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Evolution of Diadromy in Fish: Insights from a Tropical Genus (*Kuhlia* Species)

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ABSTRACT: Diadromous species undergo regular migration between fresh and marine waters. This behavior is found in many species, including fish, mollusks, and crustaceans, some of which are commercially valuable species. Several attempts to trace the evolution of this behavior have been made in Salmonidae and Galaxiidae, but ambiguous phylogenies and multiple character state changes prevented unequivocal conclusions. The Kuhlidae family consists of 12 fish species that inhabit tropical islands in the Indo-Pacific region. The species have marine, partially catadromous, or fully catadromous life histories (i.e., they migrate from rivers to the sea to reproduce). The evolution of migratory behavior was traced on a well-resolved phylogeny. Catadromous *Kuhlia* species were basal, and partially catadromous and marine species formed derived monophyletic groups. This is, to our knowledge, the first time that a clear origin and polarity for the diadromous character has been demonstrated. We propose that the relative lack of resources in tropical, inshore, marine habitats and the ephemeral and isolated nature of freshwater environments of tropical islands, combined with phenotypic plasticity of migratory traits, play key roles in driving the evolution of diadromy in the Kuhlidae and probably in other groups. This work is an important starting point to understand the role of diadromy in speciation and adaptation in unstable habitats.

Keywords: diadromy, evolution, phylogeny, ancestral character reconstruction, habitat shift, catadromy, land locking.

Introduction

The term “diadromy” was introduced by Myers to describe migrations of aquatic organisms between freshwater and

the sea (Myers 1949). Diadromy takes three distinct forms: catadromy, anadromy, and amphidromy. Catadromous and anadromous fish migrate between the marine and the freshwater biomes to reproduce. Catadromous fish move from freshwater to breed in the sea, whereas anadromous fish move from the sea to breed in freshwater habitats. Migrations of amphidromous fish are not for reproductive purposes. As defined by McDowall (2007), amphidromous fish reproduce in freshwater, and larvae drift downstream to feed at sea. After a variable amount of time, juveniles return to freshwater, where they undergo most of their somatic growth before maturing and spawning. We refer to this life cycle as freshwater amphidromy to distinguish it from marine amphidromy, which refers to reproduction at sea, followed by migration to freshwater after hatching for a variable period, then a return to the sea for additional growth and reproduction (Gross 1987).

Despite the physiological challenges presented by this tactic, diadromy has evolved multiple times in aquatic taxa, including fish, mollusks, and crustaceans, which verifies its importance. However, evolutionary pathways leading to a diadromous life cycle are unclear (McDowall 1997). Gross (1987) proposed an ecological and evolutionary model based on the principle that diadromy would evolve if the combination of reproductive success and survivorship of migrants would exceed that of individuals who do not migrate. In his model, catadromy and anadromy, respectively, are preceded by marine and freshwater amphidromy and are intermediary evolutionary steps between exclusively marine and freshwater life cycles. Additional analysis of global patterns in aquatic productivity led to the conclusion that the presence and the direction of diadromy can largely be explained by the relative availability of food resources in freshwater and marine

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Table 1: Sample, geographical location, and species name of specimens used in this study

Sample	Sampling location	Latitude	Longitude	Species identification
Kmar 1	Guam	13°26'39.5"N	144°47'37.4"E	<i>Kuhlia marginata</i>
Kmar 2	New Caledonia	20°31'28.31"S	164°46'32.56"E	<i>K. marginata</i>
Kmar 3	Pentecost, VA	15°47'0.9"S	168° 9'52.06"E	<i>K. marginata</i>
Kmar 4	Malekula, VA	16° 5'27.79"S	167°10'30.71"E	<i>K. marginata</i>
Kmar 5	Efate, VA	17°37'15.32"S	168°29'54.42"E	<i>K. marginata</i>
Kmar 6	Queensland, AU	16°27'37.1"S	145°21'22.2"E	<i>K. marginata</i>
Ksal 1	Samoa	13°54'48.3"S	171°44'5.8"W	<i>Kuhlia salelea</i>
Ksal 2	Samoa	13°54'48.3"S	171°44'5.8"W	<i>K. salelea</i>
Kmal 1	Moorea, FP	17°35'7.3"S	149°50'24.4"W	<i>Kuhlia malo</i>
Kmal2	Raiatea, FP	16°52'37.6"S	151°25'35.0"W	<i>K. malo</i>
Krup 1	Mayotte, CO	12°48'26.4"S	45°12'0.5"E	<i>Kuhlia rupestris</i>
Krup 2	Réunion, MA	21°18'32.2"S	55°24'34.5"E	<i>K. rupestris</i>
Krup 3	New Caledonia	20°31'28.31"S	164°46'32.56"E	<i>K. rupestris</i>
Krup 4	Fraser Island, AU	25° 7'40.6"S	153°17'40.4"E	<i>K. rupestris</i>
Ksau 1	Madagascar	15°26'60.0"S	47°40'0.0"E	<i>Kuhlia sauvagii</i>
Ksau 2	Madagascar	15° 8'46.9"S	49°57'29.4"E	<i>K. sauvagii</i>
Kxen 1	Hawaii	20°56'20.0"N	156°20'33.0"W	<i>Kuhlia xenura</i>
Kxen 2	Hawaii	20°56'20.0"N	156°20'33.0"W	<i>K. xenura</i>
Kmun 1	New Caledonia	20°56'14.7"S	165°22'41.4"E	<i>Kuhlia munda</i>
Kmun 2	New Caledonia	20°56'14.7"S	165°22'41.4"E	<i>K. munda</i>
Kcau 1	Réunion, MA	21°18'32.2"S	55°24'34.5"E	<i>Kuhlia caudavittata</i>
Kcau 2	Réunion, MA	21°18'32.2"S	55°24'34.5"E	<i>K. caudavittata</i>
Ksan 1	Moorea, FP	17°34'42.1"S	149°51'81.1"W	<i>Kuhlia sandvicensis</i>
Ksan 2	Tubuai, FP	23°22'29.6"S	149°29'1.0"W	<i>K. sandvicensis</i>
Knut 1	Easter Island	27° 7'16.3"S	109°21'59.1"W	<i>Kuhlia nutabunda</i>
Knut 2	Easter Island	27° 7'16.3"S	109°21'59.1"W	<i>K. nutabunda</i>
Kmug 1	Réunion, MA	21°18'32.2"S	55°24'34.5"E	<i>Kuhlia mugil</i>
Kmug 2	Réunion, MA	21°18'32.2"S	55°24'34.5"E	<i>K. mugil</i>
Kmug 3	Clipperton	10°17'5.4"N	109°12'58.5"W	<i>K. mugil</i>
Kmug 4	Clipperton	10°17'5.4"N	109°12'58.5"W	<i>K. mugil</i>
Kmug 5	New Caledonia	20°55'50.6"S	165°19'27.6"E	<i>K. mugil</i>
Kmug 6	New Caledonia	20°55'50.6"S	165°19'27.6"E	<i>K. mugil</i>
Kpet 1	Clipperton	10°17'5.4"N	109°12'58.5"W	<i>Kuhlia petiti</i>
Kpet 2	Clipperton	10°17'5.4"N	109°12'58.5"W	<i>K. petiti</i>
Kpet 3	Marquesas, FP	9°57'37.50"S	138°50'28.6"W	<i>K. petiti</i>

Note: AU = Australia; CO = Comoros; FP = French Polynesia; MA = Mascarene; VA = Vanuatu.

habitats (Gross et al. 1988). At low latitudes, freshwater productivity often exceeds marine water productivity. Gross et al. (1988) argue that this difference promotes the occasional excursion of marine fish into freshwater habitats and initiates evolution toward a fully freshwater life cycle through intermediate stages of marine amphidromy followed by catadromy. At high latitudes, the reverse applies: ocean productivity is generally higher than freshwater productivity, so the occasional excursion of freshwater fish into marine habitats initiates evolution toward an anadromous life cycle via freshwater amphidromous stages. However, the evolution of catadromy has received little attention since Gross's (1987) model was formulated. A great deal of discussion has been generated over the evolution of anadromy, and several attempts to test this model have been made (Dodson et al. 2009).

The starting point to validate Gross's (1987) model for the evolution of diadromy is to determine whether diadromous species have freshwater, marine, or diadromous ancestry. This will allow the polarity of the character (i.e., migratory behavior) to be inferred, which is the key to understanding the evolutionary scenario. One way to address these issues is to focus on the phylogeny of terminal taxa (e.g., within family or genus) to identify changes in tactics among clades (McDowall 1997) and thus the likely mode of evolution of diadromy. This method has been applied to the Salmonidae and Galaxiidae, where it was found that diadromy evolved independently in several lineages, which prevented the nonequivocal reconstruction of the ancestral state (McLennan 1994; McDowall 1997; Waters et al. 2001). These families are among the largest and oldest teleostean groups and include numerous lin-

eages, subfamilies, genera, and species distributed worldwide. Incomplete taxon sampling made ancestral state reconstructions challenging, and difficulties were also encountered in resolving deep phylogenetic relationships. Another way to answer this question is to estimate the ancestral states for a group of species with varying life histories in relation to outgroups (Maddison et al. 1984). This approach has also been applied to Salmonidae and Galaxiidae by studying the phylogenetic position of the families within the teleostean lineages. However, the different topologies obtained (Johnson and Patterson 1996; McDowall 2002; Ramsden et al. 2003) led to different conclusions. Recently, Dodson et al. (2009) suggested that the evolution of anadromy may have followed contrasting evolutionary pathways, and they proposed the complementary safe-site hypothesis. In their model, anadromy in osmeriforms has evolved in response to a selective pressure generated by the importance of safe reproductive sites for survival. However, in this study, doubts remained about whether the ancestral state for the osmeriforms was marine or diadromous. Thus, 25 years after its formulation, the model proposed by Gross (1987) remains the most comprehensive evolutionary framework to understand the evolution of diadromy, but it has yet to be tested.

The Kuhliidae family (Teleostei) is a relevant group for studying the evolution of diadromous behavior. It consists of a single genus, *Kuhlia*. The species are associated with tropical islands in the Indo-Pacific region. Importantly, they have various types of life cycles. All Kuhliidae species include a marine larval phase, but the adults of various species live in marine, estuarine, or freshwater habitats. It has been demonstrated that spawning occurs at sea in two species in which adults reside in freshwater (Hogan and Nicholson 1987; Oka and Tachihara 2001). Reproduction of other *Kuhlia* species has never been reported in rivers, despite many years spent in the field (P. Keith, personal observations), and we assume that all Kuhliidae species reproduce at sea. Thus, representatives of this family may be classified as marine (i.e., they complete their entire life cycle at sea), partially catadromous (i.e., with reproduction at sea, marine larvae, and estuarine adults), or catadromous (i.e., with reproduction at sea, marine larvae, and freshwater adults). There are 12 species currently recognized in the genus (Randall and Randall 2001; Loiselle and Stiassny 2007). Two species have an Indo-Pacific range: *Kuhlia rupestris* Lacépède, 1802; and *Kuhlia mugil* Forster, 1801, with the latter also found in the eastern Pacific. *Kuhlia sandvicensis* Steindachner, 1876; *Kuhlia munda* De Vis, 1884; *Kuhlia marginata* Cuvier, 1829; and *Kuhlia petiti* Schultz, 1943, have large distributions in the Pacific. *Kuhlia caudavittata* Lacépède, 1802, is found throughout the Indian Ocean. *Kuhlia xenura* Jordan & Gilbert, 1882; *Kuhlia salelea* Schultz, 1943; *Kuhlia malo* Valenciennes,

1831; *Kuhlia nutabunda* Randall and Radcliffe, 1912; and *Kuhlia sauvagii* Regan, 1913, are endemic to Hawaii, Samoa, French Polynesia, Easter Island, and the western Indian Ocean, respectively.

The aim of our study was to use the Kuhliidae family to test hypotheses concerning the evolution of diadromy and, in particular, catadromy. We first reconstructed the phylogenetic relationships between marine, diadromous, and partially diadromous species in this group. Then, we mapped the different life cycles onto the phylogeny obtained and applied ancestral state reconstruction methodology. The implications of the scenario found here for the evolution of diadromy and catadromy are discussed as well as the importance of the short geological history of tropical islands and the ephemeral nature of freshwater environments in driving the evolutionary history of the Kuhliidae.

Material and Methods

Sampling

All nominal species ($n = 12$) of the genus *Kuhlia* were sampled from 21 islands and mainland locations, from Mayotte (Indian Ocean) to Clipperton (Pacific Ocean; table 1). Samples for species with large geographic ranges (e.g., *Kuhlia mugil*, *Kuhlia rupestris*, and *Kuhlia marginata*; Randall and Randall 2001) were obtained from several specimens (from two to six) from various locations across the wide distributional range. Species identifications were based on field guides (Keith et al. 2002, 2006) and taxonomic literature (Randall and Randall 2001; Loiselle and Stiassny 2007) and by comparison with the species available in the collections of the Muséum National d'Histoire Naturelle of Paris (MNHN). Two species were chosen as nonmonophyletic outgroups (Yagishita et al. 2002; Darlu and Tassy 2009); *Microcanthus strigatus* Cuvier, 1831 (Kyphosidae), and *Nemadactylus monodactylus* Carmichael, 1819 (Cheilodactylidae), because they were closely related to the Kuhliidae (Yagishita et al. 2002; Li et al. 2009), and because tissues were available from the MNHN collection (table 1).

DNA Extraction, Amplification, and Sequencing

Total genomic DNA was extracted from ethanol-fixed fin clips with use of the semi-automated ABI Prism 6100 Nucleic Acid PrepStation (Applied Biosystems) following the protocol of Winnepenninckx (1993). Portions of five genes were amplified and sequenced: the mitochondrial cytochrome oxidase I (*COI*) and 16S rRNA genes and the nuclear partial rhodopsin retrogen (*Rh*), interphotoreceptor retinoid-binding protein (*IRBP*), and TMO-4C4

Table 2: Forward and reverse primers used for polymerase chain reaction of the five genes analyzed in this study

Gene: primer name	5'-3' sequences	Source
<i>COI</i> :		
CoITelF1	TCGACTAATCAYAAAGAYATYGGCAC	Dettai et al. 2011
CoITelR1	ACTTCTGGGTGNCCAAARAATCARAA	
<i>16S</i> rRNA:		
16Sarl	CGCCTGTTTATCAAAAACAT	Palumbi et al. 1991
16SbrH	CGGTCTGAACTCAGATCACGT	
<i>TMO</i> :		
TMO4C4F	CCTCCGGCCTTCCTAAAACCTCTC	Streelman and Karl 1997
TMO4C4R	CATCGTGCTCCTGGGTGACAAAGT	
<i>IRBP</i> :		
IRBPF740	AACNGCWAARTCTATCAACCC	This study
IRBPR1540	YTCCTCRAAGTCTCCRAACAT	
<i>Rh</i> :		
RhF193	CNTATGAATAYCCTCAGTACTACC	Chen et al. 2003
RhR1039	TGCTTGTTTCATGCAGATGTAGA	

(*TMO*) genes. The *TMO* gene is an anonymous, putative protein-coding locus identified and used for phylogeny by Streelman and Karl (1997). The first intron of the *IRBP* gene was amplified using primers designed for this study (table 2). Primers used and fragment lengths are listed in table 2. The PCRs were performed in a final 20- μ L volume containing 5% DMSO, 2.0 μ L of 10 \times CoralLoad buffer (Qiagen), 0.2 mM dNTP, 3.0 pM of each primer, 0.6 U of Taq (Qiagen), and 2.0 ng of DNA. The amplification products were generated by an initial denaturation for 4 min at 94°C, followed by 45 cycles of 40 s at 94°C, 40 s at 52°C, and 1 min at 72°C, with a final extension of 7 min at 72°C. Polymerase chain reaction products were purified using exonuclease I and phosphatase and sequenced using BigDyeTerminator V3.1 kit (Applied Biosystems) and the ABI3730XL sequencer. Sequences were verified by forward and reverse comparisons.

Phylogenetic Analysis

All sequences were manually aligned and edited. Eight data sets were analyzed for all individuals listed in table 1. Five data sets consisted of the independent gene analyses (*COI*, *TMO*, *IRPB*, *16S*, and *Rh*). The sixth data set, *COI*-RY, included the same set of characters as the *COI* data set, but it included transversion (R-Y) substitutions at the third codon positions for saturation correction. This matrix was constructed by replacing the third codon purines (A/G) with R and the third codon pyrimidines (C/T) with Y (Phillips and Penny 2003; Phillips et al. 2004). The last two data sets consisted of five-gene concatenated data sets; one included the regular *COI* matrix (CD), and one included the *COI*-RY matrix (CD-RY).

We evaluated saturation for the third codon position of

the gene *COI* for transitions and transversions separately. We plotted pairwise nucleotide differences against an evolutionary distance as a substitute for absolute geological time. Evolutionary distance was the gamma-corrected maximum composite likelihood distance calculated with Mega v. 4 (Tamura et al. 2007).

Using MrModeltest 2.2 (Nylander 2004), we selected a generalized time reversible model with a gamma law (Γ , four categories) and a proportion of invariants (I) as the best-fitting model of nucleotide evolution for each of the five genes analyzed. Phylogenies were constructed for each gene sequence data set and for the concatenated data sets, CD and CD-RY. They were conducted using maximum likelihood (ML) and Bayesian approaches. Analyses of *COI* (and *COI*-RY), *TMO*, and the coding region of *IRBP* were run using first and second codon and third codon positions as two different partitions. The noncoding region of *IRBP* (i.e., intron) was considered as a third partition for this gene. In the concatenated analyses, mutation rates were partitioned among genes, and the partitions among codon positions (first and second codon and third codon positions) were conserved for the different coding regions. Best-scoring ML trees were estimated for each data set using RaxML HPC2 on Teragrid, version 7.2.7, implemented in the Cyberinfrastructure for Phylogenetic Research portal, version 3.1. One hundred independent searches were made starting from distinct random trees. The robustness of nodes was assessed using the bootstrapping algorithm (1,000 replicates; Stamatakis et al. 2008). Bayesian trees were calculated using Mr. Bayes, version 3.1.2 (Huelsenbeck and Ronquist 2001). Independent analyses (default temperature), starting from distinct random trees, were run over 10 million generations and were sampled each 1,000 steps for the eight data sets. When the

log-likelihood scores were found to stabilize (i.e., after omitting the first 10% of trees as burn-in), a consensus tree was calculated. For third codon positions in the CD-RY coding data sets, we arbitrarily used A and C instead of R and Y, respectively, and set a single rate category for this partition (lset nst = 1) instead of six to avoid unnecessary estimation of transitional changes during the calculation.

Ancestral Character States Reconstruction

Recent studies have found that some individuals within species (*Kuhlia malo*, *K. rupestris*, *Kuhlia munda*, and *Kuhlia xenura*) are polytypic for migratory traits, and this primarily occurs with juvenile life stages (Benson and Fitzsimons 2002; Feutry et al. 2011, 2012a; McRae et al. 2011). In addition, juveniles of *Kuhlia caudavittata* and *K. mugil* are sometimes captured in freshwater (P. Feutry, personal observation). In this study, the migratory characteristics of the majority of the adult members of a species were used to determine the migratory status of each Kuhliidae species following McDowall's (1997) definition of diadromy. According to this classification, the species *K. mugil*, *Kuhlia petiti*, *Kuhlia sandvicensis*, *Kuhlia nutabunda*, *K. xenura*, and *K. caudavittata* were considered to be marine species, because almost no individuals migrate into rivers (Randall and Randall 2001; Benson and Fitzsimons 2002; McRae et al. 2011). The majority of *K. marginata*, *K. rupestris*, *Kuhlia malo*, *Kuhlia sauvagii*, and *Kuhlia salelea* individuals migrate into freshwater, and those species were considered to be catadromous species (Hogan and Nicholson 1987; Oka and Tachihara 2001; Oka and Tachihara 2008; Feutry et al. 2011, 2012a). *Kuhlia munda* individuals mostly live in estuaries after their larval migration from the sea. This species was considered to be partially catadromous (Feutry et al. 2012a). Each of these three life-history variants was considered as an alternate state for the reconstruction of the evolution of the migratory behavior within the *Kuhlia* genus.

Ancestral migratory states were reconstructed using the maximum likelihood method implemented in Mesquite, version 2.73 (Maddison and Maddison 2010). The migratory state of outgroups was coded as missing data, so as not to influence character reconstruction within the ingroup. The evolution of the migratory behavior assumed a Markov model with three states, and transition among states was set as equally likely (Lewis 2001). To take into account topological uncertainties, ancestral states were reconstructed for all Bayesian trees retained from the analysis of the five-gene concatenated analyses, and their mean likelihood was then plotted on the consensus tree.

Results

Sequences

Sequencing of the five genes was successful for all the individuals (European Molecular Biology Laboratory accession nos. HE798245–HE798384). No indels were found for the coding genes *COI*, *TMO*, and *Rh* or for the coding parts of *IRBP* genes. There were several indels in the non-coding part of the *IRBP* gene (1–48 base pairs [bp] long) and in the *16S* rRNA gene (1–2 bp long). However, alignments were not problematic within the ingroup (Kuhliidae) or when outgroups (Kyphosidae and Cheilodactylidae) were added to alignments. For the *COI* gene (633 bp long), 25 different haplotypes were found among the 37 specimens, displaying 185 polymorphic sites (haplotype diversity [Hd], 0.98). For the *16S* gene (586 bp long), 16 different haplotypes were found with 98 polymorphic sites (Hd, 0.94). Nuclear genes were less variable than mitochondrial genes. The *Rh* gene (795 bp long) presented 13 different haplotypes with 57 polymorphic sites (Hd, 0.91). The *IRBP* gene (740 bp long) exhibited 16 haplotypes. The coding part of *IRBP* was slightly more variable than the noncoding part, with 65 and 56 polymorphic sites and Hd of 0.92 and 0.86, respectively. Overall, the variability for the *TMO* gene (504 bp long) was less than for the other genes, with only 10 different haplotypes among the 37 specimens, 56 polymorphic sites, and Hd of 0.85.

Both pairwise transversional and transitional differences in first and second codon positions and transversional differences at third codon positions of *COI* gene increased with an increase in evolutionary distance, but transitional differences at third codon positions showed the beginning of saturation for the widest ingroup distances and were clearly saturated for outgroups compared with ingroup differences (app. A, available online). Thus, internal nodes of the tree obtained with the CD should be cautiously compared with those obtained with the CD-RY.

Phylogeny and Evolution of Diadromy

No incongruences were depicted among the topologies derived from the six single-gene analyses (app. B, figs. B1–B6, available online). However, in each of the single gene analyses, the relationships among groups were generally poorly resolved, with few well-supported clades. Therefore, we present the results obtained for the two concatenated data sets. The CD and CD-RY data sets produced phylogenetic trees with identical topologies and highly resolved relationships among both internal and external nodes (fig. 1).

The analysis of DNA sequences from five gene segments provides the first phylogeny of the Kuhliidae. It includes all known species and supports the monophyly of the family.

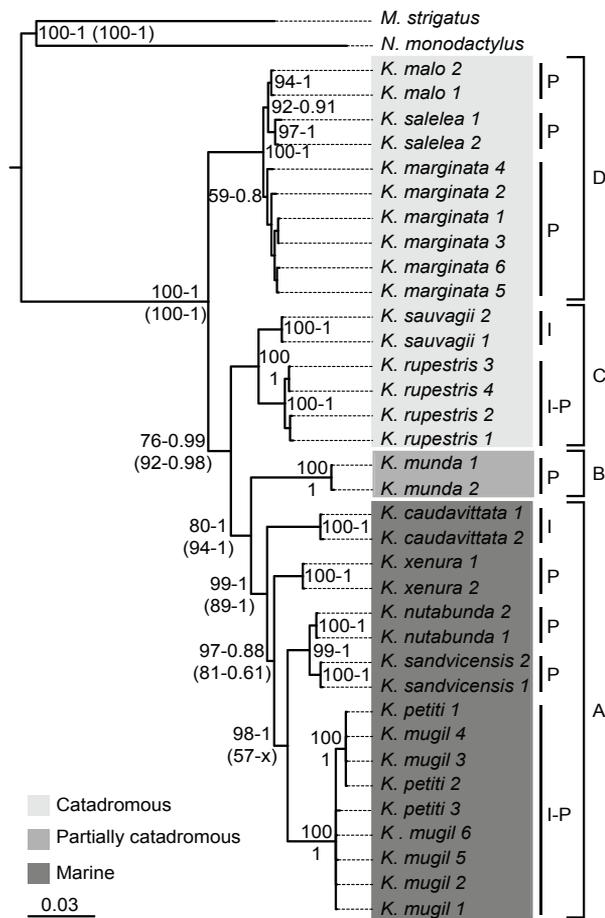


Figure 1: The 50% majority rule consensus tree obtained with the Bayesian analysis using the five-genes concatenated data set (CD). The topologies obtained by Bayesian analyses of the five-genes CD with transversion substitutions at the third codon positions of the *COI* gene (CD-RY), and maximum likelihood (ML) analyses on both the CD and the CD-RY were identical. ML bootstrap (BS) and posterior probabilities (PP) values are specified for each node in this order. For clarity, BS and PP for the CD-RY were only given for internal nodes (values between brackets) and not for species nodes. I and/or P indicate the presence of the associated clade in the Indian and/or Pacific Oceans, respectively. A, B, C, and D represent clades explained in the text.

In this phylogeny of the 12 *Kuhlia* species, 10 were found to be monophyletic and supported by high posterior probabilities and bootstrap values. The specimens that keyed to species named *K. mugil* and *K. petiti* could not be differentiated from molecular analyses. They formed a single monophyletic group, and each nominal species was polyphyletic, so they were treated as the same species in this study.

The phylogenetic tree showed that all diadromous species were contained in two highly supported monophyletic groups (clades D and C; fig. 1) that displayed a basal position

and which were separated from a third derived group that included the partially diadromous species and all marine species. Moreover, *K. munda* (group B; fig. 1), the only species with a partially diadromous life as adults, is the sister group to the derived monophyletic group that comprises all marine species (clade A; fig. 1). This intermediate position suggests a transitional step to brackish habitats before the colonization of marine habitats. Thus, all species in this family are probably derived from an ancestral diadromous *Kuhlia* species, which infers polarity in the evolution of migratory history in this family. Indeed, reconstructed migratory behavior supported this hypothesis (fig. 2). At the Kuhliidae node, the percentage of Bayesian trees for which ML ancestral character states reconstruction indicated a diadromous origin was 0.89 and was only 0.09 and 0.02 for a marine and partially diadromous origin, respectively.

Discussion

Origin and Polarity of Diadromy

The Kuhliidae proved to be a useful group to study the evolution of diadromy. To our knowledge, this is the first time that the phylogenetic origin of diadromy in any aquatic group has been demonstrated unequivocally and in which the polarity of this character can be inferred. This study makes a significant contribution to the discussion about whether diadromy is an ancestral or derived behavioral trait (McLennan 1994; Ramsden et al. 2003; Dodson et al. 2009).

Oka and Tachihara (2001) suggested that diadromous species of the family Kuhliidae evolved from marine species. Indeed, the families that, according to Yagishita et al. (2009), are known to be the closest to the Kuhliidae (Kypnosidae, Oplegnathidae, and Enoplosidae) are marine, and another closely related family (Terapontidae) includes both estuarine and marine species. Thus, the most parsimonious a priori explanation for the evolution of Kuhliidae is that the marine species were basal and that a single transition in life-history traits occurred to give rise to the diadromous derived *Kuhlia* lineage. In addition to being the most parsimonious hypothesis, this scenario conforms to Gross's (1987) model of evolution (i.e., catadromy evolved from marine life forms). Surprisingly, our phylogeny fails to support this hypothesis. We conclude that diadromy is basal for this genus, although the genus was evidently derived from marine forms. Extant *Kuhlia* marine species were more recently derived from *Kuhlia* species with diadromous life histories. The implications for the evolution of diadromy in this group are discussed below in terms of the acquisition and then the loss of the ability to migrate to freshwater.

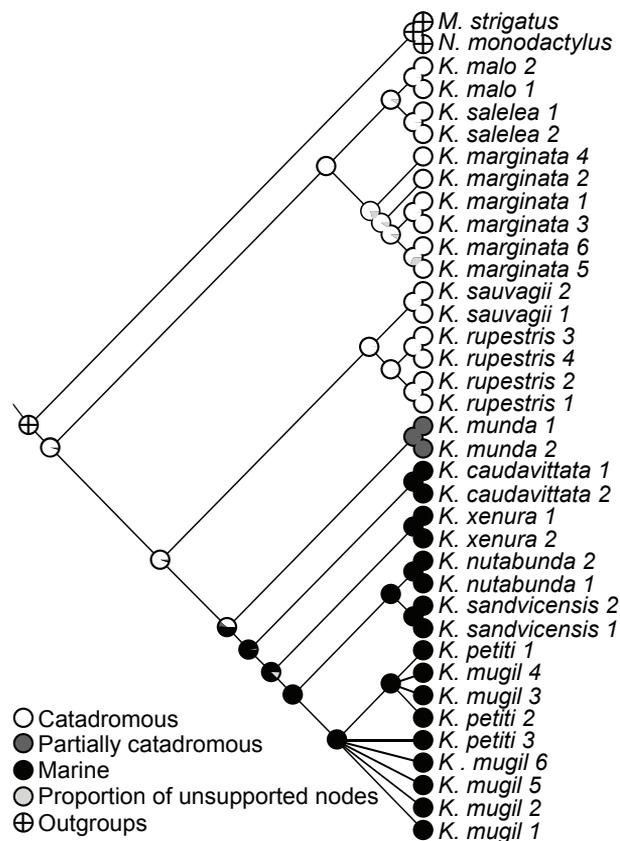


Figure 2: Reconstructed evolutionary history of migratory behavior using the maximum likelihood method implemented in Mesquite, version 2.73. The migratory behavior character had three states according to life cycles observed in genus *Kuhlia* (catadromous, partially catadromous, and marine).

Acquisition of Diadromy: The Ecological Opportunity Hypothesis

Having proposed a model of the evolution of diadromy, Gross et al. (1988) argued that the relative availability of food resources in ocean and freshwater habitats was the main factor that would favor juvenile fish deserting their biome of birth for residency in another. Thus, in the tropics, diadromous species may have evolved from marine ancestors because of higher productivity in freshwater habitats than in marine habitats. At first sight, the acquisition of catadromy (i.e., adults in freshwater with marine reproduction) in the *Kuhliidae* seems to conform to the theory of Gross et al. (1988). However, the fast-flowing streams of tropical and subtropical islands of the Indo-Pacific region inhabited by diadromous *Kuhlia* species are oligotrophic and thus do not offer a resource-rich environment. Assuming the species have had a long association with these habitats through evolutionary time, diadromy in *Kuhlia* may

not have evolved solely in response to an opportunity to colonize productive freshwater habitats. We suggest that the emergence of the genus and the appearance of diadromy could also be closely linked to the appearance of insular ecosystems. Tropical oceanic (and often volcanic) islands have unstable freshwater habitats at different timescales. Steep mountainous islands that emerge from the sea are at first largely without rivers and then are eroded within a few million years. Small rivers with large estuaries are replaced by completely marine habitat when erosion is complete (Craig 2003). At a shorter timescale, climatic events, such as storms, floods, and droughts, may lead to local freshwater extinctions in oceanic islands. Thus, these freshwater habitats commonly have depauperate fish communities (Smith et al. 2003). Despite their oligotrophic nature, the freshwater habitats offer resources not available in adjacent marine habitats. According to Lee and Bell (1999), these environmental conditions over time and stable temperatures at low latitudes are among the factors that facilitate freshwater colonization of marine-derived species. The selective pressures driving marine fishes into freshwater could include environmental changes, absence of predators, decreased disease or physiological stress, habitat loss, competition for resources, or physiological and developmental changes induced by mutations (Gross et al. 1988). Because there are no predators (except anthropogenic) for *Kuhlia* in insular streams, and because they are the only fish able to feed on surface drift (Resh et al. 1999), we suspect that the evolution of diadromy in this genus was a key innovation to respond to an ecological opportunity in these environments (Losos 2010).

This pattern of evolution could have occurred for other diadromous families in tropical islands. Various species of catadromous freshwater eels (Anguillidae) or freshwater amphidromous gobies of the subfamily Sicydiinae (Gobiidae) inhabit tropical insular systems. The common ancestor of Anguillidae species probably evolved from a marine ancestor in the tropics (Inoue et al. 2010), and the freshwater amphidromous life cycle of the Sicydiinae family is thought to be derived from marine ancestors (Thacker and Hardman 2005) and originated in the tropical Pacific region (Keith et al. 2011). The species of the Sicydiinae are the biggest contributors to the diversity of fish communities in insular systems, and their highly specialized diet, ranging from entirely herbivorous to entirely carnivorous, allows them to occupy various ecological niches (Keith and Lord 2011). Their life cycle is well suited to short and swiftly flowing coastal streams (mostly oligotrophic) but not to more productive, slower-moving rivers with large lowland and estuarine components (Thuesen et al. 2011). Thus, the ecological opportunity hypothesis (i.e., that a clade will diversify in a suite of species to take advantage of accessible resources little used

by competing taxa; Losos 2010) seems reasonable for the emergence of diadromy in this subfamily also.

Loss of Catadromy: The Sea-Locking Hypothesis

Following the evolution of catadromy in *Kuhlia*, our phylogeny suggests that a fully marine life history is an evolved character. In other words, the ability to migrate to freshwater has been lost through evolutionary time, and those species occupy marine habitats throughout their lives. The opposite mechanism (i.e., loss of anadromy) called land locking, has been well documented (McDowall 1988 and references therein) in some populations of anadromous fish and in many amphidromous fish. It is generally accepted that this mechanism can lead to speciation. Many lacustrine galaxiid species are interpreted as having an ancestry in diadromous stocks (Ovenden and White 1990). However, phylogenetic analyses are still lacking to confirm specific examples. In this study, we were interested in whether the mechanisms involved in the loss of anadromous migrations (i.e., land locking) could also apply to the loss of the catadromous migratory state and lead to what we would call the sea-locking hypothesis.

First, a high plasticity in the migratory behavior seems to be the key for a population to adapt to a novel environment, through rapid selection of nonmigratory phenotypes (fig. 3). In *Kuhlia* species, there is evidence for flexible migratory behavior and varying tolerances to salinity. Randall and Randall (2001) noted that some diadromous individuals of Kuhliidae could occupy brackish environments. A recent study based on otolith microchemistry analyses of the diadromous species *K. malo* demonstrated that, after the recruitment in estuaries, some juveniles shift to freshwater, some are able to stay in the estuary, and others share their time between fresh and brackish water (Feutry et al. 2011). Similarly, some diadromous *K. rupestris* individuals may occasionally be found in estuaries. The life cycle of partially diadromous *K. munda* individuals can include a freshwater environment (Feutry et al. 2012a), and the marine species *K. xenura* may be found in estuaries or freshwater (Benson and Fitzsimons 2002; McRae et al. 2011). Such phenotypic variability can represent the raw material of speciation processes (West-Eberhard 1989, 2005; Pigliucci et al. 2006), especially in diadromous fish (West-Eberhard 1989, 2003). In a changing environment, a better-adapted phenotype can quickly be favored by natural selection (Gross et al. 2010), and depending on the heritability of the trait, rapid divergence among populations can lead to species formation (West-Eberhard 2005; Corl et al. 2010).

Second, the main scenario under which land locking may occur is the adaptation of the fish population to the impoundment of a river system that prevents the migra-

tion to and from the sea. As mentioned above, volcanic islands are changing environments, at both short and long timescales, in which freshwater or brackish habitats often disappear. In such ecosystems, access to freshwater may become restricted, and phenotypic variants of diadromous species that are more tolerant to salinity may initiate an adaptation to the marine environment. However, this may not be a general picture, because access to freshwater habitats may not be restricted in neighboring islands. Larval migrations to other islands, with a free access to freshwater systems, could slow down genetic differentiation and adaptation to the marine environment. Under this scenario, speciation may be more likely to occur in remote volcanic islands where populations that experience a decrease in freshwater systems are isolated from populations that do not. Furthermore, Williams et al. (2011) demonstrated that, in archipelagos of oceanic islands, allopatric speciation may be common in species with low dispersal abilities. Beside habitat changeability and geographic discontinuity of island freshwater habitats, the low larval dispersal ability, often observed in *Kuhlia* diadromous species (Feutry 2011, 2012b), may strengthen geographical barriers and accelerate adaptive speciation. Thus, the hypothetical sea-locking scenario may be possible in remote tropical islands. However, land locking can sometimes occur without topographical constraints (McDowall 1988), and similarly, other factors should be considered for sea locking.

As stated previously, streams in insular systems are oligotrophic and the available food is limited. To face this, insular fish have highly specific dietary behaviors (Kido 1996; Resh et al. 1999) in relation to specific microhabitats along the river continuum. The longitudinal distribution of the aquatic fauna in tropical island streams has been well documented (Keith 2003 and references therein). Three major zones can be distinguished: the estuary, the lower freshwater reaches below the first major waterfall, and the upper reaches beyond it. To occupy these different compartments of the rivers, species diversification has been observed in numerous taxa, such as amphidromous gobies and decapod crustaceans (Fossati et al. 2002; Marquet et al. 2003). *Kuhlia* species abound in the lower reaches but are absent beyond the first major waterfall (Keith 2003). In islands with steep slopes, this freshwater lower reaches of the river is often short, and most of the habitat available for *Kuhlia* species is under tidal influence. The Kuhliidae diversification from diadromy toward marine life histories through an estuarine intermediate may be related to the search for food and diet diversification. This would imply that, initially, the diadromous Kuhliidae may have evolved to take advantage of an empty niche in insular systems, but once they occupied this limited niche, some went back to the sea in search of other niches. In fact, under this scenario without topographical constraint,

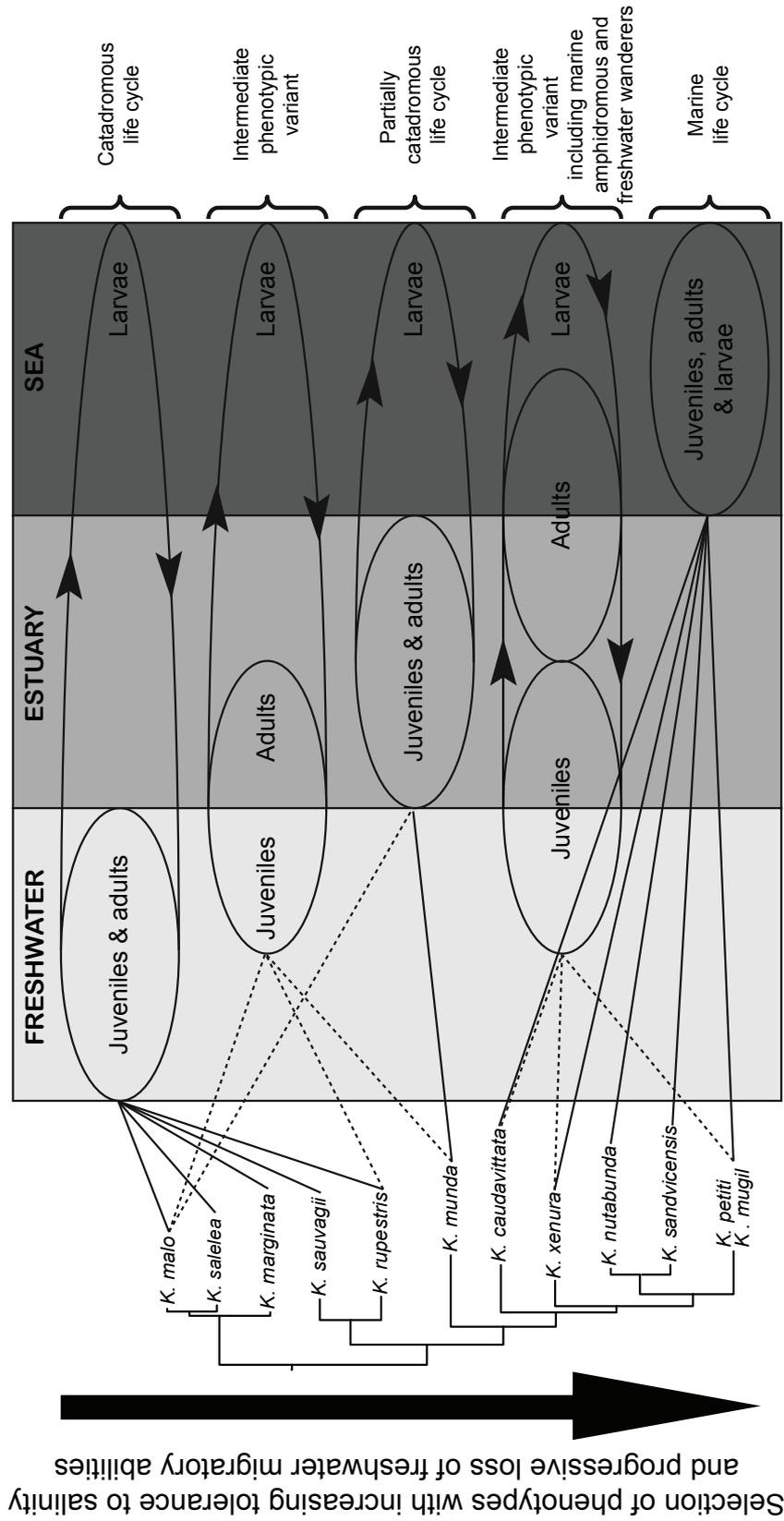


Figure 3: Evolution of diadromy in the Kuhlidae, from catadromy to marine life history through marine amphidromy and other intermediates. Solid lines indicate the main behavior found for each species. Dotted lines indicate rarer phenotypic variants.

both acquisition and loss of diadromy would be linked to the search for suitable niches. Except for *K. malo* in French Polynesia, little information on the diet of *Kuhlia* is available, and additional investigation of the diet of migratory phenotypic variants would help to test this hypothesis.

An interesting aspect of the evolutionary history of this group is that, except for the more derived *K. mugil*, all marine species have peripheral distribution. More importantly, the most basal marine species *K. caudavittata* and *K. xenura* are located on opposite sides of the Indo-Pacific region and do not share any part of their ranges with *K. munda*, the sister species of the marine clade (fig. 1). If their distributions remained identical through evolutionary times, this would imply that marine life histories are likely to have evolved multiple times in allopatry (Williams et al. 2011) and that the diadromous ancestor that gave birth to those species is now extinct. This is consistent with the first scenario proposed. An alternative theory is that marine life history only evolved once and that marine forms are more likely to invade isolated peripheral islands than the central Indopacific region. One explanation could be less competition with marine fish and higher availability of niches in peripheral regions (Randall 1998). This is consistent with either the topographical constraint or unconstrained hypotheses.

The Kuhliidae and Gross's Sequential Model of Evolution

Regardless of these evolutionary scenarios, the gradient of migratory behaviors observed in the Kuhliidae (fig. 3) is relevant to the sequence of evolution described by Gross (1987). In his model, freshwater wanderers, followed by marine amphidromous and catadromous fish, are the intermediate evolutionary states that lead from marine to freshwater life history. However, this sequence of evolution has never been validated, and McDowall (1997) argued that there are virtually no cases of amphidromous species that spawn at sea. On the contrary, some individuals of some *Kuhlia* marine species clearly exhibit such behaviors, and according to the models we developed above, we believe that they represent intermediate evolutionary steps between catadromous and marine life history (fig. 3). This is the first study to provide evidence of amphidromy as an intermediate stage of evolution. However, the major difference with Gross's (1987) model is that the direction of the evolution observed in *Kuhlia* is the opposite of what he predicted. Daverat et al. (2006) recently reported that marine amphidromy is more frequent than suspected, even among catadromous eels. However, this was not enough to support Gross's (1987) model, because the Anguillidae family does not include marine species. Other groups, such as mullets (Mugilidae) or snooks (Centropomidae), which present a wide range of migratory behaviors that include

entirely marine life history, may provide additional evidence for Gross's (1987) sequential model of evolution when the phylogenetic relationship between species is resolved.

Nevertheless, the evolutionary scenario that we proposed here remains to be validated, and future studies should focus on potential genetic divergences or differences in reproductive behavior between migratory phenotypic variants at the intraspecific level.

Conclusion

The Kuhliidae has provided new insights into the evolution of diadromous and catadromous migratory behaviors. Because the phylogeny of the family was well resolved, we were able to examine the evolution of diadromy among a large group of related species with varying migratory behaviors. Against expectations, our analysis showed that diadromy was ancestral in Kuhliidae, with subsequent reversal back to a nonmigratory state. We suggest that this mode of evolution is intimately linked to the limited and transient nature of freshwater habitats on tropical islands. This study supports the hypothesis that the evolution of diadromy in fish appears to be highly species or family specific. Multiple and nonexclusive factors may be responsible of the acquisition (e.g., decreased predation, empty niche, and relative productivity) and the loss (e.g., impoundment of a river, disappearance of freshwater habitat, and geographic isolation) of diadromous abilities depending on the group under study. We argue that the formulation of a global evolutionary framework for diadromy is based on the production of genus-level phylogenies such as this one.

Improving our knowledge of the evolution of diadromy is of major importance. This behavior is present in large and economically important organisms, such as Salmonidae, Anguillidae, and Mugilidae. Moreover, diadromous organisms constitute the major part of the indigenous aquatic fauna in tropical islands, which are naturally unstable and ephemeral ecosystems and have become even more so in recent years as a result of human alteration (Smith et al. 2003).

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