Adipose fin condition and flow regime in catfish

N.F. Temple and T.E. Reimchen

Abstract: Based on recent evidence suggesting a hydrodynamic function of the small adipose fin in salmonids to turbulent flow conditions, we test for associations between presence and absence of the adipose fin and flow regime in Siluriformes, one of the largest freshwater groups of fish with variable expression of this fin. Among 1906 species from multiple families, those living in habitats with flow (streams or rivers) exhibited an adipose fin significantly more frequently than expected relative to no-flow habitats (lakes, marine, parasitic). These trends were robust and occurred on different continents and among multiple paired comparisons within sister groups. Exceptions to these trends generally had atypical body shape or occupied divergent habitat types. These results are concordant with the hydrodynamic function of this small fin.

Résumé : Comme des données récentes attribuent une fonction hydrodynamique à la petite nageoire adipeuse des salmonidés dans des conditions d'écoulement turbulent, nous vérifions les associations entre la présence et l'absence de la nageoire adipeuse et le régime d'écoulement des eaux chez les siluriformes, l'un des groupes les plus importants de poissons d'eau douce à présenter une expression variable de cette nageoire. Parmi les 1906 espèces appartenant à de nombreuses familles, celles qui vivent dans les habitats d'eau courante (ruisseaux ou rivières) possèdent une nageoire adipeuse significativement plus fréquemment qu'attendu par comparaison à celles des habitats d'eau calme (lacs, mer, vie parasitique). Ces tendances sont robustes; elles existent sur plusieurs continents et s'observent au sein de nombreuses comparaisons appariées de groupes sœurs. Les exceptions à ces tendances concernent généralement des poissons qui ont une forme corporelle atypique ou qui vivent dans des habitats particuliers. Ces résultats sont compatibles avec la fonction hydrodynamique de cette petite nageoire.

[Traduit par la Rédaction]

Introduction

The persistence of the enigmatic adipose fin on eight orders of extant early euteleosts, including salmonids, may result from long-term continuity of the selective landscape and possibly, developmental constraints. Recently, we have shown experimental evidence that removal of this fin in juvenile salmonids reduces their swimming efficiency at multiple flow velocities (Reimchen and Temple 2004). Although the explicit functionality is obscure, this is suggestive of a hydrodynamic role to this small fin. In a broad taxonomic survey of taxa with the fin, we noticed that two of the large orders, Siluriformes and Characiformes, similar to the Salmoniformes, and one of the smaller orders, Percopsiformes, commonly inhabited current and turbulent flow conditions, suggestive of a common function for the adipose fin (Temple 2003). Recent investigations with particle imaging of salmonid swimming behaviour emphasize the complexity of flow in the region of the caudal peduncle (Liao et al.

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2003; Drucker and Lauder 2005) and where an adipose fin may improve swimming efficiency.

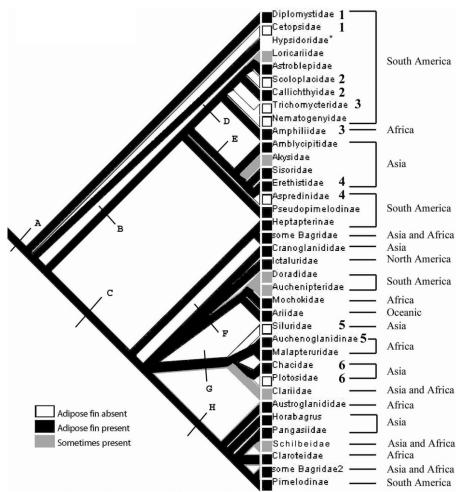
In this study, we look at associations of adipose fin condition, habitat, and body size using a qualitative assessment of all catfish species. Using existing phylogenies, we contrast presence or absence of the adipose fin with flow regime among sister groups within Siluriformes.

Materials and methods

We surveyed all species (n = 2597) within Siluriformes for maximum length, presence or absence of the adipose fin, geographic distribution, and habitat information, primarily using Fishbase (Froese and Pauly 2002). We classified habitat type into 1 of the 5 following categories: (1) lakes, bogs or swamps, (2) streams or rivers, (3) parasitic, (4) marine, or (5) unknown. These categories were additionally grouped: flow (streams or rivers) or no-flow (lakes, bogs or swamps, parasitic, and marine). Where further habitat information existed in streams and rivers (for 382 species), we distinguished slow-flow and fast-flow regimes based on descriptions given on Fishbase (e.g., found in slow-moving streams (slow-flow) or inhabits high gradient mountain streams (fast-flow)). Adipose fin condition for each species was classified as present, absent, or unknown. We excluded taxa with "unknown" data, which left data for 1906 species (1415 with adipose fin present, 491 with adipose fin absent). Fishbase is a new and expanding tool for meta-analyses of

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Fig. 1. Cladogram of catfish families redrawn using data from de Pinna (1998) showing the distribution of the adipose fin, as well as the geographic distribution of the families. Hypsidoridae* is an extinct family and the expression of the adipose fin is unknown. Uppercased letters indicate separate clades used for statistical comparisons. Numbers correspond to pairings for independent contrasts (refer to Table 1).



broad trends in ichthyological research (for example see Ruesink 2005).

We tested (χ^2) for associations between occurrences of the adipose fin and flow characteristics of the habitat at the species level for all Siluriformes. To test whether associations between adipose fin occurrence and habitat flow regime (flow or no-flow) were a consequence of a few family groups directing the trend, we repeated the analysis across multiple clades (refer to Fig. 1).

We made paired comparisons between families that were contrasting in the adipose fin trait (Fig. 1). Adipose fin expression was overlaid onto a siluriform cladogram redrawn using data from de Pinna (1998) using Mesquite software (Maddison 2000). Six phylogenetically independent paired comparisons were possible based on the Mesquite algorithm (for an explanation of pair selection and algorithm description see Maddison 2000). As it was impossible to assign a single habitat code to an entire family, we compared the relative proportion of species living in slow-flow (including no-flow) habitats in each pair. The extent of signed differences between the proportions was compared with a one-tailed sign test.

We further examined potential associations between occurrence of the adipose fin and maximum body length, as well as broad geographic region, using ANOVA. Maximum body length for each species was obtained from Fishbase and species were assigned to one of the following geographic regions: Asia, Africa, South America.

Results

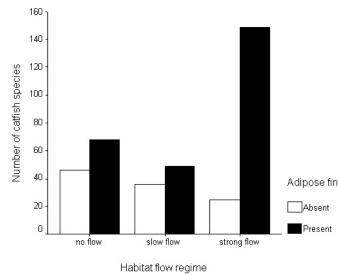
There was an association between occurrence of the adipose fin and flow regime. Across all species of catfish analyzed (n = 1906), those living in habitats with flow (streams or rivers) exhibited a greater occurrence of the adipose fin than those living in habitats without flow (lakes, marine, parasitic) ($\chi^2_{[1]} = 16.2$, P < 0.001). Among freshwater species, we found a further association between adipose fin occurrence and flow regime (no-flow, slow-flow, fast-flow) ($\chi^2_{[2]} = 32.8$, P < 0.001). Again, a high proportion of species living in swift-current habitats exhibited an adipose fin, while species living in both no-flow and slow-flow environments frequently lacked the adipose fin (Fig. 2).

Associations between adipose fin occurrence and flow regime were further observed in five of the seven clades tested within the Siluriformes. Group B, containing families from Loricariidae to Pseudopimelodinae, had 1061 valid cases for the analysis and showed a significant association (χ^2_{11} =

Sister-group comparisons	Family without adipose fin (% of species living in slow-flow regime)	Family with adipose fin (% of species living in slow-flow regime)	Difference in the proportions (%)
1	Cetopsidae (0)	Diplomystidae (0)	Tie
2	Scoloplacidae (25)	Callichthyidae (3.6)	+21.4
3	Trichomycteridae (17.6)	Amphiliidae (5)	+12.6
4	Aspredinidae (16.7)	Erethistidae (0)	+16.7
5	Siluridae (31.6)	Auchenoglanidinae (8.6)	+23.0
6	Plotosidae (54.8)	Chacidae (0)	+54.8

Table 1. Pairwise comparisons of the percentage of species living in no or little flow between two catfish families, one without an adipose fin and the other with an adipose fin.

Fig. 2. Association of the adipose fin with different flow regimes among catfish species with known flow regimes.



16.8, P < 0.001) with species exhibiting the adipose fin predominantly living in flow environments. Group C, containing families from Heptapterinae to Pimelodinae, showed the same trend among the 816 valid cases analyzed ($\chi^2_{11} = 28.5$, P < 0.001). Group D, which had three families without an adipose fin (Scoloplacidae, Trichomycteridae, and Nematogenvidae), three families with an adipose fin (Astroblepidae, Callichthyidae, and Amphiliidae), and one family with variability in the fin (Loricariidae), also showed the association between adipose fin occurrence and a flow environment $(\chi^2_{[1]} = 13.6, P < 0.001, 853$ valid cases). Group E had only one family, the Aspredinidae, that lacked the adipose fin, but among the 183 valid cases for analysis, the trend was consistent ($\chi^2_{[1]} = 9.44$, P = 0.002). Groups F and H did not have enough species without an adipose fin for comparisons; however, group G containing the Siluridae to the Clariidae had 188 valid cases for analysis and was consistent with the other groups ($\chi^2_{[1]} = 5.21$, P = 0.01).

We compared six pairs of closely related catfish families differing in the presence and absence of the adipose fin. Five of the six paired comparisons showed that the family with no adipose fin had a greater proportion of species living in no or little current (sign test, P = 0.03) (Table 1, for pairs refer to Fig. 1). The sixth comparison produced a tie.

There were significant associations between adipose fin condition and log-transformed maximum body length ($F_{1,21261} = 31.3$, P < 0.001), although trends differed among

geographical regions (interaction: $F_{[2,2126]} = 39.4$, P < 0.001). In Africa and Asia, families with an adipose fin have a smaller mean maximum length than families without an adipose fin (Africa: 24.9 cm vs. 41.8 cm, $t_{[455]} = 5.6$, P < 0.001); Asia: 30.2 cm vs. 45.6 cm, $t_{[442]} = 4.7$, P < 0.001), while in South America, the opposite occurred (19.1 cm vs. 13.0 cm, $t_{[1229]} = 4.9$, P < 0.001). Restricting comparisons to the sister families with and without adipose fins (see Table 1) shows similar trends in direction of maximum length differences (adipose condition, $F_{[1,580]} = 61.5$, P < 0.001).

Discussion

The occurrence of the adipose fin in the evolution of fishes has provided a challenge to taxonomists (Garstang 1931) and there is a general consensus that the eight orders of bony fishes with the fin share common ancestry (Garstang 1931; Sandon 1956; Rosen 1985). The adipose fin occurs in Cretaceous deposits in gymnotids (Lecointre and Nelson 1996), salmonids (Jordan 1905), and stomiatoids, suggesting that it has persisted since the Cretaceous (Garstang 1931). Groups that have retained the adipose fin generally exhibit dorsoventral asymmetry of the dorsal and anal fins with a medially or anteriorly placed dorsal fin, a posteriorly placed anal fin, and a truncated or forked caudal fin (Reimchen and Temple 2004), yet they occupy a diversity of habitats.

We looked for associations between adipose fin occurrence and habitat among the speciose order Siluriformes, as catfish species are diverse in habitat as well as in adipose fin condition. We detected broad habitat patterns among and within groups differing in the presence or absence of the adipose fin, with adipose fin presence more frequently associated with catfish species inhabiting streams or rivers compared with those in lakes. These results were robust and largely independent of family or geographic distribution.

Exceptions to this observed trend often included species that deviate from a body form typical of fish with an adipose fin, such as a centrally placed single dorsal fin and a forked or truncated caudal fin (Temple 2003). Currentdwelling Cetopsidae and Siluridae, which lack an adipose fin, both have small, anteriorly placed dorsal fins and extremely long anal fins, while Plotosidae, which also lacks the adipose fin, has an anal fin that is confluent with a long and pointed caudal fin. Other exceptions include the Trichomycteridae, which lack an adipose fin and are frequently found in fast-flowing rivers. However, most genera within this family are endoparasitic on vertebrate hosts (Nelson 1994). Within Schilbeidae, the African glass catfish (*Parailia pellucida* (Boulenger, 1901)) lives primarily in lakes yet has an adipose fin. The potamodromous behaviour of this group (Froese and Pauly 2002) might contribute to the persistence of the adipose fin.

The pervasiveness of the adipose fin among currentdwelling catfish is a phylogenetically broad association. Previous work has shown that the adipose fin may play a hydrodynamic or sensory role among salmonids in turbulent or fast-flow regimes and that its removal results in reduced swimming efficiency (Reimchen and Temple 2004). Although the adipose fin is nonrayed and passive in movement, recent evidence indicates the presence of neural tissue in the fin (Temple 2003; J. Buckland-Nicks, personal communication), which is consistent with a sensory role of the fin. Additionally, recent hydrodynamic studies using digital flow visualization techniques (Drucker and Lauder 2005) provide new evidence for the potential influence of the adipose fin on caudal vortices. Although we are unable to identify whether the adipose fin has a similar role among catfish, our results provide strong supporting evidence for functionality of this fin.

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