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Shape up or ship out: migratory behaviour predicts morphology across spatial scale in a freshwater fish

Ben B. Chapman[1,2]*, Kaj Hulthén[2], Christer Brönmark[2], P. Anders Nilsson[2,3], Christian Skov[4], Lars-Anders Hansson[2] and Jakob Brodersen[5]

[1]School of Life Sciences, University of Nottingham, Nottingham, UK; [2]Department of Biology, Aquatic Ecology Unit, Lund University, Lund, SE-223 62, Sweden; [3]Department of Environmental and Life Sciences, Karlstad University, Karlstad 651 88, Sweden; [4]National institute of Aquatic Resources, Technical University of Denmark, Silkeborg DK-8600, Denmark; and [5]Department of Fish Ecology and Evolution, EAWAG Swiss Federal Institute of Aquatic Science and Technology, Center for Ecology, Evolution and Biogeochemistry, Kastanienbaum, Switzerland

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Summary

1. Migration is a widespread phenomenon, with powerful ecological and evolutionary consequences. Morphological adaptations to reduce the energetic costs associated with migratory transport are commonly documented for migratory species. However, few studies have investigated whether variation in body morphology can be explained by variation in migratory strategy within a species.

2. We address this question in roach *Rutilus rutilus*, a partially migratory freshwater fish that migrates from lakes into streams during winter. We both compare body shape between populations that differ in migratory opportunity (open vs. closed lakes), and between individuals from a single population that vary in migratory propensity (migrants and residents from a partially migratory population). Following hydrodynamic theory, we posit that migrants should have a more shallow body depth, to reduce the costs associated with migrating into streams with higher flow conditions than the lakes the residents occupy all year round.

3. We find evidence both across and within populations to support our prediction, with individuals from open lakes and migrants from the partially migratory population having a more slender, shallow-bodied morphology than fish from closed lakes and all-year residents.

4. Our data suggest that a shallow body morphology is beneficial to migratory individuals and our study is one of the first to link migratory strategy and intraspecific variation in body shape.

Key-words: animal migration, ecomorphology, fish, geometric morphometrics, partial migration

Introduction

Each year billions of animals make migratory journeys to new habitats in step with the changing of the seasons, to track shifts in food resources, occupy optimal breeding habitats, avoid adverse climatic conditions and escape predation (Dingle 1996; Altizer, Bartel & Han 2011; Skov *et al.* 2013; Chapman *et al.* 2014). Migration is a widespread strategy across a diverse array of taxa and can have powerful ecological consequences (Brodersen *et al.* 2008b, 2011; Bauer & Hoye 2014). Migratory journeys vary in scale but all involve transport between divergent habitats, and a plethora of studies have investigated the many phenotypic adaptations that allow migrants to successfully complete their seasonal journeys. These adaptations can take a variety of forms, from physiological adaptations in, for example anadromous fishes, which allow migrants to cope with the high salinity of their migratory destination (Hinch *et al.* 2005), to the use of various cues to navigate during the migratory journey (Åkesson 2014). Many adaptations are linked with reducing the energetic cost of transport during the migratory journey. Between-species comparisons have shown that avian migrants tend to have wings of a higher aspect ratio with more pointed wingtips than resident birds, which is thought to allow faster and more efficient flight (Mönkkönen 1995; Hedenström 2008).

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*Correspondence author. E-mail: ben.chapman@nottingham.ac.uk

Whilst interspecific comparisons are useful in understanding adaptations to migration e.g. (Mönkkönen 1995), intraspecific variation in migratory behaviour can provide additional and powerful insights into the functional significance of phenotypic traits (Wilson 1998), not least because interspecific comparisons are hampered with differences in other aspects of the physiology, morphology and ecology of the species studied. Recent interest in studying intraspecific variation in migratory propensity (partial migration: Chapman *et al.* 2011a) has been assisted with new technological developments (Liedvogel *et al.* 2013; Hylander *et al.* 2014). However, despite this, few studies utilise intraspecific variation in migratory behaviour to investigate morphological adaptations to migration. Notable exceptions include recent studies that show that wing morphology varies between migratory and non-migratory populations of monarch butterflies, where migrants have larger and more elongate wings than residents (Altizer & Davis 2010). Moreover, sex differences in the wing length of migratory passerines have been related to differences in the timing of spring migration between males and females in a Swedish population of great reed warblers *Acrocephalus arundinaceus* (Tarka *et al.* 2014).

Intraspecific variation in body morphology is ubiquitous in the animal kingdom and has been particularly well studied amongst certain groups, such as freshwater fishes. Many factors have been linked with variation in body shape in this group, particularly predation (Brönmark & Miner 1992; Langerhans *et al.* 2004; Hulthén *et al.* 2014b), dietary niche (Snorrason *et al.* 1994) and habitat use (Svanbäck & Eklöv 2002). However, perhaps with the exception of the salmonidae (Fraser *et al.* 2007), few studies have investigated a link between migration and body shape at an intraspecific level in fishes (Brönmark *et al.* 2013). Migration in the dense medium of water is energetically costly, especially when migration occurs in streams and rivers, as is the case for many salmonids and cyprinids (Quinn 2005; Brodersen *et al.* 2008a; Skov *et al.* 2008; Hulthén *et al.* 2014a). Steady swimming is a mode of locomotion commonly employed during migration and when holding station against water flow (Domenici 2003). Hydrodynamic theory predicts that fish can reduce the costs of drag and recoil energy losses by adopting a shallower and more streamlined body shape that increases steady swimming performance, which may be particularly important during migration in streams and rivers (Webb 1984; Vogel 1994; Langerhans & Reznick 2010). Hence, a more shallow body depth can increase performance in certain habitats that are associated with migration in a diverse array of fish species, which has likely fitness outcomes. Many data support the link between a shallow body shape and habitat water velocity characteristics in a range of fish species (Langerhans & Reznick 2010); however, this framework has yet to be applied to explain morphological variation in species that vary in migratory behaviour.

Many fishes undertake potamodromous (i.e. freshwater) migrations, in many cases from lakes to streams (Lucas & Baras 2001; Brönmark *et al.* 2013). Following the postulates of this framework (i.e. reduced costs of migration in running water systems for shallow-bodied individuals), we predict that individuals that migrate from lakes into rivers and streams should display a more shallow body shape than all-year lake residents. In this study, we test this prediction at an intraspecific level on roach *Rutilus rutilus*, a well-studied migratory cyprinid (Brodersen *et al.* 2008a; Chapman *et al.* 2013). Roach are partial migrants, that is populations are composed of both migrants and residents (Skov *et al.* 2008), an extremely common phenomenon across the animal kingdom and in a range of fishes (Chapman *et al.* 2011a, 2012b). Each autumn roach perform short-distance migrations from shallow lakes into connected streams (Brönmark *et al.* 2008; Skov *et al.* 2008). A recent study of the flow conditions roach encounter on their migratory journey in lake Krankesjön (one of our study lakes) suggests that roach commonly encounter water velocities of $0{\cdot}15$–$0{\cdot}35\ \mathrm{ms}^{-1}$ in the streams (Brodersen *et al.* 2008c).

We first make between-population comparisons of the morphology of fish from lakes with (open) and without (closed) migratory opportunity. Secondly, we focus upon a single lake (Lake Krankesjön) where partial migration has been previously documented and studied in detail for this species (Brodersen *et al.* 2008a; Skov *et al.* 2008; Chapman *et al.* 2011b). In this population up to 70% of individuals migrate during winter into small, shallow connecting streams. In the second part of our study, we compare the morphology of migrant vs. resident individuals. We predict that fish from open lakes as well as migrants within the partially migratory population will have more shallow body morphologies compared with fish from both closed lakes and residents, respectively.

Materials and methods

SAMPLING

For our interpopulation study, we investigated roach morphology at eight Scandinavian lakes (Table 1): five closed lakes with no opportunity for migration (Fjällfota, Hale, Havgårds, Sövdeborgs, Udbyover; total $n = 108$) and three open lakes with migratory opportunity (Hinge, Loldrup, Sögard; total $n = 35$). 'Open' lakes have unimpeded access from the lake to both tributaries and outlet, whilst 'closed' lakes lack this access, as in most cases closed lakes do not have tributaries or outlets (Hale, Havgårds, Sövdeborgs, Udbyover) that would accommodate a winter stay by roach. One of the closed lakes (Fjällfota) has no external tributaries, but has an outlet stream. However, access to this outlet has been blocked for centuries by an ancient dam. We have followed and documented roach migration in three of our four open study lakes (the three for the interpopulation study and the one for the intrapopulation study) for about a decade (lake Krankesjön 2003–2015; lakes Sögaard & Loldrup 2005–2015) and have in all lakes and years recorded a high fraction of migrants among

Table 1. Characteristics of lakes included in the study. 'Open' refers to lakes with associated streams, where roach migrate into during winter, whereas 'closed' refer to lakes without associated streams, where roach stay resident in the lake during winter. Sample sizes in brackets. Z indicates lake depth, and x indicates that data are not available. Shaded cells indicate the presence of fish species

	Lake	Size (ha)	Zmean (m)	Zmax (m)	Pike	Roach	Perch	Bream	Rudd	Tench	Ruffe	C. Carp	Bleak	Zander	W. Bream	Sunbleak	Gudgeon	Carp
Open	Søgård (9)	26	1·6	2·7	▨	▨	▨	▨	▨						▨			▨
	Loldrup (10)	39	1·2	3·3	▨	▨	▨	▨	▨					▨				
	Hinge (16)	91	1·23	2·6	▨	▨	▨	▨			▨				▨		▨	
Closed	Sövdeborgs (22)	11	2·5	3·5	▨	▨	▨			▨		▨	▨					
	Hale (12)	10	x	1·1	▨	▨	▨											
	Udbyover (14)	21	1·05	2·6	▨	▨	▨					▨				▨		
	Havgårds (45)	54	3·1	6	▨	▨	▨	▨		▨	▨							
	Fjällfota (15)	155	1·4	3	▨	▨	▨	▨	▨	▨			▨	▨		▨		

the roach populations. In the last open lake (Hinge), we have observed migratory roach in the associated streams during winter and we were therefore fully convinced that roach do not perform winter migrations in any of the closed lakes, but do so in all of the open lakes.

For our comparison of migrants and residents from the same population, we captured roach from lake Krankesjön in south Sweden (residents, $n = 151$), and in its two inlet streams (Silvåkra and Länsmansbäcken: migrants, $n = 244$) during 28 and 30 November 2011. Temporal patterns of migration in this focal study population were continuously monitored by passive telemetry using RFID technology that allowed us to sample after the main autumn lake departure, that is when migrants and residents were spatially segregated and we were confident that the vast majority of fish captured in the lake were residents (Brodersen *et al.* 2008b; Skov *et al.* 2008). For both studies, roach were captured using electrofishing in the littoral zone of the lake. Sampling was haphazard and fish were captured from a variety of locations around the lakes and within the streams, and fishing continued until a sufficient number of fish were captured. Captured individuals were immediately transported to the laboratory. For our interpopulation study, all fish were frozen for storage and thawed prior to morphometric land marking. Although freezing may potentially have some effects on morphology (see, however, Valentin *et al.* 2008), all individuals were treated consistently between lakes and if any variation in morphology should be caused by freezing, it would more likely blur differences between populations rather than to falsely indicate them. For our intrapopulation study, captured individuals were immediately transported to Lund University, Sweden where they were anaesthetised using benzocaine. All fish were weighed (to the nearest 0·1 g) and measured to the nearest mm (total length, LT). In our within-lake comparisons, lake residents ($n = 151$) ranged in LT from 123 to 243 mm with a mean (± s.d.) of 164 ± 26 mm, whereas migrants ($n = 244$) ranged in LT from 124 to 221 mm with a mean of 149 ± 20 mm. In our across-lake comparisons, fish from open lakes ($n = 35$) ranged in LT from 110 to 201 mm with a mean of 133 ± 20 mm, whereas fish from closed lakes ($n = 108$) ranged in LT from 100 to 247 mm with a mean of 138 ± 25 mm. After this, all fish were placed on a white Styrofoam plate with the fins carefully pinned to the plate to optimise the accuracy of landmark placement, and laterally photographed to provide digital photos for subsequent morphological analysis.

MORPHOLOGICAL ANALYSIS

To characterise body shape variation among and within our study populations, we used geometric morphometrics, based on the analysis of landmark coordinates sampled from the digital photos. Landmark selection was based largely on prior work on this and related species and landmarks were selected to offer an adequate summary of overall body morphology. To reduce measurement error, the same person carried out the digitising of all landmarks blind, and for all specimens from the two studies. The digitisation of 13 landmarks (including five semilandmarks) along the lateral profile on each specimen (Fig. 1) was performed using Tps-Dig (Rohlf 2004b). The semilandmark technique allowed us to generate landmarks where fixed landmarks could not be assigned and hence expand the overall coverage of body shape (Webster & Sheets 2010). Prior to superimposition, semilandmarks were identified by use of a 'sliders file' in Tps-Util. The software TPS-RELW (Rohlf 2004a) was used to align, scale and rotate landmark config-

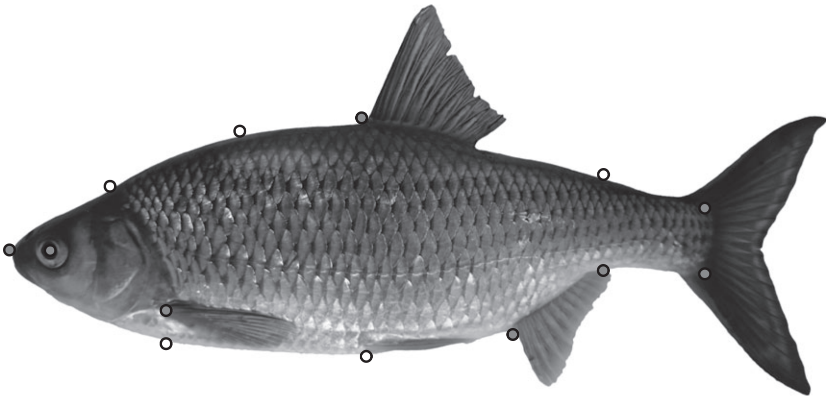

Fig. 1. Roach with landmark placement indicated. Grey points show fixed landmarks and white points semilandmarks.

urations through generalised least squares superimposition. From the superimposed specimens, we generated affine and non-affine shape components (20 partial warps and two uniform components). Shape variables (all partial warps and uniform components) together representing all information about the shape of the specimens were used as dependent variables in our subsequent multivariate analyses (Andersson, Johansson & Söderlund 2006). Variation in shape between open vs. closed lake fish, and migrants vs. residents from lake Krankesjön, was visualised using thin-plate spline transformation grids in tpsRegr (Rohlf 2004c).

STATISTICAL ANALYSIS

We carried out separate multivariate analysis of covariance (MANCOVA) on shape variables to test for morphological differences between lake types (i.e. open vs. closed lakes) and between migrants and residents within lake Krankesjön. The uniform components and partial warps were entered as the dependent variables and centroid size (the square root of the summed, squared distance of all landmarks from their centroid) were used as a covariate to control for differences in body size between and within populations. In the first model, lake type (open vs. closed) was entered as the independent factor and population as a nested factor within habitat type. In the second model, we included migratory status (migrant vs. resident) as the independent factor.

We used discriminant function analysis (DFA) to investigate how accurately individuals could be classified into their correct habitat type (open vs. closed) and migratory status (migrant vs. resident) based on overall morphology. Percent correct classifications were calculated based on a jackknifed, (i.e. leave-one-out) cross-validation process. Shape variables (uniform components and partial warps) were entered as dependent factors and habitat type and migratory status as grouping factor. All statistical analyses were performed using SPSS version 21 (SPSS, Inc., Chicago, IL, USA).

Results

COMPARISON OF OPEN VS. CLOSED LAKES

Our nested MANCOVA with shape data as response variables revealed effects of lake type, (Wilks $\lambda = 0{\cdot}376$, $F = 8{\cdot}514$, d.f. = 22,113, $P < 0{\cdot}001$: Fig. 2a,b), population nested within lake type (Wilks $\lambda = 0{\cdot}057$, $F = 3{\cdot}200$, d.f. = 132,665, $P < 0{\cdot}001$), and centroid size (Wilks

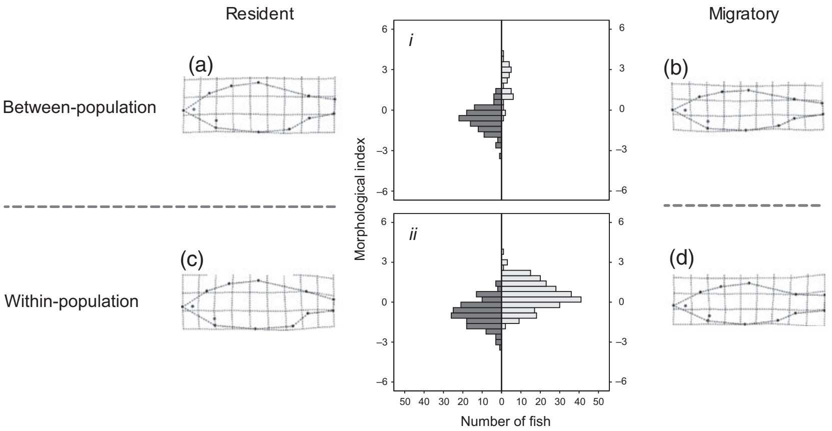

Fig. 2. Shape variation between migratory and resident fish from between-population (a, b) and within-population (c, d) comparisons. Images display the consensus body morphology for a given migratory type (at ×3 magnification for between-population and ×10 magnification for within-population images). 2i. and 2ii. Show the frequency distribution morphological index scores for resident (dark grey) vs. migrant (light grey) fish from our between- and within-population comparisons, respectively. The morphology index scores were generated from the discriminant function analysis (DFA), where all partial warps and uniform scores are combined into a single morphological index (Eklöv & Svanbäck 2006).

$\lambda = 0{\cdot}326$, $F = 10{\cdot}616$, d.f. = 22,113, $P < 0{\cdot}001$) upon body shape. The subsequent DFA analysis correctly classified 85·3% of fish to the correct lake type based on overall body morphology (Wilks $\lambda = 0{\cdot}439$, $P < 0{\cdot}001$: (Fig. 2i,ii.).

Visualisation of thin-plate spline transformations revealed that fish from open lakes had a more shallow-bodied morphology than fish from closed lakes (Fig. 2a, b).

INTRAPOPULATION COMPARISON OF MIGRANTS VS. RESIDENTS IN KRANKESJÖN

Our overall MANCOVA with shape data as response variables revealed the effects of migratory status, (Wilks $\lambda = 0{\cdot}724$, $F = 6{\cdot}423$, d.f. = 22,371, $P < 0{\cdot}001$: Fig. 2c,d) and centroid size (Wilks $\lambda = 0{\cdot}238$, $F = 54{\cdot}125$, d.f. = 22,371, $P < 0{\cdot}001$) upon body morphology. The DFA analysis correctly classified 71·4% of fish to the correct migratory status based on overall body morphology (Wilks $\lambda = 0{\cdot}707$, $P < 0{\cdot}001$: Fig. 2i,ii). Visualisation of thin-plate spline transformations revealed that migrants had a relatively shallower body depth than residents from this partially migratory population (Fig. 2c,d).

Discussion

We find evidence at two different scales (within and between population) to provide support for our prediction that fish with migratory lifestyles and/or opportunity have shallower body morphologies than non-migratory individuals. We report differences in shape between fish from open vs. closed populations (i.e. lakes with or without the opportunity for migration) and similar but more subtle differences between migrants and residents from a partially migratory population. For the between-lake comparisons, 85·3% of the roach individuals were correctly classified into lake type (open vs. closed) based on morphology, whereas in the within-population comparison, we were able to correctly classify an individual's migratory behaviour for 71·4% of fish. This is a clear indication of the powerful effect of migratory opportunity/propensity upon overall body morphology in this species.

Roach, like many other species of freshwater fishes, migrate from lakes into connected streams during winter (Skov *et al.* 2008). Swimming against a current is energetically expensive, and hence migrants should benefit from the more shallow body morphologies we report here by reducing drag and hence the cost of sustained swimming or maintaining position within flowing water. A great deal of theoretical work supports the link between increased streamlining and reduced energy expenditure to maintain position in flowing water (e.g. Webb 1984; Vogel 1994). Additionally, experimental studies have shown that the costs of swimming are related to divergent body morphologies in fishes (e.g. Facey & Grossman 1992; Pettersson & Brönmark 1999), and a recent and extensive field study revealed the impact of stream characteristics upon fish morphology across a range of species (Senay, Boisclair & Peres-Neto 2014). The morphological differences we report between migrants and residents mirror in direction the morphological differences found between fish from habitats with high vs. low flow regimes. For example, Collin & Fumagalli (2011) investigated intraspecific morphological diversification between non-migratory stream and lake minnows *Phoxinus phoxinus*. Their study revealed that populations of stream fish had more shallow bodies than their lake counterparts, which they argue is adaptive in lotic habitats such as the streams roach migrate into during the winter. There are other examples from natural systems where high water velocity is associated with a shallow body shape, for example in brook charr *Salvelinus fontinalis* (McLaughlin & Grant 1994) and pumpkinseed sunfish *Lepomis gibbosus* and rock bass *Ambloplites rupestris* (Brinsmead & Fox 2002). A recent meta-analysis of morphological variation between high vs. low flow habitats also reported that fish from a wide range of species occupying high flow habitats had a significantly more streamlined body shape than fishes occupying low flow habitats (Langerhans 2008; see also Langerhans & Reznick 2010). Hence, we suggest that a likely explanation for the morphological variation we document here between migrants and residents is that they experience divergent water velocities during the migratory period, and this variation in flow conditions drives differences in body morphology due to differences in optimal body shape in the different environments.

Whether the differences we report in body shape are plastic, and environmentally induced, or alternatively heritable, is not currently known. Many freshwater fishes have been documented as displaying morphologically plastic responses to various stimuli (e.g. Brönmark & Miner 1992). For example, fishes can developmentally modify their body shape in response to hydraulic conditions: brown trout reared under high velocity flow conditions developed more streamlined body morphologies (Pakkasmaa & Piironen 2000). Similarly, crucian carp exposed to water current developed a more shallow body shape (Johansson & Andersson 2009). There are also documented the effects of heritable differences in body shape according to habitat type (flow vs. still water). Comparisons between reservoir (i.e. standing water) and stream populations of *Cyprinella lutrensisi,* a small cyprinid fish, revealed heritable differences in morphology, with individuals from stream populations having shallower bodies (Franssen 2011).

The observed increase in streamlining to reduce the cost of locomotion and sustained swimming in lotic stream environments should also be a potentially powerful, and adaptive, explanation for the variation in body shape we report here between migrants and residents. Work on long-distance vs. short-distance migrants of brook charr, a salmonid fish, showed divergent body morphologies, with long-distance migrants having a more streamlined body shape (Fraser & Bernatchez 2005). Similarly, a study comparing the morphology of anadromous and resident brook trout found that anadromous fish had a shallower, more streamlined body shape (Morinville & Rasmussen 2008).

Besides increasing swimming performance, there are also other, possibly complementary explanations for the variation in body morphology among roach. Migration in roach provides anti-predator benefits from piscivorous birds and fish (Brodersen *et al.* 2008b; Skov *et al.* 2013), as these predators occur at much lower abundances in the streams that roach migrate into. A potential explanation for the increased body depth we report in year-round resident fish could be that this provides anti-predator benefits to gape-limited predators such as pike (Nilsson, Brönmark & Pettersson 1995; Nilsson & Brönmark 2000), which our residents and fish from closed lakes are exposed to for their entire lives. Recent work with roach has also linked variation in predation pressure to subtle variation in body morphology in roach: however, roach from a high predation lake had a more shallow body morphology than fish from less risky lakes (Scharnweber *et al.* 2013), which is suggestive that the differences we document are perhaps unlikely to be driven by predation. In addition, variation in habitat structure between lakes and streams may influence the costs and benefits of different body morphologies in these environments.

A new frontier in migration biology is integrating the many components of the 'migratory syndrome' (Dingle 2006) to provide a full and deep understanding of the many adaptations animals evolve to cope with the migratory journeys they undertake. Roach have been previously reported to exhibit behavioural differences between migrants and residents in risk-taking behaviour (Chapman *et al.* 2011b), and here we show differences in body morphology, hence highlighting the potential for a behavioural-morphological migratory syndrome in this species. Partially migratory animals make excellent 'natural experiments' to study adaptations to migration, especially amongst short-distance migrants, that tend to be less well studied than long-distance migrants. An important next step is to assess how general these migratory adaptations are. Many lacustrine freshwater fishes are partial migrants (Chapman *et al.* 2012a,b), and migrate from lakes to running water streams. Future studies could assess whether the patterns we document here can be generalised across species with similar migratory strategies. Indeed, the few studies that have focused upon intraspecific differences in morphology have shown that morphological adaptations tend to follow what we would expect from hydrodynamic/aerodynamic theory. Follow-up work for this project could be to quantify the costs and benefits of divergent body shapes from an energetic and anti-predator perspective, to attempt to shed light on the relative potential importance of these two factors in driving variation in body shape (Langerhans & Reznick 2010).

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Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.60pq3 (Chapman *et al.* 2015).

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