Contrasting Evolutionary Pathways of Anadromy in Euteleostean Fishes

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Abstract.—We develop the view, based on life cycle differences and recently published sister group relationships, that the freshwater life cycle was the ancestral character state leading to anadromy among salmoniforms, whereas the marine life cycle was the ancestral character state leading to anadromy among osmeriforms. In contrast to most salmonid fishes, the reproductive migrations of smelts are generally characterized by brief excursions to spawn in freshwater, and larvae may spend no more than 24 h in freshwater before being transported to coastal marine or estuarine environments. We reconstructed the phylogeny of the suborder Osmeroidei to establish the phylogenetic relationships among anadromous, marine, and freshwater species of this taxon. We mapped these life cycles onto phylogenetic trees of osmeriforms and salmoniforms and applied character-reconstruction methodology based on simple parsimony and likelihood methodologies. A freshwater origin of salmonids was supported by our analyses, whereas either marine or anadromous life cycles characterized the evolution of osmeroids. The possibility that the evolution of anadromy in salmonids and osmeroids followed separate paths requires a reconsideration of some generalizations concerning anadromy. We hypothesize that anadromy in osmeroids may be first and foremost an adaptation to place embryos and the early larval stages in reproductive safe sites to maximize their survival. The evolution of exclusive freshwater species of osmeriforms has occurred via anadromy through the various processes associated with landlocking. Freshwater amphidromy in osmeroids is most likely a consequence of anadromy rather than a precursor and may be contingent upon the availability of food resources in freshwater. Finally, marine osmeroids have been derived from anadromous ancestors and are "safe-site" specialists, exploiting principally the upper intertidal zone for reproduction. We also suggest that such contrasting evolutionary pathways to anadromy may provide insight into the evolution of partial migration, observed uniquely in salmonids, and the nature and extent of population genetic structure found in the two groups of fishes.

Introduction

Fishes that migrate regularly between freshwater and saltwater for the purposes of reproduction and

feeding (diadromy) exhibit three migratory patterns (Myers 1949). Anadromous fishes such as salmon move from the sea to breed in freshwater, whereas catadromous fishes such as eels move from freshwater to breed in the sea. The third category, amphidromy, is sometimes included within either anadromy or catadromy but has been considered

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as a distinct strategy (McDowall 1988). McDowall (2004) restricted the definition of amphidromy to fishes that reproduce in freshwater and drift downstream following hatching to feed at sea for variable periods of time before returning to freshwater to feed and grow to maturity. We refer to this life cycle more specifically as freshwater amphidromy to distinguish it from those diadromous fishes that reproduce at sea, migrate to freshwater early in life to feed for variable periods of time, and return to sea to feed and grow to maturity (marine amphidromy, Gross 1987). Diadromy is shown by at least 227 fish species, of which 110 are anadromous (McDowall 1988; Nelson 1994). Anadromy appears to have evolved early among fishes, as 90% of the 110 species identified by McDowall (1988) as anadromous are among either the most primitive living fishes (e.g., lampreys, sturgeons; 20 species) or the basal clupeocephalan teleosts (79 species.). However, its presence among some neoteleosts (e.g., Gasterosteiformes, Gobioidei) suggests more than one independent origin of anadromy.

One of the most influential contributions to understanding the adaptive significance and evolution of diadromy was formulated by Gross (1987). To evolve, diadromy (or any other migratory pattern) must result in a level of lifetime reproductive success (reproductive success × survivorship) exceeding that of individuals who do not migrate. The most important biological variable in explaining the presence and direction of diadromy was identified as the relative availability of food in marine and freshwater habitats (Gross et al. 1988). Marine habitats are more productive at high latitudes and less so towards the tropics, whereas the inverse occurs in freshwater. As such, anadromy is favored at high latitudes, whereas catadromy is favored at low latitudes. Gross (1987) envisioned amphidromy as the ancestral state in the evolution of anadromy and catadromy. Finally, the evolutionary scenarios proposed by Gross (1987) were based on the assumption that the ancestral state of diadromous fishes involves the reproductive environment. As such, catadromous fishes are derived from marine species that continue to exploit the ancestral reproductive environment. The ultimate derived state involves a completely freshwater life cycle. On the other hand, anadromous fishes are derived from freshwater species that continue to exploit the ancestral reproductive environment

and the ultimate derived state involves a completely marine life cycle.

Since they were first published, these comprehensive evolutionary scenarios have generated a great deal of discussion and ensuing confusion. McDowall (1997) objected to the contention that amphidromy is an intermediate stage in the evolution of anadromy on the basis that there are few documented cases of freshwater fishes becoming facultative marine wanderers, the initial stage in Gross' evolutionary pathway to anadromy. However, McDowall (1988) defined a category of freshwater fishes that occasionally move into marine waters (euryhaline wanderers) as being distinct from anadromous fishes. The well-documented ability of many freshwater species to exploit the oligohaline waters of estuaries (Moyle and Cech 2004) seems to fit the definition of euryhaline wanderers and represents a plausible evolutionary route to an anadromous life style. McDowall (1997) also stated that there is little empirical evidence that marine amphidromy is a precursor to the evolution of catadromy in formerly marine species as there are virtually no cases of amphidromous species that spawn at sea. On the contrary, recent observations reveal that marine amphidromy is more common than previously suggested, even among the catadromous anguillid eels (Daverat et al. 2006 and references therein). Despite numerous publications on the subject, we are no closer to formulating a comprehensive evolutionary framework to understand the development of diadromy beyond that provided by Gross (1987) 20 years ago. In the present paper, we aim to provide an alternative, yet complementary, model of the evolution of anadromy.

The starting point of this argument is to challenge the assumption that anadromy has been uniquely derived from freshwater origins. Several anadromous fishes such as the Atlantic tomcod *Microgadus tomcod* (Walbaum) and the clupeid shads (*Alosa* spp. and *Hilsa* spp.) appear to have been derived from marine families (McDowall 1993, 1997; Dodson 1997). Secor (2002) hypothesized that anadromy in striped bass *Morone saxatilis* (Walbaum) evolved from a marine-spawning ancestor. Gobies may represent another, more complex, example. The suborder Gobioidei is sister to the widespread, primarily marine family Apogonidae. The phylogenetic analysis of Thacker and Hardman (2005) supports the hypothesis that gobioids arose

in freshwater, from a marine ancestor, then returned to marine habitats on several occasions. Of the 42 valid genera of basal gobioid families identified by Thacker and Hardman (2005), 17 are classified as having freshwater life cycles, 17 as salt-tolerant, occurring in freshwater and estuaries, and 8 as having marine life cycles. Exclusively freshwater ecology is optimized as the condition at the root of Gobioidei, and invasion of marine habitats is hypothesized to have occurred independently on several occasions. The major radiation of Gobioidei, the gobiine gobiids, is known primarily from marine habitats. The occurrence of the anadromous life history strategy (particularly freshwater amphidromy) within this taxon thus represents a derived character state within Gobioidae. These observations also illustrate that the transition among marine, freshwater, euryhaline, and diadromous life cycles across phylogenetic history appears to be unconstrained, at least within the Gobioidae.

A serious impediment to clarifying the origins of anadromy resides in the phylogenetic reconstructions of the basal teleost fishes (Ramsden et al. 2003). The Clupeocephalan teleosts include the Tselfatiiformes, the Otocephala (Clupeomorpha and Ostariophysi), and the Euteleostei (Taverne and Gayet 2005). Without a well-supported phylogeny of these taxa, it is virtually impossible to track the evolutionary origins of anadromy. McDowall's argument that salmonids probably evolved from a diadromous ancestor (McDowall 2001) was based on the assumption that the sister group of salmonids is the family Osmeridae. However, the study by Ishiguro et al. (2003), based on mitochondrial genome sequences, concluded a sister group relationship between salmoniforms and esociforms, a group that inhabits freshwater almost exclusively. In addition, the sister of Salmoninae (*Eosalmo driftwoodensis*) included in the analysis of Ramsden et al. (2003) is considered a freshwater taxon, as fossil evidence indicates that all life history stages occurred in freshwater. These observations appear to add weight to the argument that the ancestor of the salmoniforms was a freshwater species and that anadromy evolved from freshwater origins (Ramsden et al. 2003).

The phylogenetic reconstruction of Ishiguro et al. (2003) also sheds light on the evolution of anadromy in osmeriforms. The superfamily Argentinoidae (herring smelts, deep-sea smelts, and spookfishes), a group of strictly marine fishes (Nel-

son 1994), and the suborder Osmeroidei (the diadromous smelts, galaxiids, and icefishes) are the two major clades peripheral to the basal neoteleosts, all of which are marine species. The maximum parsimony analysis of Ishiguro et al. (2003) revealed that Argentoidae is the sister group to Osmeroidei, and together, they form the sister group of neoteleosts. It thus appears plausible that anadromy among osmeroids may have evolved from marine origins. In contrast to salmoniforms, reproduction in freshwater of anadromous osmeroids may be considered the derived state. The emergence of anadromy may thus have followed very different evolutionary pathways in salmoniforms and osmeriforms.

The hypothesis presented in this paper is developed in three stages. We first reconstructed the phylogenetic history of the suborder Osmeroidae to establish the phylogenetic relationships among anadromous, marine, and freshwater species of this important group of fishes. Unlike salmonids, the osmeroids exhibit the complete range of anadromous (including amphidromous), marine, and freshwater life cycles. We mapped life cycles onto our phylogenetic reconstruction of osmeroids and onto the previously published phylogenetic reconstructions of salmoniforms (see below). We then applied ancestral character-state reconstruction methodology (see below) to test alternative hypotheses concerning the evolution of anadromy in salmonids and osmeroids. Second, we formulate an alternative hypothesis concerning the evolution of anadromy, based on the possibility that anadromy may have evolved from marine origins as well as from freshwater origins. We refer to this alternative view as the safe-site hypothesis and contrast it with the model presented by Gross (1987). Finally, we consider some important biological differences between anadromous osmerids and salmonids and discuss how these differences may be related to the hypothesized origins of anadromy in salmoniforms and osmeriforms.

Methods

Phylogenetic Reconstruction

The overall classification of euteleosts is based on Nelson (1994), with exceptions as noted (Table 1). To assess the evolution of anadromy in osmeroids, we conducted a phylogenetic reconstruction of this group based on the mitochondrial cytochrome *b*

Table 1.—Classification and common names used in this study. The nomenclature follows Nelson (1994), Ishiguro et al. (2003), and Waters et al. (2002).

Classification	Common names used
Protacanthopterygii	
Order Esociformes	Esociforms: pikes, pickerels, mudminnows
Order Osmeriformes	Osmeriforms
Superfamily Argentinoidea	Argentinoids: herring smelts, deep-sea smelts, spookfishes
Suborder Osmeroidei	Osmeroids
Family Osmeridae	Osmerids: northern smelts
Family Galaxiidae	Galaxiids
Family Retropinnidae	Retropinnids: southern smelts
Family Salangidae	Salangids: icefishes
Order Salmoniformes	Salmoniforms
Family Salmonidae	Salmonids

gene. All sequences were published in GenBank (NCBI 2005), and accession numbers of the various sequences used are listed in Table 2. All known sequences available for the family Osmeridae were used. We did not include the numerous sequences available for the galaxiid fishes. Waters and Wallis (2001) have argued that the freshwater, nonmigratory lineages among galaxiids represent independent radiations from diadromous lineages with repeated loss of diadromy. Thus, galaxiid fishes were represented here only by the anadromous Tasmanian whitebait *Lovettia sealii* (Johnston). As reported by Nelson (1994), 13 species of Osmeridae are recognized. However, taking into account the recent literature (Nishida 1988; Wilson and Williams 1991; Taylor and Bentzen 1993; Taylor and Dodson 1994; Johnson and Patterson 1996; Saruwatari et al. 1997; Ishiguro et al. 2001; Waters et al. 2002; Ishiguro et al. 2003; Skurikhina et al. 2004; Ilves and Taylor 2007), we recognized 15 valid osmerid species (excluding subspecies). Within the Osmeridae, we obtained cyt *b* sequences for 11 species. We also obtained sequences for Salangidae (icefishes) and Retropinnidae (southern smelts) (Table 2). The trees were rooted with representative species of the superfamily Argentinoidae, the sister group of suborder Osmeroidei in the maximum parsimony analysis of Ishiguro et al. (2003). Sequences were aligned using Clustal W (Thompson et al. 1994), and multiple alignments were corrected by eye using Seaview (Galtier et al. 1996). Maximum likelihood trees were generated by dnaml (PHYLIP) (Felsenstein 2005), and the robustness of tree branches was assessed using

500 bootstrap replications. Only values above 50% were reported for basal and intermediate branches. We indicated whether the species were anadromous, marine, or exclusively freshwater based on published accounts of their ecology (see McAllister 1963; FishBase, www.fishbase.org, version 12/2004).

The phylogenetic tree of the salmonid fishes used was the one obtained by Crespi and Fulton (2004; Figure 2C) from the analysis of seven nuclear DNA genes (7,530 DNA positions), involving 21 species. We also included the phylogenetic reconstruction of the esociforms (10 species of pikes, pickerels, and mudminnows; Lopez et al. 2004), as this group was identified as the sister of the salmoniforms by these authors and by Ishiguro et al. (2003). The concatenation was done by hand to produce one phylogenetic reconstruction upon which we mapped freshwater and anadromous life cycle states (there are no salmoniforms with uniquely marine life cycles). This general topology excluded branch lengths, as different sequence data were available for the two groups. Huchen *Hucho hucho* (Linnaeus) was classified as a uniquely freshwater taxon (Holcik et al. 1988). The movements of European and Siberian Hucho are quite limited and they are found in the large rivers of piedmont and upland areas. East Asian Hucho are also found far inland (M. Kottelat, independent consultant, Cornol, Switzerland, personal communication).

Reconstructing Ancestral Character States

It is well known that anadromy encompasses a wide array of behaviors. Rounsefell (1958) and Quinn

Table 2.—Species and family names and GenBank accession numbers relative to the mitochondrial cytochrome *b* (cyt *b*) gene sequences of species used to reconstruct the phylogeny of osmeriforms (Figure 1). F = freshwater life cycle; M = marine life cycle; A = anadromy/amphidromy.

Family - species	cyt *b*	Life cycle
Salangidae		
Hemisalanx brachyrostralis [Fang]	AY279372	F
Leucosoma (=*Salanx*) *reevesii* [Gray]	AY279375	F
Neosalanx jordani [Wakiya and Takahashi]	AY279374	A
Protosalanx chinensis [Basilewsky]	AY279370	F
Japanese icefish *Salangichthys microdon* [Bleeker]	NC_004599	A
Salanx ariakensis [Kishinouye]	NC_006918	A
Noodlefish *S. cuvieri* [Valenciennes]	AB196913	A
Osmeridae		
Japanese smelt *Hypomesus japonicus* [Brevoort]	AB049019	A
Wakasagi *H. nipponensis* [McAllister][a]	DQ010190	A
Pond smelt *H. olidus* [Pallas]	DQ010196	A
Delta smelt *H. transpacificus* [McAllister]	AB089609	A
Capelin *Mallotus villosus* [Müller]	AB049022	M
Arctic rainbow smelt *Osmerus dentex* [Steindachner and Kner]	AB114911	A
European smelt *O. eperlanus* [Linnaeus]	U05667	A
Rainbow smelt *O. mordax* [Mitchill]	U05666	A
Ayu *Plecoglossus altivelis* [Temminck and Schlegel]	NC_002734	A
Spirinchus lanceolatus [Hikita]	AB094410	A
Eulachon *Thaleichthys pacificus* [Richardson]	AY279378	A
Retropinnidae		
Cucumberfish *Retropinna retropinna* [Richardson]	NC_004598	A
Tasmanian smelt *R. tasmanica* [McCulloch]	AF112321	A
Galaxiidae		
Tasmanian whitebait *Lovettia sealii* [Johnston]	AF112320	A
Outgroups		
Deepsea smelt *Glossanodon semifasciatus* [Kishinouye]	NC_004595	M
Eared blacksmelt *Lipolagus* (=*Bathylagus*) *ochotensis* [Schmidt]	NC_004591	M
Robust smallmouth *Nansenia ardesiaca* [Jordan and Thompson]	NC_004596	M
Barrel-eye *Opisthoproctus soleatus* [Vaillant]	NC_004600	M
Stout blacksmelt *Pseudobathylagus milleri* [Jordan and Gilbert]	AY973046	M

[a] Identical to *Hypomesus chishimaensis* [Saruwatari, López and Pietsch] (see Ilves and Taylor 2007).

and Myers (2004) have argued that anadromy in salmonids is not a single trait, but rather represents a suite of life history traits that are expressed along a continuum. The freshwater portion of the life cycle may be limited to spawning and only several days following hatching. Anadromous individuals may coexist with freshwater residents within some or all populations of some species. One salmonid genus, *Oncorhynchus* [Suckley], illustrates the entire range of such behaviors (Quinn and Myers 2004). Freshwater residency and feeding prior to spawning, typical of freshwater amphidromy, may vary from several years (e.g., *Galaxias fasciatus* [Gray], McDowall 1988) to several weeks or months in some populations of southern smelts (Eldon and Greager 1983). Despite this diversity of life cycle characteristics, we here consider anadromy and its variants together as one evolutionary condition, the physiological capacity to exploit freshwaters to reproduce yet tolerate saline waters for varying periods of time for feeding. We thus limited our reconstruction of ancestral character states to three general categories of life cycles: freshwater, marine, and anadromous. We broadly defined the latter group to include spe-
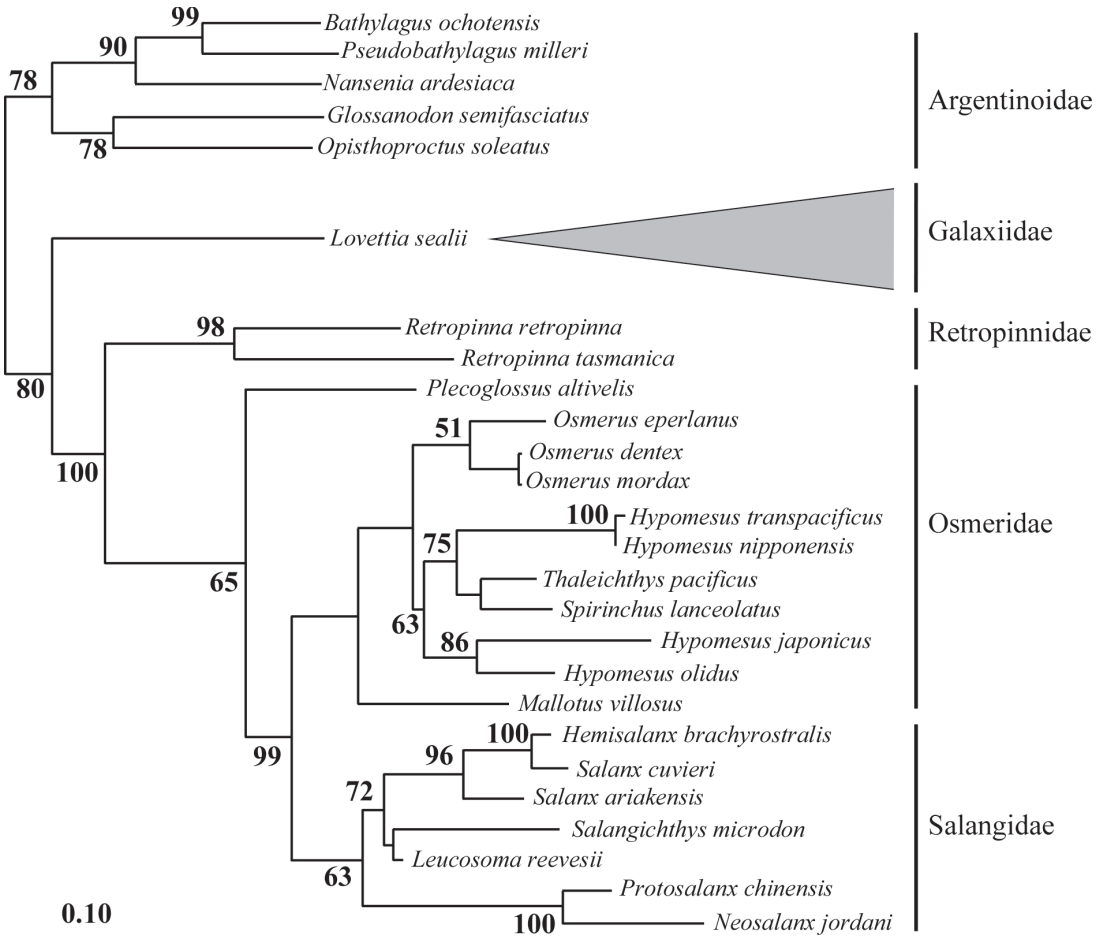
Figure 1.—Phylogenetic reconstruction of osmeriforms based on the cytochrome *b* mitochondrial gene. A total of 1,043 nucleotides were obtained from GenBank to construct a consensus tree based on 500 bootstraps. Numbers refer to the percent bootstrap support. Scale bar indicates number of changes per site.

cies with populations or population components that reproduce in freshwater and migrate to sea to feed during at least part of their life cycle.

We first reconstructed ancestral character states using maximum parsimony methods. Parsimony reconstruction finds the ancestral states that minimize the number of steps of character change given a phylogenetic tree and the observed character distribution across the terminal branches (Maddison et al. 1984). Parsimony analysis was based on simple parsimony: reversals and convergence were counted equally. Whereas parsimony implicitly assumes an equal probability of character change on all branches, Waters et al. (2002) have argued in

favor of character weighting (unequal probabilities of character change) in cases involving reductive characters and when a priori evidence suggests that homoplasy is wide-spread (e.g., losses of anadromy in galaxiid fishes, which repeatedly lose their marine life history phase; McDowall 1988). We have avoided such character weighting as counseled by Kitching (1992), Swofford et al. (1996), and Grant and Kluge (2003). In the present analysis, character weighting would necessarily be a subjective exercise. As phylogenetic hypotheses based on subjective weighting schemes run the risk of becoming self-fulfilling prophesies, we adopt the view that equal weighting of all transformations in parsimony and
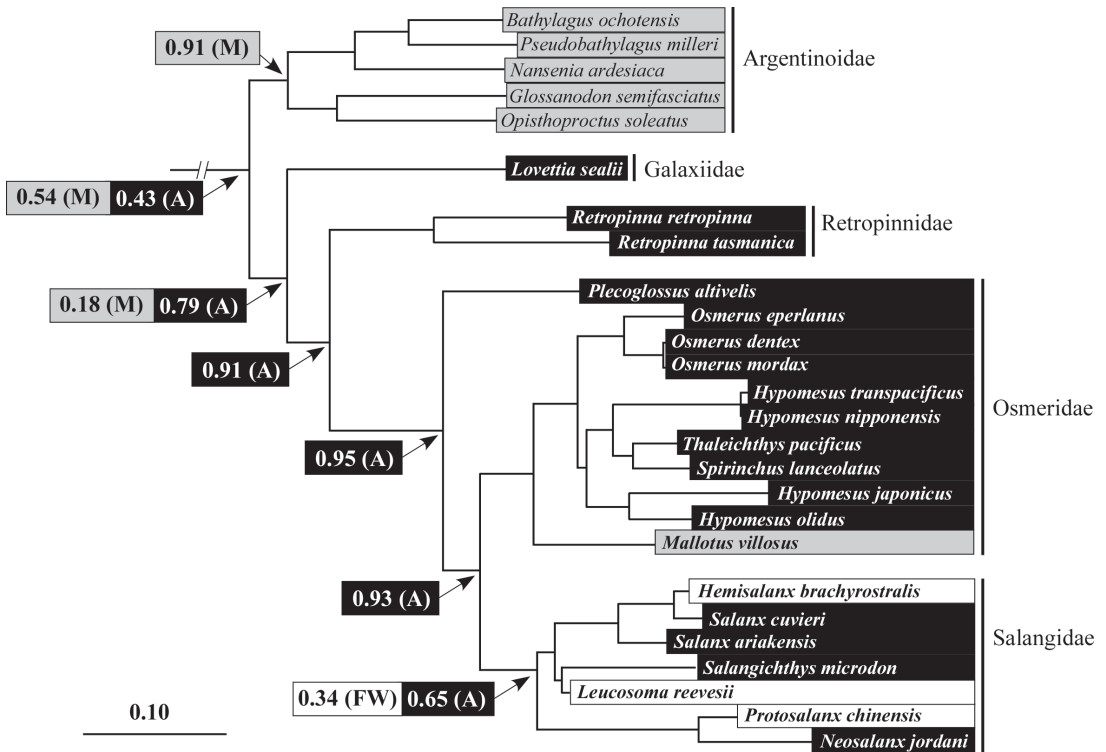
Figure 2.—Ancestral character state reconstruction of anadromous (A), marine (M), and freshwater (F) life cycles in osmeriforms based on the phylogenetic reconstruction depicted in Figure 1. Numbers at nodes represent significant liklihoods reported as proportional likelihoods. gray boxes—marine species, open boxes—freshwater species, black boxes—anadromous species.

likelihood analyses provides the least-biased test of competing hypotheses.

A fundamental problem with parsimony is that it does not account for the uncertainty in the process of character change (Huelsenbeck et al. 2003). There is always the chance that histories other than the most parsimonious one produced the observed distribution of character states. To deal with this problem, we used likelihood reconstruction methods to find ancestral states that maximize the probability that the observed states would evolve under a stochastic model of evolution (Schluter et al. 1997). For each node, the reconstruction finds the state assignment that maximizes the probability of arriving at the observed states in the terminal taxa and allowing the states at all other nodes to vary. We used the Markov k-state parameter model of evolution (Maddison and Maddison 2006). The single parameter is the rate of change and any particular

change is equally probable. All analyses were conducted using the program Mesquite (Maddison and Maddison 2006).

Results

Phylogenetic Reconstruction and the Evolution of Anadromy in Osmeroids and Salmonids

The phylogenetic reconstruction of osmeroids, based on 1,043 nucleotides of the cyt *b* gene (Figure 1), strongly supported a sister group relationship between southern smelts (Retropinnidae) and northern smelts (Osmeridae) + icefishes (Salangidae), as initially shown by Waters et al. (2002) and López et al. (2004). Poor bootstrap support was obtained for the basal nodes of Osmeridae, largely because of uncertainty concerning the placement

of capelin *Mallotus villosus* (Müller). Both northern and southern smelts are considered as anadromous. Salangidae (icefishes) are also anadromous, with some freshwater neotonic forms (Johnson and Patterson 1996; Froese and Pauly 2004). Within osmerids, four species are considered marine, but cyt *b* sequences were only available for capelin. Based on both parsimony and likelihood methodologies, anadromy is the likeliest ancestral state leading to the Osmeroidae, but there is a high degree of uncertainty in the reconstruction (likelihood ratio of 4.4:1, anadromous versus marine character state;

Figure 2). The marine life cycle is the likeliest ancestral state leading to the Argentoidae (likelihood of 0.91 for a marine origin) (Figure 2). The life history cycle of the common ancestor of the two groups is ambiguous, with a likelihood ratio of nearly 1:1 for marine or diadromous origins.

Ancestral nodes in the salmoniform reconstruction exhibited exclusively freshwater life cycles based on both parsimony and likelihood procedures. The freshwater life cycle is supported at a likelihood level of 0.91 at the root of the tree (Figure 3). Moving into the tree, the freshwater life cycle is again
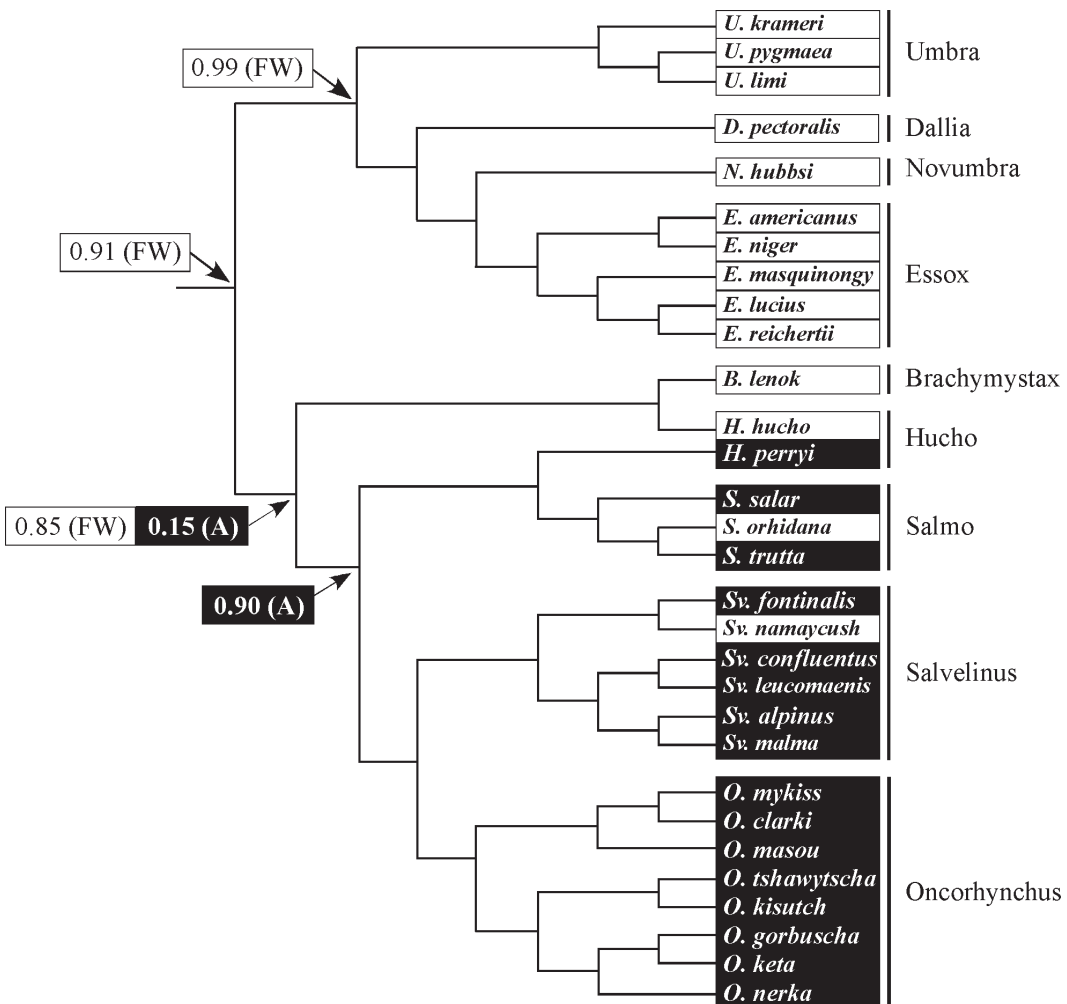

Figure 3.—Ancestral character state reconstruction of anadromous and freshwater life cycles in salmonids and esociformes. Numbers at nodes represent significant likelihoods reported as proportional likelihoods. Open boxes—freshwater species; black boxes—anadromous species.

strongly supported with a likelihood ratio of 5.6 to 1. Finally, the anadromous life cycle is strongly supported at the ancestral node of Japanese huchen *Hucho perryi*, *Salmo*, *Salvelinus*, and *Oncorhynchus*. Two species reverted independently to the freshwater life cycle.

Discussion

The Safe-Site Hypothesis

We initially proposed that the freshwater life cycle was the ancestral character state leading to salmoniform anadromy and that the marine life cycle was the ancestral character state leading to osmeriform anadromy. This prediction was partially supported by the character-state reconstruction reported here. The freshwater life cycle characterized the last common ancestor of salmoniforms and esociforms using both parsimony and likelihood reconstruction methods. In contrast, either anadromy or a marine life cycle was the ancestral state of the last common ancestor of osmeroids and argentines. Although we may neither accept nor reject a marine ancestry for osmeriform anadromy, it appears evident that anadromy among osmeriforms may have been derived without the precursor of a freshwater life cycle. The emergence of anadromy may thus have followed different evolutionary pathways in salmoniforms and osmeriforms.

The hypothesis that anadromy was derived from freshwater species to exploit the rich marine feeding grounds at high latitudes (Gross 1987; Gross et al. 1988) is consistent with the freshwater origins of salmoniforms as they appear to have experienced a strictly freshwater phase in their evolutionary history. If we assume that osmeriform anadromy was derived from a marine ancestry, we hypothesize that this evolutionary pathway represents a means of exploiting freshwater as a reproductive environment to protect the most vulnerable, early life history stages from marine predators (Figure 4). Many populations of plants and animals are controlled by heavy mortality at some life cycle stage and only individuals present in special "safe" sites may escape catastrophic mortality (Harper et al. 1961). For example, initiation of emergence and drift in beach-spawning capelin is associated with rapid wind induced water-mass exchange, which in turn results in the replacement of cold, high-saline, predator-laden waters with warmer, less-saline waters in which the abundance of predators was reduced 3–20-fold and zooplankton prey increased 2–3-fold (Frank and Leggett 1982). The abundance of eggs and larvae of 11 other marine fish species was found to be associated with the safe site water mass (Frank and Leggett 1982). The attraction to freshwater for spawning by a variety of marine fishes may be more widespread than generally believed. The groundwater seepage hypothesis (Harden Jones 1981) proposes that assembly areas, spawning areas, and spawning grounds of fishes with marine life cycles as diverse as plaice, cod, herring, pilchard, and mackerel could be identified by reference to groundwater seepage. Although Harden Jones (1981) postulated that the functional significance of groundwater seepage in spawning areas was associated with imprinting and homing to the chemicals associated with such seepages, we suggest that such seepage would also contribute to reducing the incidence of marine predators such as chaetognaths, jellyfish, and ctenophores, thus creating localized safe sites for embryos and early larvae. Given the massive mortality that occurs in marine fishes during the earliest life history stages, the transition to exploiting freshwater as a safe haven for embryos and the early larval stages would result in important fitness advantages by reducing mortality during the most vulnerable stages. Finally, the importance of estuaries to marine fish as refuges from predation has been well-established in the literature for many years (Moyle and Cech 2004).

We propose that the exploitation of low-salinity waters by some marine species led to freshwater reproduction and possibly prolonged feeding in freshwaters and the development of the amphidromous life cycle. It is no coincidence that amphidromy in osmeroids is dominated by southern hemisphere taxa. To the best of our knowledge, no salmonids have been unequivocally characterized as amphidromous. The Australian zoogeographic region has long been isolated from evolutionary events taking place elsewhere, and this is reflected in its depauperate primary freshwater fish fauna. The vast majority of this region's fish fauna is diadromous or derived from marine ancestors, reflecting the availability of freshwater niches for marine invaders. Similarly, in Patagonia, only three genera (*Aplochiton* [Jenyns], *Brachygalaxias* [Eigenmann], and *Galaxias* [Cuvier]) and eight freshwater species are present. The Andean lakes of Patagonia were formed by the last
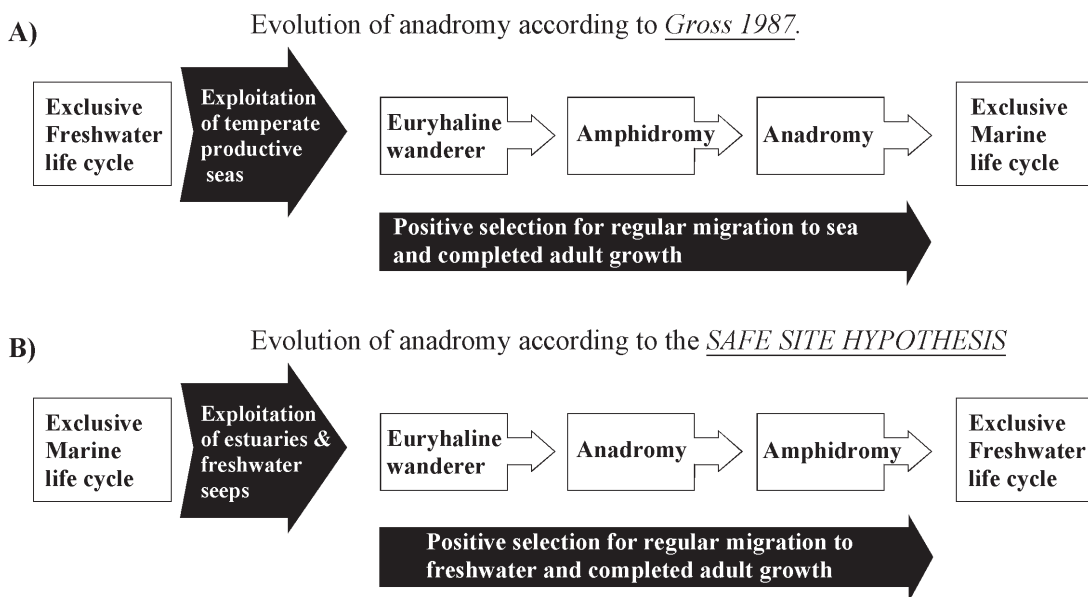
A)   Evolution of anadromy according to *Gross 1987*.

B)   Evolution of anadromy according to the *SAFE SITE HYPOTHESIS*

Figure 4.—(A) Hypothesized origins of anadromy as presented by Gross (1987) and applicable to the evolution of of salmoniform anadromy from freshwater origins. (B) The safe-site hypothesis as applied to the marine origins of osmeriform anadromy.

retreat of the Pleistocene ice sheets, some 10,000–20,000 years ago and were colonized by previously displaced gondwanic fishes (silurids and galaxiids), marine fishes (percichthiids and aterinopsiids), and marine dispersants (galaxiids) (Cussac et al. 2004). Thus, the presence of amphidromous and freshwater populations of galaxiids in Patagonia also appears to be related to a depauperate freshwater fish fauna and the availability of freshwater niches for a variety of anadromous species. This interpretation is consistent with the view of Waters and Wallis (2001) that cladogenesis of freshwater, nonmigratory, lineages among galaxiids represent independent radiations from migratory lineages with repeated loss of amphidromy.

Ecological Correlates of Contrasting Evolutionary Pathways to Anadromy

In contrast to most salmonids, the reproductive migrations of both northern and southern smelts are generally characterized by brief excursions to spawn in freshwater. Larval smelt of the subfamily Osmerinea (including *Osmerus, Allosmerus, Spirinchus,* and *Thaleichthys*) may spend no more than 24 h in

freshwater before being transported to coastal marine or estuarine environments (Hart and McHugh 1944; Ouellet and Dodson 1985; Mclean et al. 1999). In both northern and southern smelts, the establishment of landlocked populations is widespread (McDowall, 1988; Nishida 1988; Nellbring 1989; Taylor and Bentzen 1993; Bernatchez 1997). Within osmerids, four species are considered marine, but most retain some connection to fresh or brackish water. The cyt *b* sequence was available for only one marine osmerid, the capelin, a coastal marine species that spawns on the sea bottom or on beaches. Spawning beaches in Newfoundland are located at the heads of embayments having small freshwater streams percolating through the sediments (Carscadden et al. 1988). Other marine Osmerinae include the surf smelt *Hypomesus pretiosus* (Girard), a coastal species spawning in the upper surf zone (Martin and Swiderski 2001); whitebait smelt *Allosmerus elongates,* a species that inhabits freshwater at times but appears to be neither anadromous nor beach spawning (Eschmeyer 1983); and night smelt *Spirinchus starksi,* also reported to spawn in the surf zone (McAllister, 1963). The almost complete abandonment of anadromy

for a marine life cycle thus appears to have several evolutionary origins within osmerids. Most cases involve seeking safe reproductive havens in the upper intertidal reaches that may be characterized by freshwater percolation.

Another striking difference between osmeroid and salmoniform life histories concerns the phenomenon of partial migration. Salmonids are known for the occurrence in sympatry of two life history forms, one that undergoes migration to sea before returning to freshwater to reproduce (anadromous) and one that inhabits freshwater without a migration phase (resident). Moreover, experimental crosses and transplant studies have shown that juveniles from "pure" anadromous or resident crosses can either become one form or the other and that transplanted resident fish have given rise to anadromous stock or vice versa (e.g., Olsson and Greenberg 2004; Schreiber and Diefenbach 2005). By using highly polymorphic microsatellite loci and parentage analysis in a natural population of sympatric anadromous and resident brook char *Salvelinus fontinalis*, Thériault et al. (2007) found that extensive gene flow occurred between the two forms and was mediated by resident males mating with both resident and anadromous females. Furthermore, although no anadromous brook char occur further south than the Gulf of Maine, coastal resident brook char still persist (Castric and Bernatchez 2003). Assuming a reduction in the resource gradient from freshwater to the sea, the species at the southern limit of its distribution has adopted the freshwater life cycle, even though their fluvial habitats are connected to the sea. The conditional nature of anadromy in salmonids is most probably ancestral (Crespi and Teo 2002) and represents an alternative way to maximize fitness according to the metabolic status of an ancestral freshwater fish. Although osmeriforms readily establish freshwater populations through the process of landlocking, we know of no example within osmeriform fishes of the sympatric occurrence of diadromous and freshwater forms or the existence of freshwater forms that have abandoned anadromy other than by the process of landlocking. One possible exception to this is the recent demonstration that the lake-dwelling *Hypomesus chishimaensis* and and the anadromous wakasagi are not genetically distinct and do not merit separate species status (Ilves and Taylor 2007). However, similarity in mitochondrial and nuclear sequence data cannot be used to establish if life histories are under the control of a conditional strategy. Although *Hypomesus chishimaensis* may very well be an alternative ecotype of *H. nipponensis*, more work is required to demonstrate the sharing of a common gene pool in sympatry.

There also appear to be differences in the occurrence and the adaptive significance of homing to natal spawning sites between salmoniforms and osmeriforms. The cooccurrence of anadromy and homing is common in salmonid fishes and is generally believed to have evolved to facilitate adaptations to local, population-specific conditions (Leggett 1977). Recent molecular studies of population structure in salmonids and osmerids suggest that homing is not as well developed in osmerids. Although considerable population structure can be detected among populations of salmon and trout species (e.g., Fontaine et al. 1997; Shaklee et al. 1999; Castric et al. 2001), such structure is far less evident among anadromous osmerids. Studies of rainbow smelt *Osmerus mordax* (Lecomte F and J.J. Dodson unpublished data) and eulachon *Thaleichthys pacificus* (Mclean et al. 1999; Mclean and Taylor 2001; Beacham et al. 2005) reveal little genetic structuring among local populations. These local groups, or demes, may be considered to form metapopulations (Kritzer and Sale 2004) whereby extensive gene flow occurs among the demes forming the metapopulation. Anadromous salmonids bear the imprint of genetically structured freshwater species characterized by high levels of cladogenesis associated with homing to freshwater spawning sites, whereas anadromous osmerids bear the imprint of genetically less heterogeneous marine species with relatively low levels of cladogenesis associated with marine dispersal. If this assertion is correct, we would predict that allelic richness and the slope of isolation-by-distance relationships should be lower, and the extent of population differentiation (F_{st}) should be higher among anadromous salmonids relative to anadromous osmerids. However, it is difficult to find the data to test this idea. As gene flow is strongly regulated by geographic features (Bradbury et al. 2006), any comparisons between anadromous salmonids and osmerids must be carried out over the same geographical region and, ideally, in the same rivers. For example, the work of Beacham and his colleagues on the west coast of Canada has revealed that the genetic differentiation observed among steelhead *O. mykiss* populations was approximately

10 times greater than that observed among eulachon populations observed over the same coastline but in different rivers (Beacham et al. 2004; Beacham et al. 2005). Although far more research is required to evaluate the genetic structure of a variety of anadromous osmerids, we speculate that the lower levels of cladogenesis observed among anadromous osmerids studied to date is a manifestation of an ancestry that is more associated with marine than freshwater origins.

Concluding Remarks

This change in perspective regarding the evolution of anadromy identifies several promising research avenues. The impact of anadromous life cycle diversity on the comparative genetic population structure of salmonids and osmerids merits attention. Such studies may provide insights into the trade-off between homing and dispersal and its impact on the population structure and life history evolution of fishes. Far more basic biological information is required to better describe the life cycles of euryhaline species. Although there is much evidence showing the ease by which anadromous osmerids and salmonids may establish freshwater populations through the process of landlocking, little effort has been invested in exploring the ability of anadromous species to establish marine populations or the ability of marine and freshwater species to establish euryhaline populations, the most likely starting point in the evolution of anadromy. The analysis of strontium and calcium concentrations in the otoliths of some species is changing this situation and revealing brackish water life history cycles in what were previously presumed to be uniquely anadromous (ninespine stickleback *Pungitius pungitius* [Linnaeus]; Arai and Goto 2005) or even freshwater (northern pike *Esox lucius* [Linnaeus]; Westin and Limburg 2002) species. There is also evidence that estuarine environments impose distinct selective regimes, generating physiologically adapted populations divergent from their marine counterparts, and the potential for in situ speciation in complete or partial isolation (Bilton et al. 2002 and references therein). In a similar vein, the sympatric anadromous rainbow smelt populations of the St. Lawrence estuary exhibit different salinity tolerances, with the smelt population occupying the north shore of the estuary spending more time in freshwater and occupying lower salinities in the estuarine transition zone than the more marine south-shore population (Lecomte and Dodson 2005). The cryptic nature of many of these evolutionary partitions requires a much closer examination of anadromous and so-called "euryhaline" life cycles.

Acknowledgments

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