks (family Neritidae, see Abdou et al., 2015), and crustaceans (families Atyidae and Palaemonidae) (McDowall, 1997); however, in this review, we focus on fishes. More than 440 fish species have been reported to be diadromous (Table S1). These species are distributed among 58 of the 482 recognized families of fishes (Nelson, 1994); however, almost 62% of all diadromous fishes are concentrated in only seven families (Table 1).

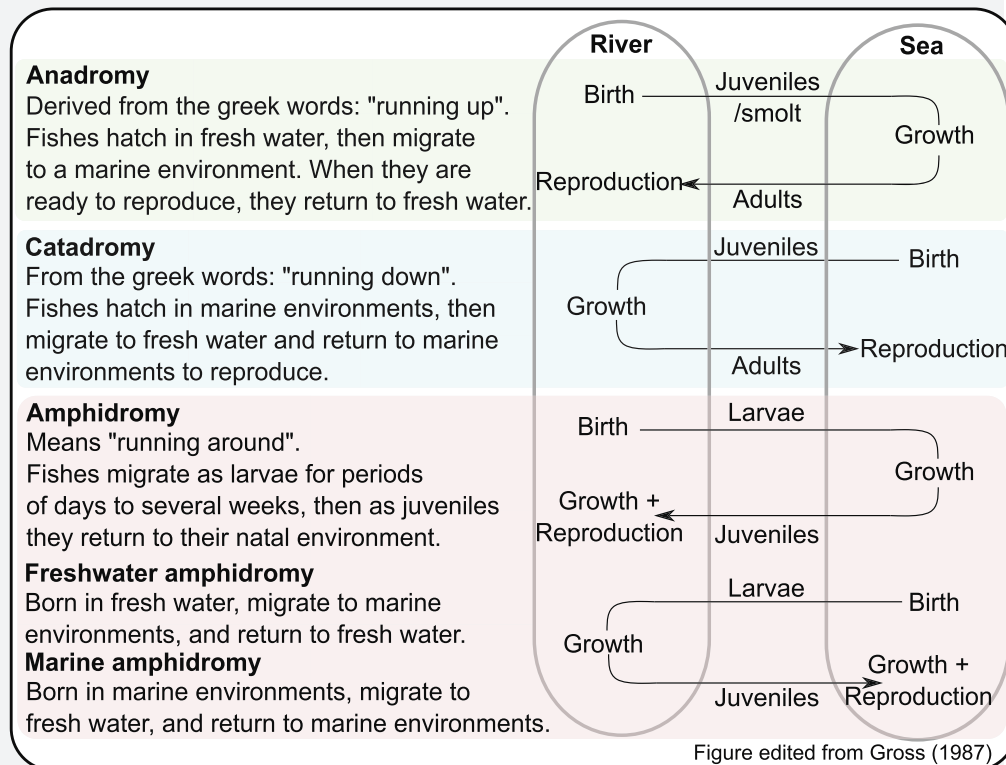
Classification

There are three categories of diadromy (Gross, 1987; McDowall, 1997); fishes can be anadromous, catadromous, or amphidromous (Box 1). Categories differ in the direction of the first migration, from rivers to the sea (i.e., anadromy and freshwater amphidromy) or vice versa (i.e., catadromy, marine amphidromy); the time of migration, particularly the life cycle stage when individuals return to their natal environment (i.e., juveniles versus adults); and the purpose of the return migration, i.e., if the return to their natal environment is for growing and/or spawning purposes.

Of the 444 species reported here as diadromous, 147 are described as anadromous, 73 as catadromous, and 224 as amphidromous (Table 1), with almost all amphidromous species reported as freshwater amphidromous. Table S1 lists species that followed McDowall’s definition of diadromy and that are referenced in a scientific paper or book; however, for many species particularly amphidromous species, little information is available (Tables 1 and S1). Although Riede (2004) reported a higher number of amphidromous species than in this paper, this was due to the use of a broader definition of amphidromy (Chalant et al., 2019). We can, however, expect the total number of diadromous (mainly amphidromous) species to increase, with the increased focus on understudied species, for instance, from the tropics.

Anadromy is the most phylogenetically widespread category, present in 29 families, but only two families (Salmonidae and Clupeidae) comprise 41% of all anadromous species. Catadromy is present in 19 families. However, two families (Mugilidae and Anguillidae) represent almost 59% of all catadromous species. Amphidromy holds the highest number of diadromous species and is present in 26 families, two of which (Elo-tridae and Gobiidae) include 62% of all amphidromous species. Although most species from the same order belong to the same category of diadromy, different categories can be present within an order or even within a family. Four orders (Clupeiformes, Gobiiformes, Mugiliformes, and Perciformes) have species of all three categories (Table 1 and Figure 1).

Box 1. Diadromous Species Classification



Phylogeny and Biogeography

Diadromy is present from agnathans to the most recent bony fishes, indicating that it is an evolutionarily successful strategy (McDowall, 1993). Despite the high cost of migration, which includes genetic, morphological, physiological, and behavioral requirements, diadromy is likely to have evolved multiple times (Corush, 2019; McDowall, 1997). The most recent Actinopterygii phylogeny developed from genomic and transcriptomic data (Hughes et al., 2018) confirms that diadromy is widespread across the fish phylogeny (Figure 1).

Anadromy is more phylogenetically widespread than catadromy or amphidromy. Although anadromy is found from lampreys, a lineage that appeared before the Actinopterygii to the most recent order, catadromy is present from the Anguilliformes order, a lineage that appeared during the Jurassic Period when marine species reappeared (Fyhn et al., 1999), to more recent families (i.e., Lutjanidae). Amphidromous species, on the other hand, are present from the order Clupeiformes to the order Perciformes (Figure 1).

From a biogeographic point of view, diadromy is widely distributed across the globe. Gross (1987) described a latitudinal shift where anadromous species are prevalent at relatively high latitudes, whereas catadromous species have a relatively high occurrence in the tropics. This pattern led to the productivity hypothesis (see "Hypotheses on the origin" section). Amphidromy also appears to be found predominantly in the tropics (McDowall, 2010). However, although categories have higher incidence at certain latitudes, diadromous species of all three categories can be found at both high and low latitudes,

Order	Family	Diadromous	Anadromous	Catadromous	Amphidromous
Acipenseriformes	Acipenseridae (R)	18	18		
	Ambassidae	4		1 ^a	3 ^a
Anguilliformes	Anguillidae (R)	16		16	
	Muraenidae	1		1	
	Ophichthidae	1	1 ^a		
Atheriniformes	Atherinidae	1			1 ^a
	Atherinopsidae	2	2 ^a		
Characiformes	Citharinidae	2	2 ^a		
Clupeiformes	Clupeidae (R)	31	26	2	3
	Engraulidae (R)	11	5	1	5 ^a
	Pristigasteridae	7	4 ^a		3 ^a
Cypriniformes	Cyprinidae (R)	6	6		
Elopiformes	Elopidae	1	1 ^a		
	Megalopidae	1		1 ^a	
Gadiformes	Gadidae	1	1		
	Lotidae (R)	1	1 ^a		
Galaxiiformes	Galaxiidae (R)	11	1		10
Gobiesoformes	Gobiesocidae (R)	1			1
Gobiiformes	Eleotridae (R)	37		5 ^a	32
	Gobiidae (R)	103	2		101
	Lutjanidae	2		2 ^a	
	Moronidae (R)	2	2		
Mugiliformes	Mugilidae (R)	34	1 ^a	27	6 ^a
Osmeriformes	Osmeridae (R)	10	10		
	Plecoglossidae	1			1
	Retropinnidae	5	1 ^a		4
	Salangidae (R)	6	6		
Perciformes	Carangidae	2			2 ^a
	Centropomidae	9		2	7 ^a
	Cheimarrichthyidae	1			1
	Cottidae	8		2	6
	Gasterosteidae (R)	2	2		
	Gerreidae	7			7 ^a
	Haemulidae	1			1 ^a
	Kuhliidae	10		5	5

Table 1. Total Number of Known Diadromous Species Reported by Family and Category

(Continued on next page)

Order	Family	Diadromous	Anadromous	Catadromous	Amphidromous
	Lateolabracidae	1		1	
	Latidae	1		1	
	Percichthyidae	1		1	
	Percidae (R)	1	1		
	Pseudaphritidae	1		1	
	Rhycichthyidae	2			2
	Scianidae	3			3 ^a
	Terapontidae	1		1 ^a	
	Tetrarogidae	1		1	
	Toxotidae	3			3 ^a
Petromyzontiformes	Geotriidae	1	1		
	Mordaciidae	2	2		
	Petromyzontidae (R)	8	8		
Pleuronectiformes	Pleuronectidae	2		2	
Salmoniformes	Salmonidae (R)	35	35		
Siluriformes	Ariidae (R)	13	3		10 ^a
	Bagridae	1	1 ^a		
	Claroteidae	1	1 ^a		
	Pangasiidae	1	1		
	Plotosidae	1			1 ^a
	Schilbeidae	1			1
Syngnathiformes	Syngnathidae	5			5
Tetraodontiformes	Tetraodontidae (R)	2	2		
Total		444	147	73	224

Table 1. Continued

The complete list of diadromous species is in [Table S1](#).

(R) report of resident populations.

^aLittle information available (e.g., no microchemistry analysis).

providing evidence against the productivity hypothesis ([Figure 2](#)). The widespread extent of diadromous species supports its important role in species dispersal, including transoceanic dispersal ([Chubb et al., 1998](#); [McDowall, 1998](#)).

Hypotheses on the Origin

Although phylogenetic data support the hypothesis that diadromy has evolved multiple times ([Figure 1](#)), the origin of diadromy and its evolutionary bases are still under debate ([Bloom and Lovejoy, 2014](#)). Below, we summarize the main hypotheses for the origin of diadromy.

- **Productivity or Resource Availability Hypothesis.** This is the most accepted hypothesis first proposed by [Gross \(1987\)](#). It is based on the findings of latitudinal trends for anadromous and catadromous species by [Baker, 1978](#) and [Northcote, 1978](#) and states that anadromous species are more prevalent at high latitudes because productivity in the sea at those latitudes is higher than in freshwater environments.

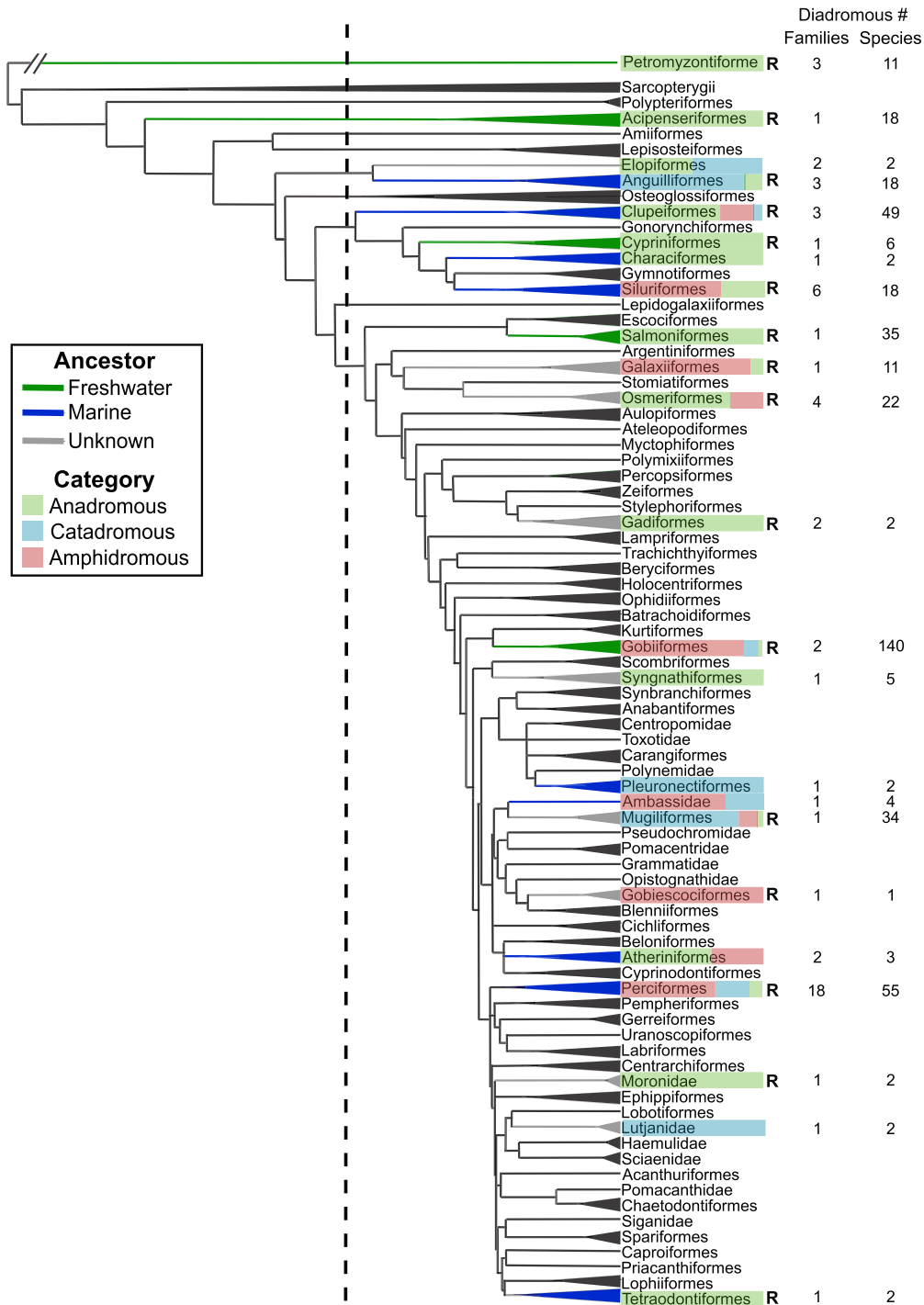


Figure 1. Actinopterygians Phylogeny Adapted from Hughes et al. (2018)

The colors in each terminal branch have been added to indicate the most likely origin of the ancestor for diadromous taxa (see Table S3 for references). Taxa exhibiting diadromy have colored background labels reflecting the category of diadromy (anadromy, catadromy, or amphidromy). Some taxa exhibit more than one form of diadromy, and their proportion is indicated by the different colors in the label backgrounds. The dotted line represents the beginning of the Jurassic Period. The R to the right states the presence of resident populations and the numbers the number of known diadromous families and species for each taxon.

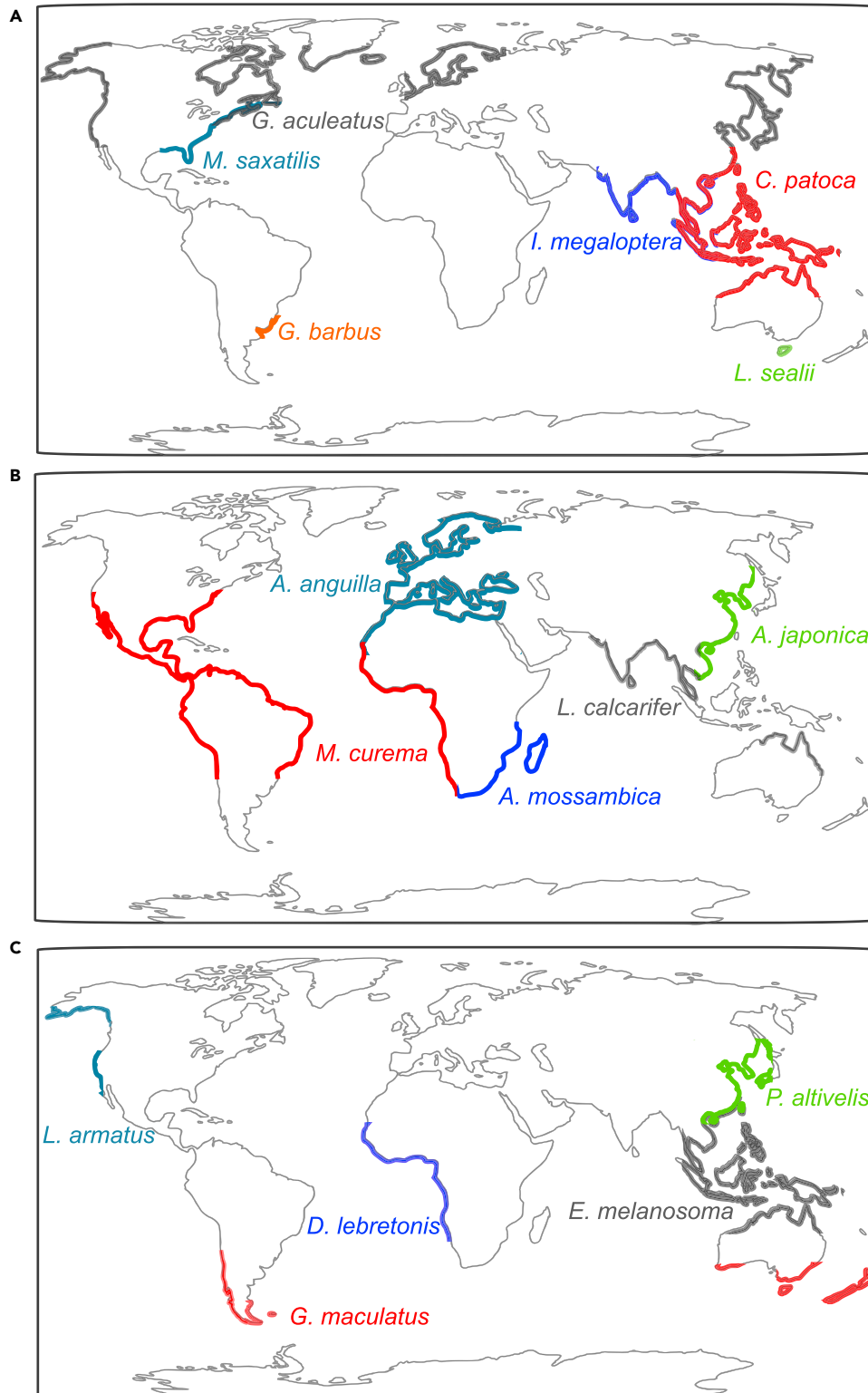


Figure 2. World Map Depicting the Distribution of Five to Six Diadromous Species Present at Different Latitudes

- (A) Anadromous species.
- (B) Catadromous species.
- (C) Amphidromous species.

Catadromy instead, is relatively common at tropical latitudes, given that the productivity of fresh water at low latitudes is higher than in the sea.

The presence of all categories of diadromy at different latitudes questions the generality of this hypothesis (McDowall 2008b; Figure 2), for example, temperate eels migrate to freshwater environments that have lower productivity than marine environments (Edeline, 2007). Bloom and Lovejoy (2014) tested this hypothesis using the phylogeny of the order Clupeiformes. Their results did not support the productivity hypothesis as the ancestry of diadromy could not be predicted based on latitude (Bloom and Lovejoy, 2014).

Historical processes including the expansion and invasion of newly available environments following post-Pleistocene deglaciation could explain the prevalence of anadromous species in northern temperate latitudes (McDowall, 2008b). Temperature and particularly temperature fluctuations could also explain the incidence of diadromy. For example, at high latitudes temperature fluctuates more in fresh water than in the sea, a factor that has led to the hypothesis that the invasion of fresh water (i.e., catadromy) is more frequent at low latitudes (Lee and Bell, 1999).

- **Random Escapement Hypothesis.** This hypothesis, proposed by Tsukamoto et al. (2009), is based on behavioral models from observations of the amphidromous Ayu (*Plecoglossus altivelis*) and argues that diadromy originated as an escapement behavior of fishes to leave unfavorable environments, instead of as migration to a more nutrient-rich habitat (i.e., productivity hypothesis). A three-step model is used to explain the start of migration. First, an individual needs to reach a threshold age or size; second, it needs to be physiologically prepared; and third, it needs to receive an endogenous or exogenous cue to initiate migration (Tsukamoto et al., 2009).

Similarly, a “safe-site” hypothesis was proposed, where migration to fresh water or a “safe haven” is a consequence of the need to protect early life history stages from marine predators. An example is the early larval migration of osmeroids, which has been hypothesized to maximize their survival, and therefore their fitness, due to the presence of safe sites (Dodson et al., 2009).

- **Ecological Opportunity Hypothesis.** Proposed by Feutry et al. (2013), this hypothesis states that diadromy appears as a response to ecological opportunities (Feutry et al., 2013). Using the case of the *Kuhlia* family, within which catadromous species migrate to nutrient-poor environments, the authors proposed that diadromy originated owing to the opportunity to colonize insular ecosystems. These isolated habitats would be characterized, for example, by an absence of predators, making them ideal for colonization. This idea to move to an ecological advantageous site is similar to the “safe-site” hypothesis.

- **Intermediate State Hypothesis.** This hypothesis states that diadromous fishes have appeared as an intermediate state between fully freshwater and fully marine fishes (Gross, 1987). Gross (1987) also proposed that amphidromy is the ancestral state of both anadromy and catadromy. The hypothesis suggested that anadromous species evolved from amphidromous species, which evolved from euryhaline wanderers that evolved from freshwater species whereas catadromy evolved from amphidromous species that originated from euryhaline wanderers that evolved from marine species (Gross, 1987). The improvement in our understanding regarding the biology of amphidromy, specifically, the short time (i.e., days or weeks) amphidromous species spend in the secondary environment, led to the rejection of the idea that amphidromy was an intermediate step between fully freshwater and marine fishes (Gross, 1997).

Recently, Corush (2019) tested this hypothesis by simulating the rate of transitions in and out of diadromy and comparing it between freshwater, marine, and diadromous fishes. Transition rates out of diadromy into strictly marine or strictly freshwater life histories were higher than transitions in the opposite directions (from marine or freshwater life histories into diadromy), leading to the conclusion that diadromy may sometimes be an intermediate state between freshwater and marine fishes, but not always (Corush, 2019).

- **Conditional Evolutionary Stable Strategy Model.** This model proposed that diadromy is a phenotypically plastic trait in which an individual expresses a migratory phenotype depending on environmental variables and will migrate if this migration leads to higher fitness (Edeline, 2007). This model is supported by the fact that the migration in diadromous species reduces inter- and intra-specific competition (Edeline, 2007). Although the Conditional Evolutionary Stable Strategy Model (CESSM) may apply for some species,

the presence of sympatric migratory and non-migratory populations that show high levels of genetic differentiation (e.g., [Salisbury et al., 2018](#); [Delgado et al., 2019](#)) suggests that in such cases the decision to migrate does not just depend on environmental variables.

Loss of Diadromy

Major reductions in dispersal ability have evolved many times across numerous taxa ([Waters et al., 2020](#)). Non-migratory (hereafter called resident) populations exist among all three categories of diadromous fish species ([Table 1](#)). Many resident populations within a species have evolved multiple independent times and derived from a common diadromous ancestor, as the case of the anadromous *Alosa pseudoharengus* in Connecticut, USA ([Palkovacs et al., 2008](#)), or the amphidromous *Galaxias maculatus* in Chile ([Delgado et al., 2019](#)). Resident populations need not be landlocked; they can inhabit environments with access to the sea despite which they do not migrate but remain in their natal habitat. Examples of resident populations have been described for all categories of diadromy as follows.

- **Anadromous Species.** Atlantic salmon (*S. salar*), brown trout (*S. trutta*), brook trout (*S. fontinalis*), Arctic charr (*S. alpinus*), white-spotted charr (*S. leucomaensis*), Dolly Varden (*S. malma*), rainbow trout (*O. mykiss*), masu salmon (*O. masau*), coastal cutthroat Trout (*O. clarki*), sockeye salmon (*O. nerka*), Chinook salmon (*O. tshawytscha*) (e.g., [Dodson et al., 2013](#)), three-spined stickleback (*G. aculeatus*) (e.g., [Bell and Foster 1994](#)), and Japanese smelt (*H. nipponensis*) (e.g., [Arai et al., 2006b](#)).

- **Catadromous Species.** European eel (*A. Anguilla*) (e.g., [Arai et al., 2006a](#)), Japanese eel (*A. japonica*) (e.g., [Tsukamoto and Arai 2001](#)), American eel (*A. rostrata*) (e.g., [Lamson et al., 2009](#)), and tupong (*P. urvillii*) (e.g., [Crook et al., 2010](#)).

- **Amphidromous Species.** Common galaxias (*G. maculatus*) (e.g., [Delgado et al., 2019](#)), spotted galaxias (*G. truttaceus*) (e.g., [Waters et al. 2001](#)), big-scaled redbfin (*T. hakonensis*) (e.g., [Sakai et al., 2002](#)), New Zealand eleotrid (*G. cotidianus*) (e.g., [Michel et al., 2008](#)), and *Rhinogobius* sp. ([Tsunagawa et al., 2010](#)).

The existence of resident populations that can migrate (i.e., inhabiting environments with access to the sea), but do not, suggests that migration may not always be beneficial and that ecological factors likely play an important role in the decision to migrate. Facultative diadromy demonstrates that there is a balance between the benefits and costs of migration and residency tactics ([Hogan et al., 2014](#)). [Ferguson et al. \(2019\)](#) introduced the threshold-trait model to explain which factors determine or affect the decision of whether or not to migrate. This model involves two components: a genetic and environmental threshold. Individuals remain resident if the energy status is high and exceeds a given threshold. Alternatively, individuals migrate if their energy status is low (i.e., nutritionally deficient).

[Gross \(1987\)](#) proposed a model to explain diadromy, which is simplified in [Figure 3](#). In basic terms, the fitness of migrating adding the cost of migration must be higher than the fitness acquired by remaining in the natal environment. Following Gross hypothesis and Ferguson's threshold model, we propose to explain the loss of diadromy from an ecological and evolutionary perspective following one or the combination of four scenarios in nature ([Figure 3](#)).

- **No Alternative - [Figure 3A](#).** There are two possible explanations for the loss of diadromy ([Figure 3A](#)). Either a population becomes physically landlocked unable to leave its natal environment or the presence of mutations makes individuals physiologically unable to migrate (i.e., the genetic component of the threshold-trait model). Mutations that would affect the ability to migrate in diadromous fishes may be linked to osmoregulatory genes, nutrient assimilation genes, and signaling (see "Molecular bases" section).

- **Increase in the Cost of Migration - [Figure 3B](#).** This could be due to changes in the river systems; for example, a change in the landscape could lead to a longer distance to reach the estuary increasing the cost of migration ([Figure 3B](#)). Natural or anthropogenic barriers such as dams would also increase the cost of migration.

- **Decrease in the Fitness of Migration - [Figure 3C](#).** This would be the product of changes in the environmental conditions of the secondary habitat, for example, reduction of food supply, an increase in the

Diadromy evolved if:

ability to migrate	+	"low" cost of migration	+	fitness of migrating	>	fitness of staying
No physical barriers		Reproduction occurs		> Food		< Food
Physiologically able:		in ancestral environment		< Competition/predation		> Competition/predation
genetic mechanisms present*				< Chances inbreeding		> Chances inbreeding

Diadromy is lost if:

	ability to migrate	+	cost of migration	+	fitness of migrating	<	fitness of staying
A	X		Landlocked				
			Physiologically				
			unable: mutations*				
B			↑		> distance to estuary		
					> challenging conditions		
C					↓	< Food	
						> Competition/predation	
D						↑	> Food
							< Competition/predation
							Locally adapted

*related to osmoregulation, nutrient assimilation, signaling and/or immune response

Figure 3. A simplified model to explain the "decision" to migrate (Diadromy) or remain in the natal environment (Loss of diadromy) from an Eco-Evo perspective.

number of predators, or an increase in parasite threats (Figure 3C). These changes would lead to a reduction in fitness and even the survival of the migrating phenotype.

● **Increase in the Fitness of Staying - Figure 3D.** Changes in the environmental conditions in the natal habitat that would lead to a higher fitness payoff for a decision to stay (i.e., the environmental component of the threshold-trait model) (Figure 3D). This could result from a decrease in the fitness value of the secondary environment (Figure 3C) or positive changes in the natal habitat. Examples of the latter are the increment in the quality and quantity of resources and a decrease in competition.

Omics Studies in Diadromous Fishes—What Current Research Tells Us?

Since the introduction of next-generation sequencing (NGS) and the drop in sequencing cost, the number of studies using DNA, RNA, and methylation to address ecological and evolutionary dynamics questions has increased. Here, we present a list of studies on diadromous species that used -omics techniques, chiefly genomics, transcriptomics, and epigenomics (Table 2). This list is based on published articles and excludes books, theses, articles in bioRxiv, and conference abstracts.

Anadromy is by far the category with the highest number of studies (Table 2). From the >120 papers listed, 84% concern anadromous species. Within anadromy, the most intensely studied species are three-spined stickleback (*Gasterosteus aculeatus*), rainbow trout (*O. mykiss*), and Atlantic salmon (*Salmo salar*). Catadromy is the second category in terms of the number of studies; however, most research on catadromy has focused on species from the *Anguilla* family, particularly, the European eel (*Anguilla anguilla*). Most genetic research on amphidromous species has thus far been based on a few mitochondrial and nuclear markers (e.g., Crandall et al., 2010; Lord et al., 2015; Taillebois et al., 2013) with studies within this group using -omics approaches being scarce (Table 2). These findings are not surprising as anadromous species are more prevalent in the Northern Hemisphere, where most research takes place, and they are of economic importance.

The type of -omics approach used is a function of the research objectives (Table 2). Box 2 lists the most common methods with Reduced Representation Sequencing (RRS) being the most widely used. RRS is a cost-effective method that provides a large but limited number of markers across the genome (Wright et al., 2019). In some cases, RRS proved to be more powerful than previous genetic markers (e.g., few microsatellites, few mitochondrial genes) in differentiating and assigning individuals to populations (e.g., Moore

Diadromy Category	-Omics Approach (Methods)	Research Objective	Species Studied	Include Residents	References Examples
Anadromy	Genomics (GBS, RADseq, ddRADseq, RADcap, SNP array, NextRAD, Pool-seq, whole-genome sequencing)	Development of molecular markers/SNP panels	<i>Salmo salar</i> ; <i>Alosa pseudoharengus</i> ; <i>Alosa aestivalis</i>	No	Houston et al. (2014); Yáñez et al. (2016); Baetscher et al. (2017)
		Applicability of SNP array from close-related species	<i>Salmo trutta</i>	No	Drywa et al. (2013)
		Assembly of a reference genome	<i>Salmo salar</i> ; <i>Oncorhynchus tshawytscha</i> ; <i>Pungitius pungitius</i>	No	Davidson et al. (2010); Christensen et al. (2018); Varadharajan et al. (2019)
			<i>Salmo salar</i>	Yes	Hauge et al. (2016)
		Assembly of mitochondrial genome	<i>Takifugu obscurus</i> ; <i>Lethenteron camtschaticum</i> ; <i>Coilia nasus</i>	No, Yes, No	Kim et al. (2014); Balakirev et al. (2016); Zhang et al. (2016)
		Development of linkage map/chromosome rearrangements	<i>Salmonidae</i>	No	Sutherland et al. (2016)
		Population diversity and structure	<i>Leuciscus idus</i> ; <i>Oncorhynchus mykiss</i> ; <i>Salvelinus fontinalis</i> ; <i>Salmo trutta</i>	Yes	Skovrind et al. (2016); Leitwein et al. (2017); Elias et al. (2018); Lemopoulos et al., 2018b
			<i>Salmo salar</i> ; <i>Salvelinus alpinus</i> ; <i>Brachymystax lenok</i> ; <i>Tenulosa ilisha</i> ; <i>Alosa pseudoharengus</i> ; <i>Alosa aestivalis</i>	No	Asaduzzaman et al. (2019); Aykanat et al. (2015); Madsen et al. (2020); Moore et al. (2017, 2014); Reid et al. (2018); Roman et al. (2018)
		Genomic divergence/local adaptation	<i>Thaleichthys pacificus</i> ; <i>Oncorhynchus tshawytscha</i>	No	Candy et al. (2015); Narum et al. (2018)
			<i>Coregonus clupeaformis</i> ; <i>Salmo salar</i> ; <i>Entosphenus tridentatus</i> ; <i>Lampetra fluviatilis</i> ; <i>Oncorhynchus nerka</i> ; <i>Lampetra planeri</i> ; <i>Salvelinus alpinus</i>	Yes	Bourret et al. (2013); Hume et al. (2018); Mateus et al. (2013); Nichols et al. (2016); O'Malley et al. (2019); Parker et al. (2019); Renaut et al. (2011); Rougemont et al. (2017); Salisbury et al. (2020); Veale and Russello (2017)
			<i>Gasterosteus aculeatus</i>	Yes	Hohenlohe et al. (2010); Jones et al. (2012); Guo et al. (2015); Ferchaud and Hansen (2016); Currey et al., 2019; Dean et al. (2019); Marques et al. (2019); Rennison et al. (2019); Terekhanova et al. (2019)
			<i>Oncorhynchus mykiss</i>	Yes	Hale et al. (2013); Hecht et al. (2013); Pearse et al.

Table 2. Representation of Research in Diadromous Fishes that Have Used an -Omics Approach

(Continued on next page)

Diadromy Category	-Omics Approach (Methods)	Research Objective	Species Studied	Include Residents	References Examples
					(2014); Bowersox et al. (2016); Matala et al. (2017); Arostegui et al. (2019)
			<i>Salmo salar</i>	Yes	Bourret et al. (2011); Culling (2013); Perrier et al. (2013)
		Introgression/hybridization	<i>Gasterosteus aculeatus</i> ; <i>Leucopsarion petersii</i> ; <i>Alosa pseudoharengus</i> ; <i>Pungitius pungitius</i>	Yes	Guo et al. (2019); Hirase et al. (2020); Reid et al. (2020); Yoshida et al. (2016)
		Genotype - migration associations	<i>Salmo salar</i> ; <i>Oncorhynchus tshawytscha</i> ; <i>Oncorhynchus mykiss</i> ; <i>Salmo trutta</i>	No	Brieuc et al. (2015); Cauwelier et al. (2018); Johnston et al. (2014); Lemopoulos et al. (2018a); Micheletti et al. (2018a); Prince et al. (2017); Thompson et al. (2020)
		Genotype - sex - migration associations	<i>Oncorhynchus mykiss</i>	Yes	Kelson et al. (2019)
		Genotype - environment associations	<i>Oncorhynchus mykiss</i> ; <i>Gasterosteus aculeatus</i>	Yes	Micheletti et al., 2018b; Stuart et al. (2017); Haenel et al. (2019)
			<i>Salmo salar</i> ; <i>Oncorhynchus mykiss</i>	No	Jeffery et al. (2017); Willoughby et al. (2018)
		Genotype - microbiota associations	<i>Gasterosteus aculeatus</i>	Yes	Steury et al. (2019)
		Sex determination	<i>Gasterosteus aculeatus</i>	No	Bissegger et al. (2019)
		Transcriptomics (RNA-seq, cDNA arrays, microarrays)	Assembly of transcriptomic profiles	<i>Oncorhynchus mykiss</i> ; <i>Salmo salar</i> ; <i>Salmo trutta</i> , <i>Salvelinus alpinus</i> , <i>Coregonus lavaretus</i> ; <i>Oncorhynchus tshawytscha</i>	Yes
	Detection of lncRNAs		<i>Oncorhynchus mykiss</i>	No	Al-Tobasei et al. (2016)
	Expression profiles of spermatogenesis		<i>Coilia nasus</i>	No	Zhou et al. (2015)
	Expression profiles before migration		<i>Salvelinus fontinalis</i>	Yes	Boulet et al. (2012)
	Expression profiles of infection response		<i>Gasterosteus aculeatus</i> ; <i>Oncorhynchus mykiss</i> ; <i>Salmo salar</i> & <i>Salmo trutta</i>	Yes	Lenz et al. (2013); Sutherland et al. (2014)
	Expression profiles hatchery versus wild		<i>Salmo salar</i> ; <i>Oncorhynchus mykiss</i>	No	Bicskei et al. (2014); Fox et al. (2014)
Expression profiles juvenile brains	<i>Oncorhynchus mykiss</i>		Yes	Hale et al. (2016)	

Table 2. Continued

(Continued on next page)

Diadromy Category	-Omics Approach (Methods)	Research Objective	Species Studied	Include Residents	References Examples
		Expression profile hybrids	<i>Salvelinus fontinalis</i>	Yes	Mavarez et al. (2009)
		Genomic population/divergence	<i>Coregonus clupeaformis</i> ; <i>Alosa pseudoharengus</i> ; <i>Oncorhynchus nerka</i> ; <i>Salmo salar</i>	Yes; No	Jeukens et al. (2010); Czesny et al. (2012); Lemay et al. (2013); Warren et al. (2014)
		Salinity adaptation	<i>Alosa pseudoharengus</i> ; <i>Gasterosteus aculeatus</i> ; <i>Salmo salar</i>	Yes	Lemmetynen et al. (2013); Gibbons et al. (2017); Kusakabe et al. (2017); Rastorguev et al. (2017); Velotta et al. (2017)
		Temperature adaptation	<i>Salmo trutta</i> ; <i>Gasterosteus aculeatus</i>	Yes	Meier et al. (2014); Morris et al. (2014)
		Migratory life history	<i>Salmo trutta</i> ; <i>Salmo Salar</i>	Yes	Giger et al. (2008)
		Environmental stress associations	<i>Takifugu obscurus</i>	No	Xu et al. (2018)
		Freshwater colonization	<i>Gasterosteus aculeatus</i> & non-diadromous sister species	Yes	Kitano et al., 2019; Ishikawa et al. (2019)
	Proteomics	Salinity adaptation	<i>Coregonus lavaretus</i>	Yes	Papakostas et al. (2012)
	Epigenomics (RRBS, MSAP)	Genotype - environment associations/stressors	<i>Gasterosteus aculeatus</i> ; <i>Salmon trutta</i>	No	Aniagu et al. (2008); Morán et al. (2013); Fellous and Shama (2019)
		Genotype-phenotype associations	<i>Salmon trutta</i> ; <i>Gasterosteus aculeatus</i>	No; Yes	Covelo-Soto et al. (2015); Smith et al. (2015)
		Salinity adaptation	<i>Gasterosteus aculeatus</i>	Yes	Artemov et al. (2017)
		Migration effects	<i>Oncorhynchus mykiss</i>	Yes	Baerwald et al. (2016)
		Hatchery effects	<i>Oncorhynchus kisutch</i> ; <i>Oncorhynchus mykiss</i>	No	Le Luyer et al. (2017); Gavery et al. (2018)
	Catadromy	Genomics (genome sequencing, RADseq, Pool-seq)	Molecular markers development	<i>Anguilla japonica</i>	No
Assembly of mitochondrial genome			<i>Trachidermus fasciatus</i>	No	Zhu et al. (2018)
Population structure			<i>Mugil cephalus</i> ; <i>Anguilla japonica</i> ; <i>Anguilla anguilla</i> & <i>Anguilla rostrata</i> ; <i>Trachidermus fasciatus</i>	No	Krück et al. (2013); Igarashi et al. (2018); Gong et al. (2019); Li et al. (2019)
Adaptive divergence			<i>Anguilla rostrata</i> ; <i>Cottus asper</i>	Yes	Pavey et al. (2015); Dennenmoser et al. (2017)
Hybridization			<i>Anguilla anguilla</i> & <i>Anguilla rostrata</i>	No	Pujolar et al. (2014); Nikolic et al., 2020
Transcriptomics (RNA-seq, cDNA array)		Transcriptomic profiles	<i>Anguilla anguilla</i> ; <i>Trachidermus fasciatus</i>	No	Churcher et al. (2015); Ma et al. (2018)

Table 2. Continued

(Continued on next page)

Diadromy Category	-Omics Approach (Methods)	Research Objective	Species Studied	Include Residents	References Examples
		Genotype-phenotype associations	<i>Anguilla rostrata</i>	No	Côté et al. (2014)
	Proteomics	Salinity acclimation	<i>Anguilla marmorata</i> ; <i>Trachidermus fasciatus</i>	No	Jia et al. (2016) ; Ma et al. (2018)
	Epigenomics (MSAP)	Methylation changes between life stages	<i>Anguilla anguilla</i>	No	Trautner et al. (2017)
Amphidromy	Genomics (genome sequencing, RADcap)	Development of molecular markers	<i>Oncorhynchus clarki lewisi</i>	No	Campbell et al. (2012)
		Assembly of mitochondrial genome	<i>Sicyopterus lagocephalus</i>	No	Chiang et al. (2015)
		Phylogeny (mitogenome)	<i>Sicyopterus genus</i>	No	Lord et al. (2019)
		Populations diversity and structure	<i>Galaxias maculatus</i>	Yes	Delgado et al. (2019)
		Salinity adaptation	<i>Galaxias maculatus</i>	Yes	Delgado et al. (2020)
Transcriptomics (transcriptome sequencing)	Salinity adaptation	<i>Plecoglossus altivelis</i>	Yes	Lu et al. (2016)	

Table 2. Continued

[et al., 2014](#); [Candy et al., 2015](#); [Yoshida et al., 2016](#)), yet this is not necessarily always the case as shown by a study based on a relatively larger number of sequenced microsatellite markers ([Layton et al., 2020](#)). An alternative to RSS is whole-genome sequencing, and this can be done sequencing individuals or pools of individuals (Pool-seq) ([Fuentes-Pardo and Ruzzante, 2017](#)). However, given its cost, it has been used mainly in economically important species.

Genomic approaches allow the exploration of both neutral and adaptive markers, thus facilitating the examination of the genetic bases and mechanisms of adaptation ([Orsini et al., 2013](#)). Markers distributed across the genome have been used to estimate levels of genetic diversity (e.g., [Bowersox et al., 2016](#); [Gong et al., 2019](#)), effective populations size (e.g., [Li et al., 2019](#)), bottlenecks (e.g., [Ferchaud and Hansen 2016](#)), and fine-scale populations structure or lack thereof (e.g., [Mateus et al., 2013](#); [Aykanat et al., 2015](#); [Skovrind et al., 2016](#)) in many diadromous species (Table 1). Outlier markers are used for the assessment of genetic divergence among populations (e.g., [Box 3A](#)). Estimating this divergence can provide information on the colonization history of diadromous species, the description of glacial lineages, and the effects of secondary contact (e.g., [Bourret et al., 2013](#); [Dean et al., 2019](#)). Genome-wide studies have also revealed the molecular mechanisms (i.e., genes or islands of differentiation) supporting population divergence (e.g., [Larson et al., 2016](#)). Genetic markers differentiating phenotypes and populations can be used to assist in the assessment of relevant traits for fisheries/production (e.g., [Yáñez et al., 2016](#)), in the assignment of regional fisheries stocks (e.g., [Baetscher et al., 2017](#)), in the detection of introgression (e.g., [Bourret et al., 2011](#)), in the assessment of hybridization due to secondary contact (e.g., [Reid et al., 2020](#)), and in the detection of anthropogenic effects (e.g., [Leitwein et al., 2017](#)); this type of genotype-phenotype association studies has also given insights on which genes (i.e., loci under selection) underpin migratory behavior (e.g., [Micheletti et al., 2018a](#)).

The facultative nature of diadromy in many species suggests that variation between migratory and resident behavior could happen at a transcriptional (i.e., transcriptome) or post-transcriptional (i.e., epigenome) level; thus, the molecular variation would be found in the expression of genes rather than genes themselves. Transcriptomic studies in diadromous species have been used to examine differences in gene expression between populations, revealing critical genes involved in, for example, spermatogenesis ([Zhou et al., 2015](#)), and also involved in processes related to migratory behavior including

Box 2. Most Common Methods Used in -Omics Studies about Diadromous Species

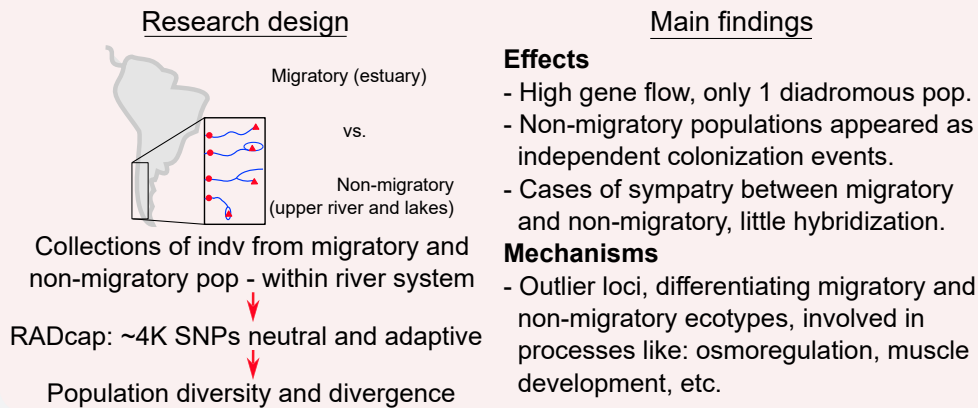
A Genomics		Pros/Cons	
● RRS: RADseq, ddRAD, RADcap	+ "Thousands" of markers located genome-wide.	- Chance of missing informative/adaptive markers.	
● Whole genome Individuals or pools (Pool-Seq)	+ Complete genomic information for the species.	- Expensive.	
B Transcriptomics		Pros/Cons	
● RRS: RNA-seq	+ Allows <i>de novo</i> assembly, great for non-model organisms.	- Bioinformatically challenging, eg: repetitive sequence, isoforms, etc.	
● Microarrays	+ Species-specific arrays provide high reliability.	- Require prior knowledge of the genome.	
C Epigenomics		Pros/Cons	
● RRS: Bisulfite Sequencing (RRBS)	+ High resolution, single base.	- Chance of missing methylation sites.	
● Methylation Sensitive Amplified Polymorphism (MSAP)	+ No need for genomic information and inexpensive.	- Low resolution.	

osmoregulation (Velotta et al., 2017), signaling or sensory perception (how fishes process light [Hale et al., 2016]), nutrient assimilation (Ishikawa et al., 2019), immune response (Lenz et al., 2013), and growth (Box 3B). These studies have also highlighted the importance of regulatory regions and their effects (e.g., Czesny et al., 2012). Furthermore, transcriptomics has been used to study salinity and temperature can affect the expression of genes differentially across populations (e.g., Meier et al., 2014 and Côté et al., 2014: Box 3B). This information is likely to be useful for predicting responses to changes in environmental conditions.

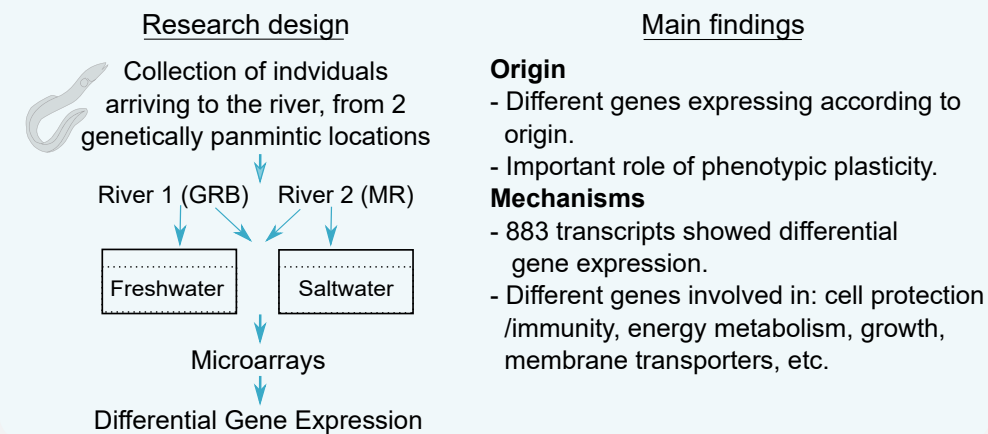
Phenotypic variance in migratory traits can be a product of genetics but may also be solely due to phenotypic plasticity as a response to environmental triggers, suggesting the important role of epigenetics (Merlin and Liedvogel, 2019). Epigenetics focuses on modifications of genetic material due to environmental factors (Merlin and Liedvogel, 2019). Research in this area is more recent and, therefore, less

Box 3. Examples of -Omics Research in Diadromous Species

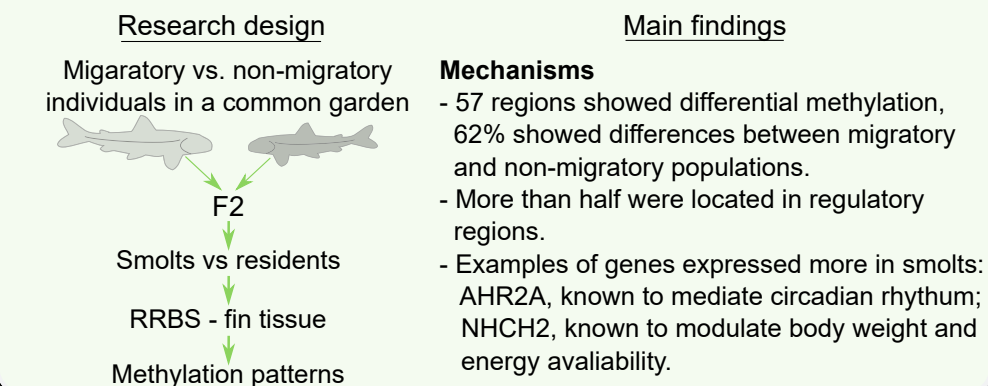
A Genomics.- amphidromous *G. maculatus* (Delgado *et al.* 2019)



B Transcriptomics.- catadromous *A. anguilla* (Côté *et al.* 2014)



C Epigenomics.- anadromous *O. mykiss* (Baerwald *et al.* 2016)



developed than genomics or transcriptomics. However, research has been conducted in some diadromous species to examine the effects of migration in reared individuals providing clues about the molecular mechanisms that distinguish migratory and resident populations. For instance, the primary location of methylation modifications that distinguish diadromous from resident populations varies in diadromous species, whereas these modifications are found predominantly within genes in three-spined sticklebacks (Smith et al., 2015) and in Rainbow Trout they are found largely in regulatory regions (Baerwald et al., 2016 -Box 3C).

Life History

Genomic analyses have been conducted to assess population structure and contribute to our understanding of migration in numerous diadromous species including the anadromous hilsa shad (*Tenulosa ilisha*) (Asaduzzaman et al., 2019), the catadromous Japanese eel (*Anguilla japonica*) (Igarashi et al., 2018), and the amphidromous common galaxias (*Galaxias maculatus*) (Box 3A). For example, site fidelity led to genetic differentiation in hilsa shad (Asaduzzaman et al., 2019) and Japanese eel (Igarashi et al., 2018) populations, whereas the presumed absence of site fidelity perhaps combined with a relatively large effective population size in common galaxias resulted in a panmictic or nearly panmictic migratory systems among diadromous collections (Delgado et al., 2019).

These genomic results regarding gene flow can also contribute to corroborate the classification of diadromous species. Common galaxias, for instance, has been classified as a marginal catadromous species as it was hypothesized that larvae only migrate to the estuaries (without reaching the ocean) and after a few weeks migrate back up the river streams (McDowall, 2009). The fact that populations across their Chilean distribution showed high levels of gene flow support the amphidromous nature of the common galaxias and is consistent with the hypothesis that larvae do indeed enter the ocean (Delgado et al., 2019).

The analyses of genomic markers have also provided information on species dispersal and reproductive behavior beyond that obtained through other methods such as telemetry. For example, a telemetry study in Arctic charr showed high dispersal levels, yet this high dispersal did not lead to high gene flow (Moore et al., 2017). This result is consistent with the notion that Arctic charr, an anadromous species, overwinters in non-natal freshwater environments in years when they do not reproduce (Jørgensen and Johnsen, 2014). Additionally, information on successful dispersal contributes to our understanding of the balance regarding the costs and benefits of this complex life history trait.

Facultative Behavior

Although some diadromous species like Atlantic salmon (*Salmo salar*) and Arctic cisco (*Coregonus autumnalis*) are considered obligatory diadromous, others like the goby *Awaous stamineus* do not need to visit the marine environment to complete their life cycle (Hogan et al., 2014). The importance of migration for an individual's development thus appears to vary depending on the species or family. The presence of sympatric diadromous and resident populations with little genetic differentiation (e.g., Rainbow trout, Kendall et al., 2014) suggests that migrating is not a requisite for the development of individuals and that diadromy can in some groups be facultative. From an ecological perspective, facultative diadromy may be beneficial as the decision to migrate would depend on environmental pressures.

In some species, resident populations are clearly genetically divergent from their diadromous counterparts (e.g., common galaxias; Delgado et al., 2019). In Arctic charr, sympatric anadromous and resident populations were until recently considered genetically indistinguishable, yet recent genomic data revealed genetically differentiated sympatric anadromous and resident populations in Labrador (Salisbury et al., 2019, 2020). Sockeye Salmon (*O. nerka*) on the other hand, exhibits examples of both genetically differentiated and non-differentiated sympatric resident and anadromous populations (Nichols et al., 2016). These differences in genetic differentiation between diadromous and resident populations are likely the product of local adaptation and/or genetic drift, implying that the ability to migrate can be maintained or lost as a result of selection or random processes.

Common garden studies have been conducted to test individual fitness in different environmental conditions, and the use of reaction norms has helped determine that diadromous species evolved a plastic response to different environmental variables. Examples are the studies on the response to varying salinities in three-spined stickleback (McCairns and Bernatchez, 2010) and the response to different temperatures in

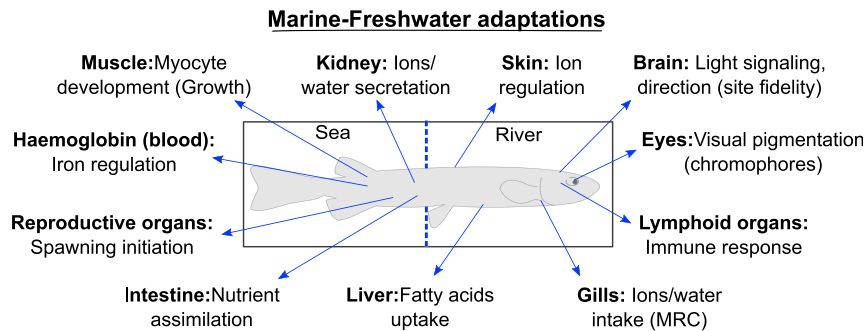


Figure 4. Examples of physiological adaptations necessary to survive in marine and freshwater environments.

brown trout (Meier et al., 2014). Both studies showed that diadromous individuals exhibit higher fitness when reared under a variety of environmental conditions than do resident individuals and are thus more plastic than resident individuals. The plastic nature of diadromy has also been demonstrated in steelhead, where diadromous or resident parents can express alternative offspring (e.g., Zimmerman et al., 2009).

Reciprocal transplant experiments with common galaxias under laboratory conditions also revealed that resident populations can differ in their response to salinity changes with some populations maintaining their osmoregulatory performance necessary for migration and others not being able to survive such changes (Delgado et al., 2020). Given that these populations were similarly genetically differentiated from their diadromous counterpart, we suspect genetic drift may be one of the factors playing an important role in determining whether the ability to migrate is maintained or lost. Yet, other forms of relaxed selection could also be playing a role in the differences in persistence and loss of salinity adaptation found between these two populations (Lahti et al., 2009). The loss of osmoregulatory capacity can also be partial as revealed by gene expression studies with alewives (*Alosa pseudoharengus*) resident populations (Velotta et al., 2014).

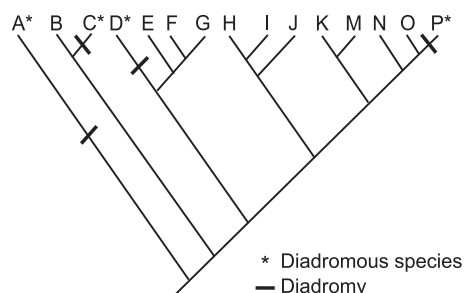
Molecular Bases

The physiological adaptations required to survive in both marine and freshwater habitats are extensive (Figure 4). Freshwater species rely on adaptations related to ions uptake (specific type mitochondria-rich cells, Bartels et al., 2017) and visual pigmentations (specific types of chromophores, Toyama et al., 2008). Although many genes described as relevant to marine-freshwater adaptations have been reported in diadromous species (Table S3), the genetic variation responsible for this migratory behavior is still unknown. This raises the question of whether there is one “diadromous” gene or genes (i.e., islands of differentiation).

Research on stickleback sister species provides a clear example of a gene essential for the ability to colonize fresh water: *Fads2* (Ishikawa et al., 2019). This gene, involved in the assimilation of fatty acids, highlights the importance of food resources in the evolution of diadromous behavior, as well as the significance of one gene (or copy number variant) to promote or constrain the dispersal to a new environment. However, the fact that diadromous species should have evolved all these adaptations (Figure 4) required to survive in freshwater and marine environments at one point seems unlikely. A more plausible scenario is that adaptations such as wide osmoregulatory capacity may be inherited before a species becomes diadromous and that what makes a species to become diadromous must be a gene or genes related to signaling that would start the migration. In birds, for instance, it has been hypothesized that a gene related to behavior such as circadian behavior or photoreceptors may be responsible for migratory behavior (Lugo Ramos et al., 2017).

Migratory genes may be linked together in chromosomal rearrangements and genomic islands of differentiation (Wellenreuther and Bernatchez, 2018), as it has been suggested that these associations of genes in genomic regions facilitate the selection in favor of or against complex life history traits. Chromosomal rearrangements including inversions and duplications appear to maintain co-adapted alleles facilitating adaptation in many contexts (Sutherland et al., 2016; Varadharajan et al., 2019; Wellenreuther and Bernatchez, 2018). Genomic islands of differentiation also appear to play key roles in linking co-adaptive traits in diadromous species (e.g., Veale and Russello 2017). For example, the *Omy5* linkage group, a large

A Diadromy appeared in multiple independent events

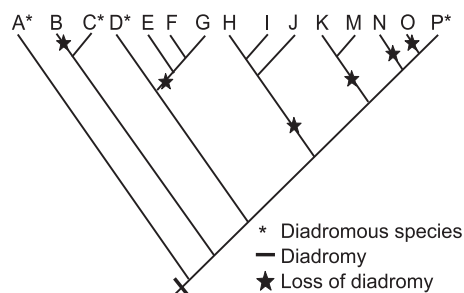


Evolved multiple times, for a given taxa may be a response to:

- Search for > food/resources
Productivity hypothesis (Gross, 1987)
- Leave unfavorable environments
Random escapement hypothesis (Tsukamoto et al. 2009)
- Search new niches/shelter
Ecological opportunity hypothesis (Feutry et al. 2013)
- Change of habitat
Intermediate state hypothesis (Gross, 1987)

* Diadromous species
— Diadromy

B Diadromy, ancestral trait that has been lost multiple times



Loss multiple times, for a given taxa may be a response to:

- Local adaptation to their natal habitat
- Inability to migrate (mutations in genes associated to survival in recipient environment)

* Diadromous species
— Diadromy
★ Loss of diadromy

Figure 5. Hypotheses Regarding the Origin of Diadromy

(A) Diadromy appeared in multiple events as a response to different scenarios (one or more of previously proposed hypotheses). (B) Diadromy is an ancestral trait that has been lost multiple times in fish phylogeny.

region located in chromosome 5 of steelhead shows a strong non-random association with life history differentiation between anadromous and non-migratory populations (Pearse et al., 2014). A small genomic region (~30 kb) was recently shown to also be closely associated with spawning migration timing in Chinook salmon (Thompson et al., 2020).

Genomic and transcriptomic analyses have revealed many putative genes that differentiated migratory and resident populations; these genes are related to osmoregulation and muscle contraction, among other processes (Table S4). Research in salmonids has shown little parallelism in genes differentiating diadromous and resident populations across species (Schneider et al., 2019). Even within the same species, replicate resident populations show that local adaptation and genetic drift can lead to different genes being fixed or lost (Delgado et al., 2020; Salisbury et al., 2020). Thus, further research on a variety of species and tissues including brain is necessary to improve our understanding of the genes that may be common among diadromous species. Such efforts could help address the overarching question of whether or not there is a “diadromous gene” or gene complex.

Origin and Ancestry

The fact that diadromy is present only in a small percentage of species, yet it is widely present across the phylogeny of fishes (Figure 1), would suggest that diadromy could have originated in either of two scenarios (Figure 5). The first hypothesis posits that diadromy appeared multiple independent times across the phylogeny of fishes; the second hypothesis instead posits that diadromy is ancestral and has been lost on multiple occasions (Figure 5).

The second hypothesis, common to other migratory taxa including birds, assumes that species have an ancestral migratory predisposition; therefore, migration, in theory, could appear in many lineages (Zink, 2011). In fishes, the rarity of diadromy (<1%) and the lack of parallelism in genes associated with a migratory phenotype suggest that diadromy may not be predisposed in all lineages. Although the loss of diadromy does appear to be common in diadromous species, as seen by the existence of resident populations in many diadromous species across the phylogeny (Figure 1), many more instances of loss of diadromy are required under this second hypothesis than are instances of the appearance of diadromy under the first

hypothesis. The hypothesis that diadromy appeared multiple independent times across the phylogeny of fishes thus seems more parsimonious.

Under the multiple appearance hypothesis, it can be also assumed that in some lineages/orders where this life history was advantageous, it rapidly expanded, resulting in a relatively large number of related species evolving from a common diadromous ancestor. Examples could include the Gobiiformes and Salmoniformes, where single families within each of these orders exhibit a high number of diadromous species (Figure 1). The first hypothesis also assumes the independence of each diadromy appearance events, suggesting that any of the proposed hypotheses on the origin of diadromy (see “Hypothesis on the origin” section), all of which have evidence for and against, may be true for a given taxon. This is also consistent with the suggestion that no single hypothesis explains the origin of diadromy for all diadromous species adding support to the first hypothesis. Recently, Alò and collaborators tested different hypotheses (e.g., productivity and genetic predisposition) to find one comprehensive migration model. Their results, however, showed that different migratory strategies including the different categories of diadromy cannot be explained by a single model but by different environmental, phylogenetic, and productivity variables (Alò et al., 2020).

There is also an ongoing debate about the salinity at which the ancestors of diadromous species lived. The ancestors have been hypothesized to be of freshwater, marine, or diadromous origin (McDowall, 1997). The ancestor species can be assumed to be of freshwater or marine environment as a function of the hypothesis of the origin of diadromy. For instance, under the intermediate state hypothesis, anadromy is derived from a freshwater ancestor, but under the safe-site hypothesis, anadromy derives from a marine ancestor. Depending on the taxa, both assumptions can be valid.

The phylogenetic tree suggests that both anadromous and amphidromous species appear to have both marine and freshwater ancestors (Figure 1). Catadromous species, on the other hand, appear to be present mainly in clades where the most recent ancestor was of marine origin (Figure 1). For most clades, however, there is no consensus on the habitat of the ancestral species. Indeed, we were unable to find information on the habitat of the ancestor for many taxa (Table S2). Although no single hypothesis explains diadromy for every diadromous species, the presence of a marine ancestor for catadromous species suggests that diadromous species may migrate for ecological reasons (i.e., increase fitness) but return to their natal habitat because they lack adaptations that would allow them to reproduce in the secondary environment. Thus, catadromous and marine amphidromous likely have a marine ancestor that passed on the ability to reproduce in marine environments, and similarly, anadromous and freshwater amphidromous most likely have a freshwater ancestor. However, there are notable exceptions like the order Clupeiformes, which held mostly anadromous species yet its most recent ancestor is marine.

The presence of marine ancestry for some anadromous or freshwater amphidromous could be explained by novel mutations that allow these species to reproduce in fresh water or by standing genetic variation of a slightly older freshwater ancestor. The appearance of novel mutations seems unlikely as these mutations would have had to appear multiple times in different lineages. The latter hypothesis (standing genetic variation) seems more plausible, as it is known that most actinopterygians are derived from a common freshwater ancestor (Vega and Wiens, 2012). The presence of pre-existing or cryptic genetic variation could explain why some anadromous and freshwater amphidromous species from multiple and independent lineages have a recent marine ancestor. This idea that most actinopterygians have standing genetic variation to reproduce in fresh water may also explain why anadromy and freshwater amphidromy are more prevalent than catadromy (<20% of diadromous species are catadromous, Table S2). However, the higher prevalence of anadromous versus catadromous species could also be explained by the higher speciation rate of anadromous species as the consequence of more opportunities to isolate and differentiate in freshwater environments than in marine environments.

Future Directions of Diadromy in an -Omics Era—What We Can Learn?

Research using -omics approaches regarding diadromy is still in its infancy. Further research on different species from all three categories of diadromy would help answer questions on the origin and molecular bases of diadromy. Questions such as whether diadromy evolved multiple independent times or is an ancestral trait could be addressed by having more genomic data of diadromous species within and among different orders, as thus far, most research has focused on Salmoniformes. Genomic data of species from

different categories of diadromy from the same and different orders or even families (e.g., Clupeidae) would also contribute to resolving the question of whether the different categories of diadromy have the same genomic bases. Also, studies focusing on orders that show rapid diversification (i.e., Gobiiformes) could shed light on questions such as why freshwater amphidromy is more prevalent than other categories.

Transcriptomic and epigenomic research with diadromous and resident populations exhibiting little genetic differentiation, and which therefore have not undergone local adaptation, would help assess which differentially expressed genes are responsible for this migratory behavior and if indeed there is a “diadromous” gene(s) or gene complex. Research thus far has focused on osmoregulatory organs (i.e., gills); however, wide resistance to osmoregulatory changes is present too in non-diadromous species as well, suggesting that this adaptation is an ancestral trait. Thus, examining other organs including brains where genes related to signaling and photoreceptor are expressed may provide an answer to the question of what gene is responsible for starting the migration of larvae/juveniles.

Research on ecological factors that may influence the decision to migrate, including the presence of predators or the influence of parasites, may also lead to improvements in our understanding of the facultative nature of diadromy, which is present in many diadromous species. Finally, understanding the evolutionary consequences of diadromy and its loss as a source of genetic diversity and also considering the increased risk of extinction that this life history trait carries can be important to predict the evolution of these species.

CONCLUDING REMARKS

Diadromy is a life history trait that has an important role in the distribution and even diversification of species in aquatic systems, directly influencing the ability of populations to disperse and colonize new habitats and niches. This migratory behavior involved a series of adaptations that grants individuals the ability to survive in such different environments. And, although many questions regarding the origin, genetic bases, and evolutionary consequences of diadromy still need an answer, our understanding of diadromy has improved during the last decade thanks to advances in sequencing technologies. For example, research has revealed key genes and processes responsible for these adaptations. Also, studies suggest that diadromy may have appeared convergently in different taxa, proving to be an important source of genetic variation in fishes. Unfortunately, many diadromous species have experienced population declines throughout the last century (Duarte, 2018; McDowall, 2009; Righton et al., 2012), and many diadromous species are in peril owing to their migratory nature. Conservation strategies for a diadromous species require the preservation not only of their natal and secondary environment but also the connection between them (McDowall, 1999) as well as the consideration of future climate-driven changes in both freshwater and marine environments (Walter et al., 2012). Thus, given the conservation status of many diadromous species and the current climate change scenario, understanding the variability and potential to adapt to different environments of diadromous species is crucial for their preservation.

METHODS

All methods can be found in the accompanying [Transparent Methods supplemental file](#).

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.isci.2020.101837>.

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AUTHOR CONTRIBUTIONS

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Supplemental Information

**Investigating Diadromy in Fishes
and Its Loss in an -Omics Era**

M. Lisette Delgado and Daniel E. Ruzzante

Table S1. List of known diadromous species. Related to Table 1.

Species	Family	Category	Little information available (e.g. no microchemistry analysis)	References	Resident populations
<i>Acipenser baerii</i>	Acipenseridae	anadromous		(Rodríguez et al., 2002)	yes
<i>Acipenser brevirostrum</i>	Acipenseridae	anadromous		(Kynard, 1997)	
<i>Acipenser dabryanus</i>	Acipenseridae	anadromous		(Kynard et al., 2003)	
<i>Acipenser gueldenstaedtii</i>	Acipenseridae	semi-anadromous		(Arai and Miyazaki, 2001)	yes
<i>Acipenser medirostris</i>	Acipenseridae	anadromous		(Allen et al., 2009)	
<i>Acipenser mikadoi</i>	Acipenseridae	anadromous		(Koshelev et al., 2012)	
<i>Acipenser naccarii</i>	Acipenseridae	semi-anadromous		(Martínez-Álvarez et al., 2005)	
<i>Acipenser nudiventris</i>	Acipenseridae	anadromous		(Acolas and Lambert, 2016)	
<i>Acipenser oxyrinchus</i>	Acipenseridae	anadromous		(Allen et al., 2014)	
<i>Acipenser persicus</i>	Acipenseridae	anadromous		(Acolas and Lambert, 2016)	
<i>Acipenser schrenckii</i>	Acipenseridae	anadromous		(Koshelev et al., 2014)	
<i>Acipenser sinensis</i>	Acipenseridae	anadromous		(Zhuang et al., 2002)	
<i>Acipenser stellatus</i>	Acipenseridae	anadromous		(Honț et al., 2019)	
<i>Acipenser sturio</i>	Acipenseridae	anadromous		(Acolas et al., 2012)	
<i>Acipenser transmontanus</i>	Acipenseridae	anadromous		(McEnroe and Cech, 1985)	
<i>Huso dauricus</i>	Acipenseridae	anadromous		(Koshelev et al., 2014)	
<i>Huso huso</i>	Acipenseridae	anadromous		(Honț et al., 2019)	
<i>Scaphirhynchus suttkusi</i>	Acipenseridae	anadromous		(Acolas and Lambert, 2016)	
<i>Arius madagascariensis</i>	Ariidae	anadromous	X	(Acolas and Lambert, 2016; Milton, 2009)	
<i>Genidens barbatus</i>	Ariidae	anadromous		(Avigliano et al., 2017)	yes
<i>Neoarius graeffei</i>	Ariidae	anadromous	X	(Milton, 2009)	
<i>Atherinella chagresi</i>	Atherinopsidae	anadromous	X	(Milton, 2009)	
<i>Atherinella guatemalensis</i>	Atherinopsidae	anadromous	X	(Milton, 2009)	
<i>Mystus gulio</i>	Bagridae	anadromous	X	(Acolas and Lambert, 2016; Bijoy Nandan et al., 2012)	
<i>Citharinus citharus</i>	Citharinidae	anadromous	X	(Riede, 2004)	
<i>Citharinus eburneensis</i>	Citharinidae	anadromous	X	(Acolas and Lambert, 2016)	
<i>Clarotes laticeps</i>	Claroteidae	anadromous	X	(Acolas and Lambert, 2016)	
<i>Alosa aestivalis</i>	Clupeidae	anadromous		(Limburg, 2001)	yes
<i>Alosa alabamae</i>	Clupeidae	anadromous		(Schaffler et al., 2015)	
<i>Alosa alosa</i>	Clupeidae	anadromous		(Baglinière et al., 2003)	yes

<i>Alosa fallax</i>	Clupeidae	anadromous		(Aprahamian et al., 2003)	
<i>Alosa immaculata</i>	Clupeidae	anadromous		(Acolas and Lambert, 2016)	
<i>Alosa kessleri</i>	Clupeidae	anadromous		(Kuzishchin et al., 2020)	
<i>Alosa mediocris</i>	Clupeidae	anadromous		(McBride and Holder, 2008)	
<i>Alosa pseudoharengus</i>	Clupeidae	anadromous		(Walters et al., 2009)	
<i>Alosa sapidissima</i>	Clupeidae	anadromous		(McBride and Holder, 2008)	
<i>Alosa tanaica</i>	Clupeidae	anadromous		(Acolas and Lambert, 2016)	
<i>Alosa volgensis</i>	Clupeidae	anadromous		(Acolas and Lambert, 2016)	
<i>Anodontostoma chacunda</i>	Clupeidae	anadromous	X	(Milton, 2009)	
<i>Anodontostoma thailandiae</i>	Clupeidae	anadromous	X	(Acolas and Lambert, 2016; Milton, 2009)	
<i>Clupanodon thrissa</i>	Clupeidae	anadromous	X	(Riede, 2004)	
<i>Clupeonella cultriventris</i>	Clupeidae	anadromous		(Bloom and Lovejoy, 2014)	
<i>Dorosoma cepedianum</i>	Clupeidae	anadromous	X	(Acolas and Lambert, 2016)	
<i>Dorosoma petenense</i>	Clupeidae	anadromous	X	(Acolas and Lambert, 2016)	
<i>Herklotsichthys gotoi</i>	Clupeidae	anadromous	X	(Milton, 2009)	
<i>Hilsa kelee</i>	Clupeidae	anadromous	X	(Milton, 2009)	
<i>Nematalosa galathea</i>	Clupeidae	anadromous	X	(Acolas and Lambert, 2016; Milton, 2009)	
<i>Nematalosa nasus</i>	Clupeidae	anadromous	X	(Acolas and Lambert, 2016; Milton, 2009)	
<i>Pellonula leonensis</i>	Clupeidae	anadromous	X	(Milton, 2009)	
<i>Pellonula vorax</i>	Clupeidae	anadromous	X	(Acolas and Lambert, 2016; Milton, 2009)	
<i>Tenualosa ilisha</i>	Clupeidae	anadromous		(Arai et al., 2019)	yes
<i>Tenualosa reevesii</i>	Clupeidae	anadromous		(Blaber et al., 2003)	
<i>Tenualosa toli</i>	Clupeidae	anadromous		(Milton et al., 1997)	
<i>Leuciscus idus</i>	Cyprinidae	semi-anadromous		(Skovrind et al., 2016)	yes
<i>Pelecus cultratus</i>	Cyprinidae	anadromous		(Acolas and Lambert, 2016)	
<i>Rutilus frisii</i>	Cyprinidae	anadromous		(Kohestan-Eskandari et al., 2014)	
<i>Tribolodon brandtii</i>	Cyprinidae	anadromous		(Sakai and Imai, 2005)	
<i>Tribolodon hakonensis</i>	Cyprinidae	anadromous		(Sakai et al., 2002)	yes
<i>Vimba vimba</i>	Cyprinidae	anadromous		(Łuszczek-Trojnar et al., 2008)	
<i>Elops hawaiiensis</i>	Elopidae	anadromous	X	(Milton, 2009)	
<i>Anchoviella lepidentostole</i>	Engraulidae	anadromous		(Milton, 2009)	
<i>Colia ectenes</i>	Engraulidae	anadromous		(Duan et al., 2012)	
<i>Coilia nasus</i>	Engraulidae	anadromous		(Dou et al., 2012)	yes
<i>Lycengraulis grossidens</i>	Engraulidae	anadromous		(Mai and Vieira, 2013)	
<i>Stolephorus commersonii</i>	Engraulidae	anadromous	X	(Bijoy Nandan et al., 2012)	

<i>Microgadus tomcod</i>	Gadidae	anadromous		(Couillard et al., 2011)	
<i>Lovettia sealii</i>	Galaxiidae	semi-anadromous		(Schmidt et al., 2014)	
<i>Gasterosteus aculeatus</i>	Gasterosteidae	anadromous		(Arai et al., 2003)	yes
<i>Pungitius pungitius</i>	Gasterosteidae	anadromous		(Arai and Goto, 2008)	yes
<i>Geotria australis</i>	Geotriidae	anadromous		(Miles et al., 2014)	
<i>Leucopsarion petersii</i>	Gobiidae	anadromous		(Kokita and Nohara, 2011)	
<i>Luciogobius guttatus</i>	Gobiidae	anadromous		(Miyazaki and Terui, 2016; Riede, 2004)	
<i>Lota lota</i>	Lotidae	anadromous	X	(Rohtla et al., 2014)	yes
<i>Mordacia lapicida</i>	Mordaciidae	anadromous	X	(McDowall, 1999)	
<i>Mordacia mordax</i>	Mordaciidae	anadromous		(Miles et al., 2014)	
<i>Morone americana</i>	Moronidae	anadromous		(Acolas and Lambert, 2016)	
<i>Morone saxatilis</i>	Moronidae	anadromous		(Secor et al., 1995)	yes
<i>Rhinomugil corsula</i>	Mugilidae	anadromous	X	(Acolas and Lambert, 2016)	
<i>Pisodonophis boro</i>	Ophichthidae	anadromous	X	(Acolas and Lambert, 2016)	
<i>Hypomesus japonicus</i>	Osmeridae	anadromous		(Dodson et al., 2009)	
<i>Hypomesus nipponensis</i>	Osmeridae	anadromous		(Katayama et al., 2000)	yes
<i>Hypomesus olidus</i>	Osmeridae	anadromous		(Acolas and Lambert, 2016)	yes
<i>Hypomesus transpacificus</i>	Osmeridae	anadromous		(Acolas and Lambert, 2016)	
<i>Osmerus dentex</i>	Osmeridae	anadromous		(Dodson et al., 2009)	
<i>Osmerus eperlanus</i>	Osmeridae	anadromous		(Lyle and Maitland, 1997)	
<i>Osmerus mordax</i>	Osmeridae	anadromous		(Bradbury et al., 2008)	yes
<i>Spirinchus lanceolatus</i>	Osmeridae	anadromous		(Yatsuyanagi et al., 2020)	
<i>Spirinchus thaleichthys</i>	Osmeridae	anadromous		(Acolas and Lambert, 2016)	yes
<i>Thaleichthys pacificus</i>	Osmeridae	anadromous		(Clarke et al., 2007)	
<i>Pangasius krempfi</i>	Pangasiidae	anadromous		(Hogan et al., 2007)	
<i>Perca fluviatilis</i>	Percidae	semi-anadromous		(Nesbø et al., 1998)	yes
<i>Caspiomyzon wagneri</i>	Petromyzontidae	anadromous		(Mark Shrimpton, 2012)	
<i>Entosphenus tridentatus</i>	Petromyzontidae	anadromous		(Clemens et al., 2013)	
<i>Lampetra ayresii</i>	Petromyzontidae	anadromous		(Acolas and Lambert, 2016)	
<i>Lampetra fluviatilis</i>	Petromyzontidae	anadromous		(Morris and Pickering, 1976)	
<i>Lampetra tridentata</i>	Petromyzontidae	anadromous		(Beamish and Levings, 1991)	
<i>Lethenteron camtschaticum</i>	Petromyzontidae	anadromous		(Acolas and Lambert, 2016)	yes
<i>Lethenteron reissneri</i>	Petromyzontidae	anadromous		(Acolas and Lambert, 2016)	
<i>Petromyzon marinus</i>	Petromyzontidae	anadromous		(Waldman et al., 2008)	
<i>Ilisha filigera</i>	Pristigasteridae	anadromous	X	(Milton, 2009)	

<i>Ilisha megaloptera</i>	Pristigasteridae	anadromous	X	(Milton, 2009)	
<i>Ilisha sirishai</i>	Pristigasteridae	anadromous	X	(Milton, 2009)	
<i>Pellona ditchela</i>	Pristigasteridae	anadromous	X	(Milton, 2009)	
<i>Retropinna tasmanica</i>	Retropinnidae	anadromous	X	(Miles et al., 2014)	
<i>Hemisanx prognathus</i>	Salangidae	anadromous		(Zhang et al., 2007)	
<i>Neosalanx jordani</i>	Salangidae	anadromous		(Dodson et al., 2009)	
<i>Neosalanx reganius</i>	Salangidae	anadromous		(Acolas and Lambert, 2016)	
<i>Salangichthys microdon</i>	Salangidae	anadromous		(Yamaguchi et al., 2004)	yes
<i>Salanx ariakensis</i>	Salangidae	anadromous		(Shiao et al., 2016)	yes
<i>Salanx cuvieri</i>	Salangidae	anadromous		(Dodson et al., 2009; Riede, 2004)	
<i>Brachymystax lenok</i>	Salmonidae	anadromous	X	(Riede, 2004)	
<i>Coregonus albula</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	
<i>Coregonus artedii</i>	Salmonidae	anadromous		(Morin et al., 1982)	
<i>Coregonus autumnalis</i>	Salmonidae	anadromous		(Wilson, 1984)	
<i>Coregonus clupeaformis</i>	Salmonidae	anadromous		(Morin et al., 1982)	
<i>Coregonus huntsmani</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	
<i>Coregonus laurettae</i>	Salmonidae	anadromous		(Brown et al., 2008)	
<i>Coregonus lavaretus</i>	Salmonidae	anadromous		(Lehtonen et al., 1992)	
<i>Coregonus muksun</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	
<i>Coregonus nasus</i>	Salmonidae	anadromous		(Brown et al., 2008)	yes
<i>Coregonus oxyrinchus</i>	Salmonidae	anadromous		(Borcherding et al., 2014)	
<i>Coregonus pallasii</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	
<i>Coregonus peled</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	
<i>Coregonus pidschian</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	
<i>Coregonus sardinella</i>	Salmonidae	anadromous		(Brown et al., 2008)	
<i>Hucho perryi</i>	Salmonidae	anadromous		(Edo et al., 2005)	
<i>Oncorhynchus clarkii</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Oncorhynchus gorbuscha</i>	Salmonidae	anadromous		(Gallagher et al., 2013)	
<i>Oncorhynchus keta</i>	Salmonidae	anadromous		(Wood and Foote, 1996)	yes
<i>Oncorhynchus kisutch</i>	Salmonidae	anadromous		(Dodson et al., 2013)	
<i>Oncorhynchus masou</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Oncorhynchus mykiss</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Oncorhynchus nerka</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Oncorhynchus tshawytscha</i>	Salmonidae	anadromous		(Dodson et al., 2013)	
<i>Salmo labrax</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	

<i>Salmo marmoratus</i>	Salmonidae	anadromous		(Acolas and Lambert, 2016)	
<i>Salmo salar</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Salmo trutta</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Salvelinus alpinus</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Salvelinus confluentus</i>	Salmonidae	anadromous		(Austin et al., 2019; Dodson et al., 2013)	yes
<i>Salvelinus fontinalis</i>	Salmonidae	anadromous		(Dodson et al., 2013)	yes
<i>Salvelinus leucomaenis</i>	Salmonidae	anadromous		(Dodson et al., 2013)	
<i>Salvelinus malma</i>	Salmonidae	anadromous		(Dodson et al., 2013)	
<i>Salvelinus namaycush</i>	Salmonidae	semi-anadromous		(Kissinger et al., 2016)	yes
<i>Stenodus leucichthys</i>	Salmonidae	anadromous		(Brown et al., 2008)	
<i>Takifugu obscurus</i>	Tetraodontidae	anadromous		(Jeong et al., 2014)	yes
<i>Takifugu ocellatus</i>	Tetraodontidae	anadromous		(Yang and Chen, 2008)	
<i>Ambassis interrupta</i>	Ambassidae	catadromous	X	(Milton, 2009)	
<i>Anguilla anguilla</i>	Anguillidae	catadromous		(Arai et al., 2006)	yes
<i>Anguilla australis</i>	Anguillidae	catadromous		(Miles et al., 2014)	
<i>Anguilla bengalensis</i>	Anguillidae	catadromous		(Bijoy Nandan et al., 2012; Milton, 2009)	
<i>Anguilla bicolor</i>	Anguillidae	catadromous		(Arai and Chino, 2019)	yes
<i>Anguilla celebesensis</i>	Anguillidae	catadromous		(Milton, 2009)	
<i>Anguilla dieffenbachii</i>	Anguillidae	catadromous		(Arai et al., 2003)	
<i>Anguilla interioris</i>	Anguillidae	catadromous		(Arai and Chino, 2012)	
<i>Anguilla japonica</i>	Anguillidae	catadromous		(Tsukamoto and Arai, 2001)	yes
<i>Anguilla malgumora</i>	Anguillidae	catadromous		(Arai and Chino, 2012)	
<i>Anguilla marmorata</i>	Anguillidae	catadromous		(Arai et al., 2013)	yes
<i>Anguilla megastoma</i>	Anguillidae	catadromous		(Arai and Chino, 2012)	
<i>Anguilla mossambica</i>	Anguillidae	catadromous		(Whitfield, 2005)	
<i>Anguilla nebulosa</i>	Anguillidae	catadromous		(Arai and Chino, 2012)	
<i>Anguilla obscura</i>	Anguillidae	catadromous		(Miles et al., 2014)	
<i>Anguilla rheinhardtii</i>	Anguillidae	catadromous		(Miles et al., 2014)	
<i>Anguilla rostrata</i>	Anguillidae	catadromous		(Jessop et al., 2007)	yes
<i>Centropomus undecimalis</i>	Centropomidae	catadromous		(Lowerre-Barbieri et al., 2014)	
<i>Centropomus pectinatus</i>	Centropomidae	catadromous	X	(Milton, 2009)	
<i>Ethmalosa fimbriata</i>	Clupeidae	catadromous		(Bloom and Lovejoy, 2014)	
<i>Potamalosa richmondia</i>	Clupeidae	catadromous		(Miles et al., 2014)	
<i>Cottus kazika</i>	Cottidae	catadromous		(Augspurger et al., 2017)	
<i>Trachidermus fasciatus</i>	Cottidae	catadromous	X	(Milton, 2009)	

<i>Eleotris annobonensis</i>	Eleotridae	catadromous	X	(Milton, 2009)	
<i>Eleotris balia</i>	Eleotridae	catadromous	X	(Milton, 2009)	
<i>Eleotris pisonis</i>	Eleotridae	catadromous	X	(Milton, 2009)	
<i>Eleotris senegalensis</i>	Eleotridae	catadromous	X	(Milton, 2009)	
<i>Eleotris vittata</i>	Eleotridae	catadromous	X	(Milton, 2009)	
<i>Thryssa scratchleyi</i>	Engraulidae	catadromous		(Miles et al., 2014)	
<i>Kuhlia marginata</i>	Kuhliidae	catadromous		(Feutry et al., 2013)	
<i>Kuhlia malo</i>	Kuhliidae	catadromous		(Feutry et al., 2013)	
<i>Kuhlia rupestris</i>	Kuhliidae	catadromous		(Augspurger et al., 2017)	
<i>Khulia salelea</i>	Kuhliidae	catadromous		(Feutry et al., 2013)	
<i>Khulia sauvagii</i>	Kuhliidae	catadromous		(Feutry et al., 2013)	
<i>Lateolabrax japonicus</i>	Lateolabracidae	catadromous		(Fuji et al., 2018)	
<i>Lates calcarifer</i>	Latidae	catadromous		(Miles et al., 2014)	yes
<i>Lutjanus goldiei</i>	Lutjanidae	catadromous	X	(Milton, 2009)	
<i>Lutjanus maxweberi</i>	Lutjanidae	catadromous	X	(Milton, 2009)	
<i>Megalops cyprinoides</i>	Megalopidae	catadromous	X	(Miles et al., 2014)	
<i>Agonostomus monticola</i>	Mugilidae	catadromous	X	(Tulkani, 2017)	
<i>Agonostomus telfairii</i>	Mugilidae	catadromous	X	(Milton, 2009)	
<i>Aldrichetta forsteri</i>	Mugilidae	catadromous		(Chang and Iizuka, 2012)	
<i>Chelon labrosus</i>	Mugilidae	catadromous		(Gordoa, 2009)	
<i>Crenimugil heterocheilos</i>	Mugilidae	catadromous	X	(Milton, 2009)	
<i>Ellochelon vaigiensis</i>	Mugilidae	catadromous	X	(Milton, 2009)	
<i>Joturus pichardi</i>	Mugilidae	catadromous	X	(Tulkani, 2017)	
<i>Liza alata</i>	Mugilidae	catadromous		(Villamarín et al., 2016)	
<i>Liza aurata</i>	Mugilidae	catadromous		(Como et al., 2018)	
<i>Liza falcipinnis</i>	Mugilidae	catadromous		(Milton, 2009)	
<i>Liza grandisquamis</i>	Mugilidae	catadromous		(Milton, 2009)	
<i>Liza haematocheila</i>	Mugilidae	catadromous		(Chang and Iizuka, 2012)	
<i>Liza macrolepsis</i>	Mugilidae	semi-catadromous		(Bijoy Nandan et al., 2012; Chang and Iizuka, 2012)	
<i>Liza parsia</i>	Mugilidae	catadromous		(Bijoy Nandan et al., 2012)	
<i>Liza ramada</i>	Mugilidae	catadromous		(Filipe et al., 2009)	
<i>Liza richardsonii</i>	Mugilidae	catadromous		(Chang and Iizuka, 2012)	
<i>Liza rumadu</i>	Mugilidae	catadromous		(Almeida, 1996)	
<i>Liza subviridis</i>	Mugilidae	catadromous		(Chang and Iizuka, 2012)	

<i>Mugil cephalus</i>	Mugilidae	catadromous		(Bijoy Nandan et al., 2012)	yes
<i>Mugil curema</i>	Mugilidae	catadromous		(Albieri et al., 2010)	
<i>Mugil liza</i>	Mugilidae	catadromous		(Garbin et al., 2014)	
<i>Mugil soiuy</i>	Mugilidae	catadromous		(McDowall, 1997)	
<i>Mugil trichodon</i>	Mugilidae	catadromous		(Mai et al., 2018)	
<i>Myxus capensis</i>	Mugilidae	catadromous		(Strydom, 2003)	
<i>Trachystoma petardi</i>	Mugilidae	catadromous		(Miles et al., 2018)	yes
<i>Valamugil cunnesius</i>	Mugilidae	catadromous		(Bijoy Nandan et al., 2012)	
<i>Valamugil speigleri</i>	Mugilidae	catadromous		(Bijoy Nandan et al., 2012)	
<i>Gymnothorax polyuranodon</i>	Muraenidae	catadromous		(Tsukamoto et al., 2014)	
<i>Macquaria novemaculeata</i>	Percichthyidae	catadromous		(Chenoweth and Hughes, 1997)	
<i>Platichthys flesus</i>	Pleuronectidae	catadromous		(Trancart et al., 2012)	
<i>Rhombosolea retiaria</i>	Pleuronectidae	catadromous		(McDowall, 2000)	
<i>Pseudaphritis urvillii</i>	Pseudaphritidae	catadromous - female		(Crook et al., 2010)	
<i>Terapon jarbua</i>	Terapontidae	catadromous	X	(Musarrat-ul-Ain et al., 2015; Riede, 2004)	
<i>Notesthes robusta</i>	Tetrarogidae	catadromous		(Milton, 2009)	
<i>Ambassis miops</i>	Ambassidae	amphidromous	X	(Miles et al., 2014; Milton, 2009)	
<i>Ambassis gymnocephalus</i>	Ambassidae	amphidromous	X	(Milton, 2009)	
<i>Ambassis kopsii</i>	Ambassidae	amphidromous	X	(Milton, 2009)	
<i>Ameiurus melas</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Arius jella</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Cephalocassia jatia</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Cochlefelis burmanica</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Hemiarius sona</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Hexanematichthys sagor</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Nemapteryx caelata</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Netuma thalassina</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Plicofollis platystomus</i>	Ariidae	amphidromous	X	(Milton, 2009)	
<i>Plicofollis tenuispinis</i>	Ariidae	amphidromous		(Hashemi et al., 2013; Milton, 2009)	
<i>Atherina boyeri</i>	Atherinidae	amphidromous	X	(Filipe et al., 2009)	
<i>Carangaoides malabaricus</i>	Carangidae	amphidromous	X	(Bijoy Nandan et al., 2012)	
<i>Caranx sexfasciatus</i>	Carangidae	amphidromous	X	(Bijoy Nandan et al., 2012)	
<i>Centropomus ensiferus</i>	Centropomidae	amphidromous		(McBride and Matheson, 2011; Milton, 2009)	
<i>Centropomus medius</i>	Centropomidae	amphidromous	X	(Milton, 2009)	
<i>Centropomus nigrescens</i>	Centropomidae	amphidromous	X	(Milton, 2009)	

<i>Centropomus parallelus</i>	Centropomidae	amphidromous		(McBride and Matheson, 2011; Milton, 2009)	
<i>Centropomus pectinatus</i>	Centropomidae	amphidromous		(McBride and Matheson, 2011)	
<i>Centropomus robalito</i>	Centropomidae	amphidromous	X	(Milton, 2009)	
<i>Centropomus undecimalis</i>	Centropomidae	amphidromous	X	(Milton, 2009)	
<i>Cheimarrichthys fosteri</i>	Cheimarrichthyidae	amphidromous		(Augspurger et al., 2017; McDowall, 2000)	
<i>Clupea harangus</i>	Clupeidae	amphidromous		(Augspurger et al., 2017)	
<i>Sardinella melanura</i>	Clupeidae	amphidromous		(Elahi et al., 2017; Milton, 2009)	
<i>Sprattus sprattus</i>	Clupeidae	amphidromous		(Augspurger et al., 2017)	
<i>Cottus aleuticus</i>	Cottidae	amphidromous		(Augspurger et al., 2017)	
<i>Cottus amblystomopsis</i>	Cottidae	amphidromous		(Augspurger et al., 2017)	
<i>Cottus asper</i>	Cottidae	amphidromous		(Augspurger et al., 2017)	
<i>Cottus hangiongensis</i>	Cottidae	amphidromous		(Augspurger et al., 2017; Miyazaki and Terui, 2016)	
<i>Cottus pollux</i>	Cottidae	amphidromous		(Augspurger et al., 2017; Goto and Arai, 2003)	yes
<i>Leptocottus armatus</i>	Cottidae	amphidromous		(McDowall, 1997)	
<i>Bostrychus africanus</i>	Eleotridae	amphidromous	X	(Milton, 2009)	
<i>Bostrychus sinensis</i>	Eleotridae	amphidromous	X	(Milton, 2009)	
<i>Bunaka gyrinoides</i>	Eleotridae	amphidromous	X	(Miles et al., 2014; Milton, 2009)	
<i>Bunaka pinguis</i>	Eleotridae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)	
<i>Butis amboinensis</i>	Eleotridae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)	
<i>Butis butis</i>	Eleotridae	amphidromous		(Bijoy Nandan et al., 2012; Milton, 2009)	
<i>Butis humeralis</i>	Eleotridae	amphidromous	X	(Milton, 2009)	
<i>Butis koilomatodon</i>	Eleotridae	amphidromous	X	(Milton, 2009)	
<i>Butis melanostigma</i>	Eleotridae	amphidromous	X	(Milton, 2009)	
<i>Dormitator latifrons</i>	Eleotridae	amphidromous		(Augspurger et al., 2017; McDowall, 2009)	
<i>Dormitator maculatus</i>	Eleotridae	amphidromous		(Augspurger et al., 2017; Milton, 2009)	
<i>Eleotris acanthopoma</i>	Eleotridae	amphidromous		(Milton, 2009; Shen et al., 1998)	
<i>Eleotris amblyopsis</i>	Eleotridae	amphidromous		(Augspurger et al., 2017; Nordlie, 2012)	
<i>Eleotris fusca</i>	Eleotridae	amphidromous		(Bijoy Nandan et al., 2012; Mennesson et al., 2015)	
<i>Eleotris melanosoma</i>	Eleotridae	amphidromous		(Maeda and Tachihara, 2005)	
<i>Eleotris oxycephala</i>	Eleotridae	amphidromous	X	(Xia et al., 2015)	
<i>Eleotris perniger</i>	Eleotridae	amphidromous		(Frotté et al., 2019)	
<i>Eleotris picta</i>	Eleotridae	amphidromous		(Augspurger et al., 2017)	
<i>Eleotris sandwicensis</i>	Eleotridae	amphidromous		(Heim-Ballew et al., 2020)	yes
<i>Giuris margaritacea</i>	Eleotridae	amphidromous	X	(Miles et al., 2014)	

<i>Gobiomorphus australis</i>	Eleotridae	amphidromous	X	(Miles et al., 2014)	
<i>Gobiomorphus cotidianus</i>	Eleotridae	amphidromous		(Augspurger et al., 2017)	yes
<i>Gobiomorphus gobioides</i>	Eleotridae	amphidromous		(Augspurger et al., 2017)	
<i>Gobiomorphus hubbsi</i>	Eleotridae	amphidromous		(Augspurger et al., 2017; Jarvis et al., 2018)	
<i>Gobiomorphus huttoni</i>	Eleotridae	amphidromous		(Augspurger et al., 2017)	
<i>Gobiomorus dormitor</i>	Eleotridae	amphidromous		(Augspurger et al., 2017; Smith and Kwak, 2014)	
<i>Gobiomorus maculatus</i>	Eleotridae	amphidromous		(Augspurger et al., 2017)	
<i>Guavina guavina</i>	Eleotridae	amphidromous		(Augspurger et al., 2017; Milton, 2009)	
<i>Hypseleotris cyprinoides</i>	Eleotridae	amphidromous		(Donaldson and Myers, 2002)	
<i>Hypseleotris guentheri</i>	Eleotridae	amphidromous		(Donaldson and Myers, 2002)	
<i>Ophieleotris aporos</i>	Eleotridae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)	
<i>Ophiocara porocephala</i>	Eleotridae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)	
<i>Thryssa dussumieri</i>	Engraulidae	amphidromous	X	(Bijoy Nandan et al., 2012; Milton, 2009)	
<i>Thryssa gautamiensis</i>	Engraulidae	amphidromous	X	(Milton, 2009)	
<i>Thryssa hamaltonii</i>	Engraulidae	amphidromous	X	(Milton, 2009)	
<i>Thryssa kammalensoides</i>	Engraulidae	amphidromous	X	(Milton, 2009)	
<i>Thryssa malabarica</i>	Engraulidae	amphidromous	X	(Bijoy Nandan et al., 2012)	
<i>Aplochiton taeniatus</i>	Galaxiidae	amphidromous		(Alò et al., 2019; Augspurger et al., 2017)	
<i>Aplochiton marinus</i>	Galaxiidae	amphidromous		(Alò et al., 2019)	
<i>Aplochiton zebra</i>	Galaxiidae	amphidromous		(Augspurger et al., 2017)	
<i>Galaxias argenteus</i>	Galaxiidae	amphidromous		(Augspurger et al., 2017)	
<i>Galaxias brevipinnis</i>	Galaxiidae	amphidromous		(Augspurger et al., 2017)	
<i>Galaxias fasciatus</i>	Galaxiidae	amphidromous		(Augspurger et al., 2017)	
<i>Galaxias maculatus</i>	Galaxiidae	amphidromous		(Augspurger et al., 2017; Hickford and Schiel, 2016)	yes
<i>Galaxias postvectis</i>	Galaxiidae	amphidromous		(Franklin and Gee, 2019)	
<i>Galaxias truttaceus</i>	Galaxiidae	amphidromous		(Augspurger et al., 2017)	yes
<i>Neochanna cleaveri</i>	Galaxiidae	amphidromous		(McDowall, 2004; Miles et al., 2014)	
<i>Eucinostomus melanopterus</i>	Gerreidae	amphidromous	X	(Milton, 2009)	
<i>Gerres cinereus</i>	Gerreidae	amphidromous	X	(Milton, 2009)	
<i>Gerres erythrourus</i>	Gerreidae	amphidromous	X	(Bijoy Nandan et al., 2012)	
<i>Gerres filamentosus</i>	Gerreidae	amphidromous	X	(Milton, 2009)	
<i>Gerres limbatus</i>	Gerreidae	amphidromous	X	(Milton, 2009)	
<i>Gerres longirostris</i>	Gerreidae	amphidromous	X	(Milton, 2009)	
<i>Gerres seifer</i>	Gerreidae	amphidromous	X	(Bijoy Nandan et al., 2012; Milton, 2009)	

<i>Gobiesox cephalus</i>	Gobiesocidae	semi-amphidromous		(Frotté et al., 2019)	yes
<i>Acantrogobius caninus</i>	Gobiidae	amphidromous		(Palavai, 2009)	
<i>Acanthogobius lactipes</i>	Gobiidae	amphidromous		(Miyazaki and Terui, 2016)	
<i>Awaous acritosus</i>	Gobiidae	amphidromous		(Augspurger et al., 2017)	yes
<i>Awaous banana</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Smith and Kwak, 2014)	yes
<i>Awaous bustamantei</i>	Gobiidae	amphidromous	X	(Schliewen, 2012)	
<i>Awaous grammepomus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Awaous guamensis</i>	Gobiidae	amphidromous		(Augspurger et al., 2017)	
<i>Awaous lateristriga</i>	Gobiidae	amphidromous	X	(Schliewen, 2012)	
<i>Awaous melanocephalus</i>	Gobiidae	amphidromous		(Shen et al., 1998; Shiao et al., 2015)	
<i>Awaous ocellaris</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Awaous stamineus</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Hogan et al., 2017)	yes
<i>Awaous tajasica</i>	Gobiidae	amphidromous		(Trevisan dos Santos, 2016)	
<i>Awaous transandeanus</i>	Gobiidae	amphidromous	X	(Lyons and Schneider, 1990)	
<i>Cotylopus acutipinnis</i>	Gobiidae	amphidromous		(Milton, 2009; Teichert et al., 2014)	
<i>Glossogobius aureus</i>	Gobiidae	amphidromous		(Miles et al., 2014; Shiao et al., 2015)	
<i>Glossogobius celebius</i>	Gobiidae	amphidromous		(Milton, 2009; Shen et al., 1998)	
<i>Glossogobius giuris</i>	Gobiidae	amphidromous		(Miles et al., 2014; Milton, 2009)	
<i>Gobioides broussonnetii</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Gobioides sagitta</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Gobionellus occidentalis</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Gobionellus oceanicus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Gobionellus thoropsis</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Gymnogobius petschiliensis</i>	Gobiidae	amphidromous		(Oto, 2019)	
<i>Gymnogobius opperiens</i>	Gobiidae	amphidromous		(Miyazaki and Terui, 2016)	
<i>Gymnogobius urotaenia</i>	Gobiidae	amphidromous		(Miyazaki and Terui, 2016)	
<i>Lentipes armatus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Lentipes concolor</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Heim-Ballew et al., 2020)	yes
<i>Lentipes whittenorum</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Oligolepis acutipennis</i>	Gobiidae	amphidromous		(Shen et al., 1998)	
<i>Parasicydium bandama</i>	Gobiidae	amphidromous	X	(Schliewen, 2012)	
<i>Periophthalmus argentilineatus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Periophthalmus barbarus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Periophthalmus malaccensis</i>	Gobiidae	amphidromous	X	(Milton, 2009)	

<i>Periophthalmus modestus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Periophthalmus novemradiatus</i>	Gobiidae	amphidromous		(Milton, 2009; Rahman et al., 2015)	
<i>Periophthalmus weberi</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Periophthalmodon schlosseri</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Periophthalmodon septemradiatus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Porogobius schlegelii</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Pseudapocryptes elongatus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Pseudogobius javanicus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Pseudogobius melanostictus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Pseudogobius poicilosoma</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Redigobius balteatus</i>	Gobiidae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)	
<i>Redigobius bikolanus</i>	Gobiidae	amphidromous		(Shen et al., 1998)	
<i>Redigobius dispar</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Redigobius horiae</i>	Gobiidae	amphidromous		(Donaldson and Myers, 2002)	
<i>Redigobius macrostoma</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Redigobius roemeri</i>	Gobiidae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)	
<i>Redigobius sapangus</i>	Gobiidae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)	
<i>Rhinogobius brunneus</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Iguchi and Mizuno, 1999)	
<i>Rhinogobius giurinus</i>	Gobiidae	amphidromous		(Shiao et al., 2015)	
<i>Rhinogobius similis</i>	Gobiidae	amphidromous		(Iida et al., 2017)	
<i>Rhinogobius sp.</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Tsunagawa and Arai, 2008)	yes
<i>Schismatogobius sp.</i>	Gobiidae	amphidromous		(Keith, 2003)	
<i>Schismatogobius roxasi</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicydium brevifile</i>	Gobiidae	amphidromous	X	(Schliewen, 2012)	
<i>Sicydium bustamantei</i>	Gobiidae	amphidromous	X	(Schliewen, 2012)	
<i>Sicydium crenilabrum</i>	Gobiidae	amphidromous	X	(Schliewen, 2012)	
<i>Sicydium multipunctatum</i>	Gobiidae	amphidromous	X	(González-Murcia and Álvarez, 2018)	
<i>Sicydium plumieri</i>	Gobiidae	amphidromous		(Frotté et al., 2019; Milton, 2009)	
<i>Sicydium punctatum</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Bell et al., 1995)	
<i>Sicydium salvini</i>	Gobiidae	amphidromous		(Lyons and Schneider, 1990)	
<i>Sicyopterus aiensis</i>	Gobiidae	amphidromous		(Augspurger et al., 2017)	
<i>Sicyopterus cynocephalus</i>	Gobiidae	amphidromous	X	(Ebner et al., 2017)	
<i>Sicyopterus fuliag</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopterus griseus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	

<i>Sicyopterus japonicus</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Shen et al., 1998)	
<i>Sicyopterus lacrymosus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopterus lagocephalus</i>	Gobiidae	amphidromous		(Augspurger et al., 2017)	
<i>Sicyopterus macrostetholepis</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopterus micrurus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopterus rapa</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopterus sarasini</i>	Gobiidae	amphidromous		(Augspurger et al., 2017)	
<i>Sicyopterus stimpsoni</i>	Gobiidae	amphidromous		(Heim-Ballew et al., 2020)	
<i>Sicyopus auxilimentus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopus jonklaasi</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopus leprurus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Sicyopus zosterophorum</i>	Gobiidae	amphidromous		(Augspurger et al., 2017; Taillebois et al., 2015)	
<i>Smilosicyopus chloe</i>	Gobiidae	amphidromous		(Taillebois et al., 2015)	
<i>Stenogobius blokzeyli</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Stenogobius fasciatus</i>	Gobiidae	amphidromous	X	(McBride and Matheson, 2011)	
<i>Stenogobius fehlmanni</i>	Gobiidae	amphidromous		(Donaldson and Myers, 2002)	
<i>Stenogobius genivittatus</i>	Gobiidae	amphidromous		(Shen et al., 1998; Shiao et al., 2015)	
<i>Stenogobius grammepomus</i>	Gobiidae	amphidromous		(Palavai, 2009)	
<i>Stenogobius hawaiiensis</i>	Gobiidae	amphidromous		(Heim-Ballew et al., 2020)	yes
<i>Stiphodon alcedo</i>	Gobiidae	amphidromous		(Maeda et al., 2011)	
<i>Stiphodon aureorostrum</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Stiphodon caeruleus</i>	Gobiidae	amphidromous		(Chabarria et al., 2014)	
<i>Stiphodon elegans</i>	Gobiidae	amphidromous		(Milton, 2009; Shiao et al., 2015)	
<i>Stiphodon larsen</i>	Gobiidae	amphidromous		(McDowall, 2010)	
<i>Stiphodon niraikanaiensis</i>	Gobiidae	amphidromous		(Maeda, 2014)	
<i>Stiphodon percnopterygius</i>	Gobiidae	amphidromous		(Iida et al., 2017; McDowall, 2009)	
<i>Stiphodon rutilaureus</i>	Gobiidae	amphidromous	X	(Ebner and Thuesen, 2011)	
<i>Stiphodon semoni</i>	Gobiidae	amphidromous		(Keith, 2003)	
<i>Stiphodon surrufus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Taenoides cirratus</i>	Gobiidae	amphidromous		(Bijoy Nandan et al., 2012)	
<i>Taenoides buchanani</i>	Gobiidae	amphidromous		(Bijoy Nandan et al., 2012)	
<i>Tridentiger brevispinis</i>	Gobiidae	amphidromous		(Miyazaki and Terui, 2016)M	
<i>Tridentiger kuroiwae</i>	Gobiidae	amphidromous		(Iida et al., 2017)	
<i>Zappa confluentus</i>	Gobiidae	amphidromous	X	(Milton, 2009)	
<i>Pomadasy maculatus</i>	Haemulidae	amphidromous	X	(Ahmed and Bat, 2016; Riede, 2004)	

<i>Kuhlia caudavittata</i>	Kuhliidae	amphidromous		(Augspurger et al., 2017)
<i>Kuhlia mugil</i>	Kuhliidae	amphidromous		(Augspurger et al., 2017)
<i>Kuhlia petiti</i>	Kuhliidae	amphidromous		(Augspurger et al., 2017)
<i>Kuhlia sandvicensis</i>	Kuhliidae	amphidromous		(Benson and Michael Fitzsimons, 2002; Milton, 2009)
<i>Kuhlia xenura</i>	Kuhliidae	amphidromous		(Augspurger et al., 2017)
<i>Agonostomus monticola</i>	Mugilidae	amphidromous		(Frotté et al., 2019)
<i>Liza macrolepis</i>	Mugilidae	amphidromous	X	(Milton, 2009)
<i>Liza melinoptera</i>	Mugilidae	amphidromous	X	(Milton, 2009)
<i>Liza subviridis</i>	Mugilidae	amphidromous	X	(Milton, 2009)
<i>Liza vaigiensis</i>	Mugilidae	amphidromous	X	(Milton, 2009)
<i>Valamugil buchanani</i>	Mugilidae	amphidromous	X	(Milton, 2009)
<i>Plecoglossus altivelis</i>	Plecoglossidae	amphidromous		(Arai, 2006; Murase and Iguchi, 2019)
<i>Plotosus canius</i>	Plotosidae	amphidromous	X	(Samani et al., 2016)
<i>Ilisha kampeni</i>	Pristigasteridae	amphidromous	X	(Milton, 2009)
<i>Ilisha melastoma</i>	Pristigasteridae	amphidromous	X	(Milton, 2009)
<i>Ilisha novacula</i>	Pristigasteridae	amphidromous	X	(Milton, 2009)
<i>Prototroctes maraena</i>	Retropinnidae	amphidromous		(Augspurger et al., 2017)
<i>Prototroctes oxyrhynchus</i>	Retropinnidae	amphidromous		(Augspurger et al., 2017)
<i>Retropinna retropinna</i>	Retropinnidae	amphidromous		(Augspurger et al., 2017)
<i>Retropinna semoni</i>	Retropinnidae	amphidromous		(Augspurger et al., 2017)
<i>Rhyacichthys aspro</i>	Rhyacichthyidae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)
<i>Rhyacichthys guilberti</i>	Rhyacichthyidae	amphidromous		(Milton, 2009; Tabouret et al., 2014)
<i>Johnius belangerii</i>	Sciaenidae	amphidromous	X	(Bijoy Nandan et al., 2012)
<i>Johnius coitor</i>	Sciaenidae	amphidromous	X	(Sakar et al., 2018)
<i>Otolithoides biauritus</i>	Sciaenidae	amphidromous	X	(Bijoy Nandan et al., 2012)
<i>Silonia silondia</i>	Schilbeidae	amphidromous		(Flura et al., 2018)
<i>Hippichthys cyanospilus</i>	Syngnathidae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)
<i>Hippichthys spicifer</i>	Syngnathidae	amphidromous		(Donaldson and Myers, 2002; Milton, 2009)
<i>Microphis brachyurus</i>	Syngnathidae	amphidromous		(McBride and Matheson, 2011)
<i>Microphis leiaspis</i>	Syngnathidae	amphidromous		(Ishihara and Tachihara, 2008; Milton, 2009)
<i>Syngnathus abaster</i>	Syngnathidae	amphidromous		(Filipe et al., 2009)
<i>Toxotes blythii</i>	Toxotidae	amphidromous	X	(Milton, 2009)
<i>Toxotes chatareus</i>	Toxotidae	amphidromous	X	(Milton, 2009)
<i>Toxotes jaculatrix</i>	Toxotidae	amphidromous	X	(Milton, 2009)

Table S2. References of diadromous taxa's ancestral environment from Figure 1.

Taxa	Origin	Reference
Acipenseriformes	Fresh water	Sulak & Randall 2002
Ambassidae	Marine	Martin 1990
Anguilliformes	Marine	Corush 2019
Atheriniformes	Marine	Campanella <i>et al.</i> 2015
Characiformes	Marine	Chen <i>et al.</i> 2013
Clupeiformes	Marine	Bloom & Lovejoy 2014
Cypriniformes	Fresh water	Imoto <i>et al.</i> 2013
Elopiformes	Unknown	
Gadiformes	Unknown	
Galaxiiformes	Unknown	Vega & Wiens 2012
Gobiesoformes	Unknown	
Gobiiformes	Fresh water	Thacker 2009
Lutjanidae	Unknown	
Moroniformes	Unknown	
Mugiliformes	Unknown	
Osmeriformes	Unknown	Vega & Wiens 2012
Perciformes	Marine/Catadromous	Cottidae (Dickman, 1995), Terapontidae (Davis <i>et al.</i> , 2012)/Kuhliidae (Feutry <i>et al.</i> , 2013)
Petromyzontiformes	Fresh water	Bartels <i>et al.</i> 2017
Pleuronectiformes	Marine	Azevedo <i>et al.</i> 2008
Salmoniformes	Fresh water	Wang <i>et al.</i> 2011
Siluriformes	Marine	Betancur-R 2010
Syngnathiformes	Unknown	
Tetraodontiformes	Marine	Yamanoue <i>et al.</i> 2011

Table S3. A representation of putative genes that differentiate migratory vs. non-migratory populations reported by different studies.

Function	Example of putative genes	Reference
Cell junction/adhesion	Tight junction protein ZO-3, Occludin, Protocadherin-18, Cadherin-8	Hale <i>et al.</i> 2013; Kozak <i>et al.</i> 2014
Cell proliferation	Epidermal growth factor receptor kinase	Kozak <i>et al.</i> 2014
Cytoskeletal connections	Obscurin-like 1	Morris <i>et al.</i> 2014
Reproduction	Zonadhesin-like, Estrogen receptor, MORC family CW-type zinc finger, Round spermatid basic protein 1-like, RING finger protein 114, life history divergence [9], Gonadotropin-releasing hormone (GnRH), Sperm-associated antigen 16, Gonadotropin subunit beta-2	Mavarez <i>et al.</i> 2009; Hale <i>et al.</i> 2013; Mateus <i>et al.</i> 2013; Kozak <i>et al.</i> 2014
Growth/differentiation factor, hormone, FSH inhibitor	Inhibin, alpha, growth hormone 2 (GH2)	Hale <i>et al.</i> 2013; Morris <i>et al.</i> 2014
Involved in immunity	NOD-like receptor family CARD domain containing 5, Immunoglobulin heavy chain (IgD-A) gene, MHC class I a region	Hale <i>et al.</i> 2013; Morris <i>et al.</i> 2014
Ion transport	ATPase, Na ⁺ /K ⁺ transporting alpha 1, Solute carrier family 9, 10, 12 (Na ⁺ /H ⁺ exchanger), ATPase, H ⁺ transporting, Sodium/potassium/calcium exchanger, Potassium voltage-gated channel subfamily H, Na ⁺ /Cl ⁻ cotransporter	Mavarez <i>et al.</i> 2009; Hale <i>et al.</i> 2013; Dennenmoser <i>et al.</i> 2017; Velotta <i>et al.</i> 2017; Brennan <i>et al.</i> 2018; Willoughby <i>et al.</i> 2018; Delgado <i>et al.</i> 2019
Microtubule attachment to the centromere	Bardet-Biedl syndrome 4 protein	Kozak <i>et al.</i> 2014
Enzymes	Glutamate dehydrogenase (GDH), d1-pyrroline-5-carboxylase synthase (P5CS), Carbonic anhydrase, Malate dehydrogenase, FMS-related tyrosine kinase 4, Alkaline ceramidase 1, Protein kinase D3	Hale <i>et al.</i> 2013; Dennenmoser <i>et al.</i> 2017; Debiasse <i>et al.</i> 2018; Willoughby <i>et al.</i> 2018
Myocyte cytoskeletal development	SPEG, Myosin regulatory light chain 2, Myostatin 2b (MSTN2)	Hale <i>et al.</i> 2013; Morris <i>et al.</i> 2014
Negative regulator of cell proliferation	Insulin-like growth factor-binding protein 1, 2a, 5	Morris <i>et al.</i> 2014; Kusakabe <i>et al.</i> 2017; Velotta <i>et al.</i> 2017
Osmosensing	Interleukin receptor 17c, 22a, Mitogen-activated protein kinase 1, 8, 13	Velotta <i>et al.</i> 2017
Osmotic/salinity stress	Glucocorticoid receptor, Aldehyde dehydrogenase 7, 9, Vasotocin	Mavarez <i>et al.</i> 2009; Mateus <i>et al.</i> 2013; Kozak <i>et al.</i> 2014
Regulation of immune cell proliferation	SAM and SH3 domain-containing protein	Kozak <i>et al.</i> 2014; Guo <i>et al.</i> 2015
Regulator of fatty acid uptake, intracellular binding	Peroxisome proliferator-activated receptor alpha a, Fatty acid-binding protein, adipocyte (AFABP)	Mavarez <i>et al.</i> 2009; Morris <i>et al.</i> 2014
Tight junction	Claudin 1, 3, 4, 7, 8, 10, 15	Kozak <i>et al.</i> 2014; Dennenmoser <i>et al.</i> 2017; Kusakabe <i>et al.</i> 2017; Velotta <i>et al.</i> 2017
Water transport	Aquaporin 3	Velotta <i>et al.</i> 2017

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