Hydrodynamic and phylogenetic aspects of the adipose fin in fishes

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Abstract: The adipose fin on fishes is a highly conserved and enigmatic, small, non-rayed fin that has persisted from the Mesozoic on some basal teleosts such as salmonids. Using juvenile steelhead, *Oncorhynchus mykiss* (Walbaum, 1792), ranging from 5 to 18 cm standard length, we experimentally test the effects of adipose fin removal on swimming performance in a variable velocity flow chamber and quantify, with seven independent trials, amplitude and frequency of caudal fin movement at multiple flow velocities (range 10–39 cm·s^{-1}). Results demonstrate that adipose fin removal on smolts produces an average 8% (range –3% to 23%) increase in caudal fin amplitude relative to unclipped fish across all velocities. However, we observed no effects in trials with smaller fish (<7 cm) or larger fish (>12 cm). Consistent with speculations in the literature, our results show that the adipose fin may function to control vortices enveloping the caudal fin during swimming or, alternatively, function as a passive precaudal sensor of turbulent flow. Phylogenetic persistence of this trait among multiple groups of early bony fishes is probably due to its hydrodynamic attributes rather than developmental constraints, and the current widespread practice in fisheries of removing the adipose fin as a marking technique may have significant biological costs.

Résumé : La nageoire adipeuse chez les poissons est une petite nageoire sans rayons qui est énigmatique, mais fortement conservée au cours de l'évolution, car elle persiste depuis le mésozoïque chez quelques téléostéens primitifs, tels que les salmonidés. Nous avons vérifié expérimentalement les effets de l'ablation de la nageoire adipeuse sur la performance de la nage chez de jeunes truites arc-en-ciel anadromes, *Oncorhynchus mykiss* (Walbaum, 1792), de longueur standard de 5 à 18 cm dans une enceinte à débit variable; nous avons quantifié, dans sept essais indépendants, l'amplitude et la fréquence des mouvements de la nageoire caudale dans une gamme de plusieurs vitesses de courant (étendue 10–39 cm·s^{-1}). Les résultats indiquent que l'ablation de la nageoire adipeuse chez les saumoneaux cause un accroissement moyen de 8 % (étendue de –3 % à 23 %) de l'amplitude du mouvement de la nageoire caudale, par comparaison à des poissons ayant conservé leur nageoire adipeuse, et ce à toutes les vitesses de courant. Cependant, il n'y a aucun effet discernable chez les poissons plus petits (<7 cm) ou plus grands (>12 cm). En accord avec les spéculations trouvées dans la littérature, nos résultats montrent que la nageoire adipeuse peut servir à contrôler les tourbillons qui entourent la nageoire caudale durant la nage; elle peut aussi servir de senseur passif du débit turbulent en position pré-caudale. La persistance au cours de l'évolution de ce caractère chez de nombreux groupes de poissons osseux primitifs s'explique probablement par ses qualités hydrodynamiques, plutôt que par des contraintes de développement. La pratique courante et répandue d'enlever la nageoire adipeuse comme technique de marquage peut probablement entraîner des coûts biologiques significatifs.

[Traduit par la Rédaction]

Introduction

Small plesiomorphic and seemingly trivial structures originating in ancestral forms and persisting through extended geological periods provide a continued focus for discussion on the role of conserved characters in evolution. Persistence can result from developmental constraints (Schlichting and Pigliucci 1998) or comprise an evolutionary trade-off between constraints and functionality (Futuyma 1998; Galis et al. 2001). The adipose fin of fishes is an enigmatic, small, non-rayed fin usually located medially between the dorsal and caudal fins and has a very restricted taxonomic occurrence (Nelson 1994). It occurs among eight extant groups of basal euteleosts (Fig. 1), including the Characiformes (characins), the Siluriformes (catfish), the Salmoniformes (salmonids), and the Myctophiformes (lanternfish); and within some of these groups, the adipose fin is variable in expression among closely related taxa. It is uniformly absent in all modern teleosts. No function has yet been identified for this small fin and it represents an important trait for distinguishing major taxonomic groups and affinities (Helfman et al. 1997).

The small size of the adipose fin and its passive motion during swimming appear to limit its role in stability, drag, or thrust, which are the major functions of medial fins in fishes (Webb 1975; Aleyev 1977). It may simply be a phylogenetic vestige of a formerly larger posterior dorsal fin (Sandon 1956; Kosswig 1965) that has persisted among extant groups owing to epistatic effects and constraints (for review see

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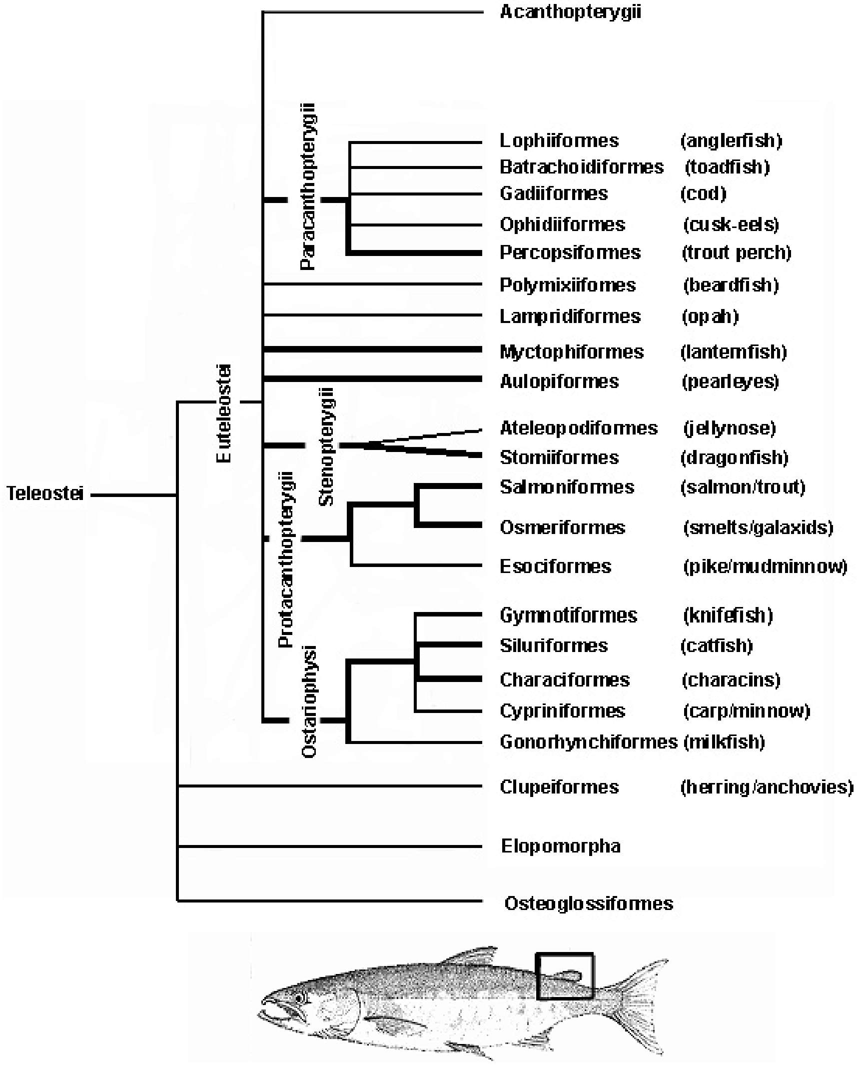
Fig. 1. Abbreviated phylogeny of Teleostei (modified from Nelson 1994). Taxa with an adipose fin shown with bold lines. Representative adipose fin shown on salmon illustration (reproduced with permission from S.D. Douglas).



Schlichting and Pigliucci 1998). Gosline (1971) suggests that the adipose fin may be important in juvenile age classes for generating a dorsal thrust vector symmetrical to that of the ventral anal fin during swimming. Webb (1975), Aleyev (1977), and Blake (1983) speculate that the adipose fin may influence vortices and flow regime to the caudal fin and potentially reduce cross-flow and boundary layer separation around the caudal peduncle just like the dorsal and ventral finlets of tuna-like fishes. The position and passive nature of the adipose fin could be equivalent to the 5th finlet of scombrids, which redirects cross-peduncular flow during steady swimming (Nauen and Lauder 2001). Whatever the function of the adipose fin might be, the benefits are thought to be small and, as in juvenile salmonids in Europe and North America, the routine clipping of the adipose fin is the dominant marking technique in fisheries science (Hammer and Blankenship 2001).

Several lines of evidence encouraged us to further develop some of the speculations regarding the functionality of the adipose fin. Firstly, there is size variation in the adipose fin within species (Martinez 1984; Nelson 1994; Petersson et al. 1999), and it seems probable that over the 70+ million years of history of the groups there would be sufficient variability to favor further reduction in size or elimination of the adipose fin if it was metabolically costly to produce. Secondly, any medial appendage would not persist from the Mesozoic to the present in multiple taxonomic groups unless it provided a benefit that offset the presumed drag-related costs. Thirdly, in salmon and trout, there is sexual dimorphism in the size of the adipose fin (Beacham and Murray 1983) that is accentuated prior to migration up the spawning rivers (Beacham and Murray 1986). In this paper, we present new experimental evidence that adipose fin removal on juvenile salmonid results in reduced swimming efficiency relative to control fish in flow chambers across multiple flow velocities.

Materials and methods

To evaluate swimming behaviour, we videotaped using a Sony Handycam at 30 frames/s swimming juvenile steelhead, *Oncorhynchus mykiss* (Walbaum, 1792), in a rectangu-

Table 1. Trial characteristics of protocol and results.

	Trial						
Protocol	A	B	C	D	E	F	G
Number of fish	9	21	11	10	16	8	37
Mean standard length (cm) (range)	11.8 (10.3–13.3)	8.5 (7.3–9.6)	11.0 (8.1–12.8)	10.7 (8.0–12.9)	16.4 (13.9–17.9)	6.7 (6.0–7.6)	5.4 (4.5–6.2)
Flow velocity categories ($cm \cdot s^{-1}$)	9.7, 11.3, 15.6, 20.3, and 25.3	9.7, 11.3, 15.6, 20.3, and 25.3	15.8 and 27.1	17.4 and 27.6	21.8, 31.7, 36.7, and 39.2	13.1, 14.8, 15.8, 18.7, 21.8, and 27.1	10.4 and 14.7
Protocol differences	MS222	MS222	Temperature controlled;* MS222; fish restricted to the front of the chamber	Temperature controlled;* eugenol; turbulent flow regime introduced	Temperature controlled;* eugenol	Temperature controlled;* eugenol; small fish	Temperature controlled;* MS222; includes injury treatment group
Average percent change in amplitude[†] (range)	17 (13–23)	17 (16–18)	–1 (–3 to 1)	10 (9–12)	3 (–3 to 6)	1 (0–5)	0 (–1 to 0)
Significance	$P < 0.001$	$P < 0.001$	$P = 0.77$	$P = 0.002$	$P = 0.02$	$P = 0.25$	$P = 0.81$

Note: MS-222 and eugenol were the anaesthetics used in the trials.

*Temperature was controlled using a cooling unit (Universal Marine Industry Inc., San Leandro, California) and a pump to maintain water temperature at 12 ± 1 °C.

[†] Relative increase in amplitude among clipped fish relative to the fishes in the control group after treatment.

lar plexiglass flow chamber (96 cm long × 10 cm wide × 15 cm high) over seven trials. Water turbulence from the pump was greatly reduced by forcing water through two sequential plates of thin tubes (20 mm long, 2 mm diameter) at the entrance of the flow chamber. A 2.5-mm grid was placed on the underside of the flow chamber against which each fish was videotaped. Flow velocities ranging from 9.7 through to 39.2 $cm \cdot s^{-1}$ were tested. Fishes were obtained from local hatchery stocks and held in circulating fresh water at 12 °C. Fishes ranged in standard lengths from 4.5 to 17.9 cm. A fish was arbitrarily chosen from the holding tank and placed in the flow chamber at zero flow rates. The fish was individually identified by natural pigmentation markings on the dorsal and left lateral surface. After the fish had acclimated and showed no visible signs of agitation (usually around 2 min), water velocity was increased to the first velocity category, which varied with trial (refer to Table 1). The fish was then videotaped for 1 min. Occasionally, the fish became agitated and did not maintain the same position in the current, and in these situations, videotaping was continued until at least 1 min of normal swimming was recorded. The procedure was repeated for all velocity categories (Table 1), after which the fish was removed and placed in a holding tank. This procedure was carried out for all fishes in the trial sequentially and then replicated in 24 h. After 1 week, all fishes were anaesthetized using MS-222 (tricaine methanesulfonate) (75 $mg \cdot L^{-1}$) or eugenol (50 $mg \cdot L^{-1}$). Fishes were arbitrarily picked from the holding tank and measured for standard length. On half the fishes, the adipose fins were clipped off at the base and then the fishes were returned to the holding tank for recovery. Previous studies (Anderson et al. 1997) demonstrate that swimming performance in trout is unaffected following 1-h recovery time from anaesthesia. However, to ensure that the fish had recovered from the additional stress of handling, we allowed an average of 51 h for recovery (range 48–56 h). After this duration, arbitrarily chosen fishes were individually placed in the flow chamber, identified from pigmentation, and videotaped at each of the velocity categories. Experiments were replicated after 24 h.

We analyzed swimming behaviour on video-playback on a high-resolution monitor (73.7-cm RCA Colortrak). Video images were scored without knowledge of group identity to avoid potential methodological bias; presence or absence of the adipose fin could not be determined from the videotapes. For each fish, at each velocity, we recorded tail-beat frequency and caudal peduncle amplitude. Tail-beat frequency was measured as the number of complete caudal fin oscillations over 10 s. Mean frequency was determined from five sequential time periods for each velocity. Maximum amplitude of the propulsive wave in each 10-s period was extracted from frame-by-frame analysis when the fish was holding its position in the current. Amplitude was measured at the narrowest region of the caudal peduncle against the 2.5-mm grid that was placed on the bottom of the flow chamber. We also recorded location of the fish in the flow chamber (distance from edge of chamber, distance from back of chamber). For statistical analyses, we calculated specific amplitude (amplitude / standard length) and compared different treatments across all trials with split-plot repeated measures ANCOVA using SPSS version 10.0 (SPSS Inc. 1999). Differences between clipped and control fishes after treatment were tested using ANCOVA for each trial.

Seven trials were completed in total, with variations in protocol with respect to flow velocity, fish size and number, anaesthetic, and temperature range (Table 1). Trial G included an additional treatment group that was given (under anaesthetic) a 3-mm epidermal scratch immediately behind the adipose fin, rather than the removal of the adipose fin, to evaluate possible subtle effects of stress associated with invasive procedures. In trial D, we maximized turbulence in the flow chamber by removing the thin tube plates and introducing a 2.5-cm diameter pipe in the middle of the flow chamber immediately anterior to the swimming fish.

Results

Among the seven trials that we conducted, the effects of adipose fin removal on swimming mode were highly variable and ranged from no responses (trials C, F, G) through to strong influences (trials A, B, D, E). When all trials were grouped, fishes with clipped adipose fin had specific amplitudes 8% higher than those in the control groups ($P < 0.01$). Within individual trials, the change in amplitude among clipped fishes ranged from –3% to 22%, with four of the seven trials showing a significant increase ($P < 0.05$) (Table 1). Fishes in trials A and B, which were not temperature controlled, exhibited the greatest increase in amplitude among clipped fishes across all velocity categories (Fig. 2). We also tested the fish in turbulent flow (trial D) and observed a significant increase in amplitude following adipose removal relative to the fish in the control group. The fish in the injury treatment group in trial G showed no significant difference in specific amplitude when compared with the fish in the control group ($P = 0.388$). We observed no significant associations between tail-beat frequencies and fin removal or injury ($P = 0.89$).

We examined whether these trends were associated with differences in body length of the fish. Our multiple trials suggest that the effect of adipose fin removal was greatest on medium-sized fish (7–12 cm) and was reduced or absent on smaller and larger fishes (Fig. 3).

Although the flow regime in the flow chamber appeared to be generally uniform, it seemed probable that the velocity would be reduced near the edge as a result of boundary layer effects, and turbulence would be greater near the back of the flow chamber. Consequently, we examined specific amplitude data in relation to the position of the fish in the flow chamber. There were no significant differences between the middle and the edge of the flow chamber ($P = 0.34$), althought there was a marginal but nonsignificant increase in amplitude at the back of the flow chamber ($P = 0.09$). However, when analyses were done using only individuals from the middle of the flow chamber (i.e., not at the back or the edge), higher amplitudes were observed for the clipped fishes ($F_{[3]} = 85.62$, $P < 0.001$).

Discussion

Our results demonstrated that the removal of the adipose fin on juvenile salmon produced variable responses in the swimming mode, which ranged from an absence of detectable effects through to a 22% increase in caudal fin amplitude, relative to those in the control group during sustained swimming behaviour. The strength of these effects appeared to depend on multiple criteria. No effects were observed in the two trials using small-bodied salmonids (<7 cm) or in the trial where the fishes were restricted in the front of the flow chamber where the most laminar flow regime is located. Among the fishes in the remaining trials, adipose removal resulted in an average 10% increase in caudal amplitude during sustained swimming relative to the fishes in the control group with an adipose fin, and these effects occurred over a threefold range of velocities. Because increased caudal amplitude requires increased energetic expenditure of the fish (Webb 1971; Yates 1983; Wolfgang et al. 1999), it suggests that the presence of the adipose fin allows for improved swimming performance over the range of velocities used in these experiments.

We were not able to identify the proximal mechanism for the increased tail-beat amplitude when the adipose fin was removed. Our results were consistent with a previous hypothesis of a vortex dampener comparable to the finlets of tuna and other high-speed fishes that use these small fins to control turbulent flow over the caudal fin (Webb 1975; Aleyev 1977; Blake 1983; Nauen and Lauder 2001). If so, then the removal of the adipose fin would result in reduced control of turbulence, leading to a corresponding reduction in thrust and velocity. The elevated caudal amplitude would reflect a compensatory response to increase thrust and maintain position in the flow chamber. In addition to this possible role as a vortex dampener, we began to suspect over the duration of our observations that the fin might also operate as a precaudal flow sensor which allows adjustments of the caudal fin motion in turbulent waters. If so, the effects of removal result in larger caudal amplitudes to generate the additional thrust required to hold the fish's position in the flow. Recent hydrodynamic analyses of swimming in a teleost indicate asymmetrical movement of the caudal fin including elevated amplitude and extension of the dorsal lobe relative to the ventral lobe (Lauder 2000). Detection or control of the vortices by the adipose fin before these envelop the caudal fin could produce a significant advantage to the fish. This could be particularly important in salmonids, which use environmental vortices to facilitate thrust in turbulent flow (Liao et al. 2003). We have preliminary evidence that suggests innervation at the base of the adipose fin, which would be consistent with a role as a flow sensor.

It is possible that our results are an artifact of the experimental protocols. Although we used anaesthetics on all fishes (control and test groups), which eliminated fish movement during handling, the process of adipose fin clipping might nevertheless lead to elevated stress hormones (e.g., Gamperi et al. 1994), and if so, reduce swimming performance during subsequent trials independent of the adipose fin condition. We cannot exclude this possibility; however, when we tested for this effect by making a small epidermal scratch near the adipose fin yet leaving it unaltered (trial G), there were no significant differences in caudal amplitude between the test and control groups. Temperature regime in the flow chambers could be contributory, as we obtained the greatest amplitude effects in the first two trials where water temperature was allowed to rise gradually over the duration of each daily trail (from 10 to 15 °C). However, it is not clear how this could account for the effects, as both control and clipped fishes were subjected to these elevated temperatures. Variability in turbulence was another factor that could have influenced results within and among trials. Turbulence was reduced in most trials by forcing flow through narrow hollow tubes, yet our results were comparable in the trial where turbulence was maximized.

The adipose fin of adult salmonids is sexually dimorphic, with males developing a disproportionately larger adipose

Fig. 2. Relationship between specific amplitude (amplitude / standard length) and flow velocity (range 9.7–25.3 cm·s^{-1}) in treatment groups of juvenile salmonids for trials A and B. Nine fish (3 control and 6 clipped) were used in trial A and 21 fish (10 control and 11 clipped) were used in trial B.

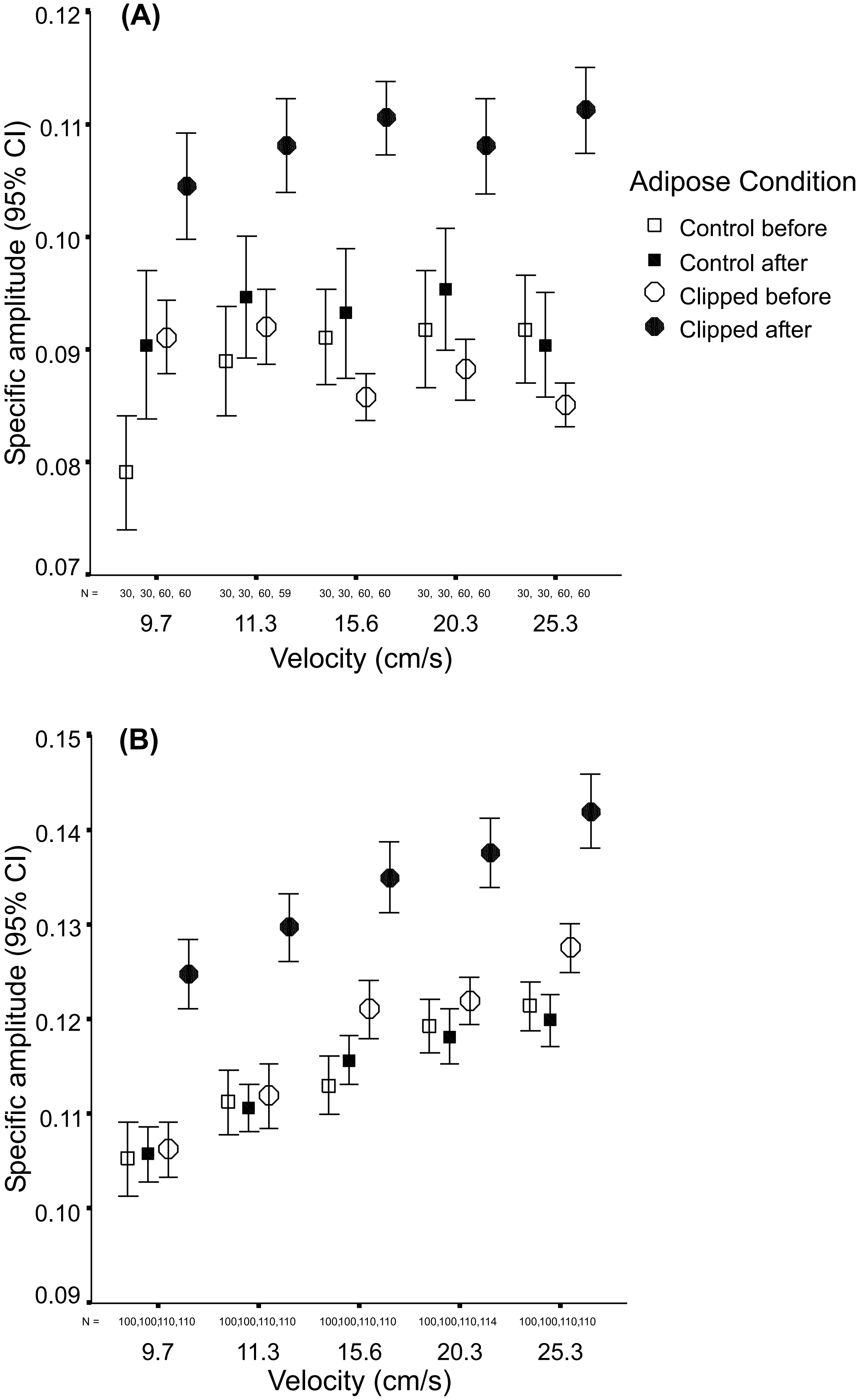
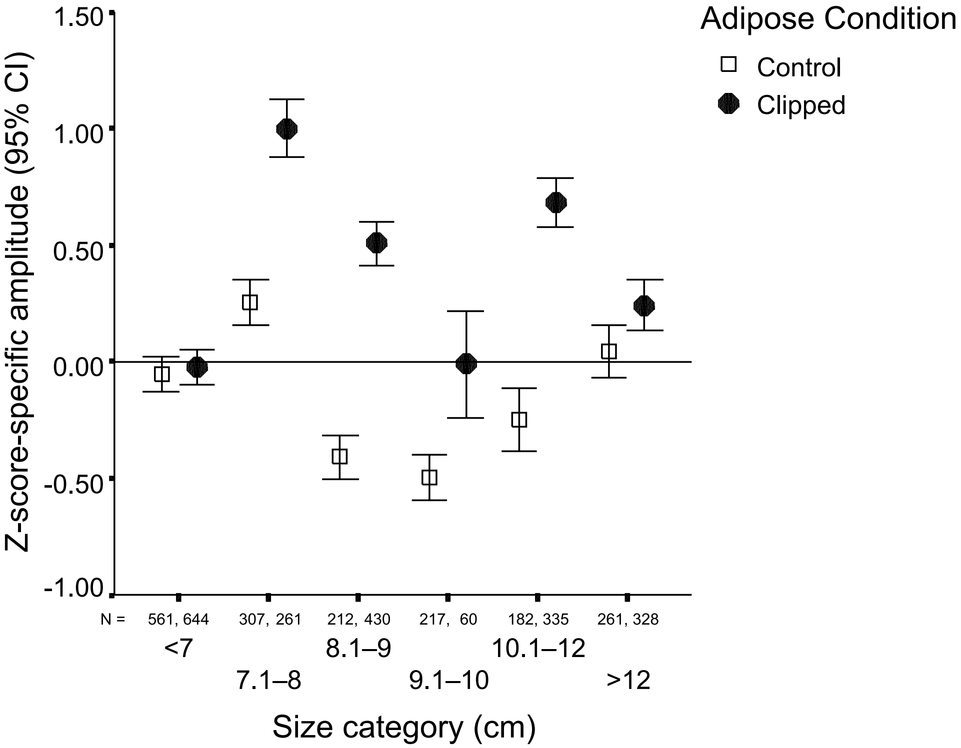


Fig. 3. Relationship between specific amplitude using *Z* scores standardized for velocity and size class of fish.



fin than females (Beacham and Murray 1983); effects that are accentuated during reproduction (Beacham and Murray 1986). Sexual selection might be a contributory process to the persistence of the adipose fin, as spawning females exhibit a slight tendency to pair with males with larger adipose fins (Petersson et al. 1999). Our hydrodynamic data suggest an additional hypothesis for the dimorphic adipose fin. Male salmon enter the spawning streams earlier than females, remain reproductively active for longer in the streams than individual females, and move more extensively around the stream than females during courtship and agonistic displays. We propose that the enlarged adipose fin on male salmon is a hydrodynamic adaptation to deal with the greater swimming demands, and if true, this would provide the selective mechanism for female choice of males with a larger adipose fin.

Our data also suggest insight into the phylogenetic distribution of the adipose fin in the basal teleosts. The majority of taxa with the adipose fin, comprising eight orders, have a single centrally placed dorsal fin, a single posterior ventral anal fin, and a truncated or forked caudal fin, whereas those related groups without the adipose fin exhibit departures from this general plan. For example, the Osmeriformes, which are closely related to the Salmoniformes, exhibit an adipose fin in 8 of 13 families, including the diadromous smelts that have similar life histories to salmonids which involve migratory and other sustained swimming behaviour. Among the five families where the adipose fin is absent, the dorsal fin is displaced posterior and the caudal fin is rounded, both traits of which are associated with the fast-start swimming mode rather than the sustained swimming mode (Aleyev 1977). In the Esociformes (pike and mudminnows), which is a second sister group of the Osmerifomes, the adipose fin is always absent; in each taxa, the dorsal fin is displaced caudally and is positioned symmetrically to the anal fin, which is also concordant with the fast-start swimming mode of this group (Aleyev 1977). The Ostariophysi, which is a large monophyletic group that comprises 64% of all freshwater fish species, exhibit major variability in the occurrence of the adipose fin. Among the Characiformes (characins and piranhas) that are found in streams and lakes of South America, the adipose fin occurs in 9 of 10 families, including the Citharinidae, which is the postulated ancestral group (Fink and Fink 1981). The Erythrinidae, the group consistently lacking the adipose fin, is the only characin with a rounded caudal fin similar to that of the Osmeriformes and mudminnows (Esociformes), which also lack the adipose fin. Among the Siluriformes (catfish), 25 of 34 families have the adipose fin, including the ancestral Diplomystidae (Grande 1987). Many of the South American catfish with the adipose occupy fast-flowing streams comparable to the salmonids of the northern hemisphere. All of the Siluriformes lacking an adipose fin exhibit one or more departures from the typical body form (e.g., the Siluridae (sheatfish) and the Claridae (airbreathing catfish) have unusually long dorsal or anal fins). Caudal fin shape is also predictive as eight of the nine catfish families without an adipose fin have a rounded caudal fin, which is comparable to trends in the Characiformes, the Esociformes, and the Osmeriformes and is indicative of the fast-start rather than sustained swimming modes. Each of these trends is consistent with our hypothesis coupling adipose presence with turbulent flow regimes or sustained swimming.

Although the hypothesis has predictive power for examining taxonomic differences in adipose fin, there are exceptions among the basal teleosts (see Fig. 1). The Gonorhynchiformes (milkfish), the Cypriniformes (minnows), and the Clupeiformes (herrings, smelts) each exhibit the typical body shape with a mid-positioned single dorsal and a posterior anal fin, yet each group lacks the adipose fin. This seems particularly puzzling for the Cypriniformes that occupy turbulent stream habitats similar to those of the Siluriformes and the Characiformes. Another exception is the Myctophiformes (lanternfish), which have a well-developed adipose fin but inhabit the nonturbulent waters of the open oceanic mesopelagic zone (200–1000 m deep). Evaluating these apparent exceptions would require comparative data on caudal flow regimes among the groups.

Within the Salmoniformes, our data support a functional role for the adipose fin based on changes in caudal fin amplitude during sustained swimming at multiple velocities. Predictions extending from these experiments also provide insight into the taxonomically variable expression of the adipose fin in the Characiformes, the Siluriformes, and the Osmeriformes. Recent advances in digital particle image velocimetry for analyzing flow regimes over the fish (Lauder 2000; Nauen and Lauder 2001; Lauder et al. 2002) offer the potential for identifying hydrodynamic components to the adipose fin among different body shapes.

These results support previous speculations on a hydrodynamic function to the adipose fin (Webb 1975; Aleyev 1977; Blake 1983) and suggest that the persistence of the synapomorphy among the basal teleosts is due to function rather than developmental constraints. Further efforts are in progress to identify sensory components to the adipose fin and the relationship to caudal fin motion. The current data suggest that clipping of the adipose fin, which is the major method in fisheries science for marking millions of young salmonids in Europe and North America, may have important biological and economic costs.

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