

Phenotypic traits meet patterns of resource use in the radiation of “sharpfin” sailfin silverside fish in Lake Matano

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Abstract Disruptive natural selection on traits related to resource exploitation may lead to differential adaptation and finally to speciation. Trait utility, the performance of traits in terms of fitness, is a central criterion for the recognition of adaptive radiation. Utility of morphological structures involved in foraging can be detected by relating their variation to individual resource use. Here, we test for trophic adaptations in the radiation of “sharpfin” sailfin silversides (Atheriniformes: Telmatherinidae), endemic to ancient graben-lake Matano in central Sulawesi (Indonesia). This small species-flock is characterized by high phenotypic diversity, including traits most likely related to feeding ecology. Previous analyses suggest that species boundaries are porous, indicating very recent or possibly ongoing processes of species flock formation. To test for adaptation to resource use in this radiation, we compared morphological traits among trophic groups of individuals as identified by stomach content analyses. We analyzed variation in candidate structures or structural complexes commonly recognized as indicative of trophic adaptation in fish radiations, including shapes of body, oral and pharyngeal jaws, gill rakers and body size. We found fine-scaled morphological differentiation according to feeding habits, covering all traits analyzed. Fish-, shrimp- and egg-feeders were most distinct, with major axes of morphological variation fitting patterns of adaptation reported from other lacustrine fish radiations. Thus, the present results are consistent with fine-scaled morphological adaptation to resource use, supporting the adaptive character of the sharpfin sailfin silverside radiation.

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Introduction

Adaptive radiations are prime models for the analysis of speciation processes in nature (Schluter 2000). Natural selection is commonly discussed as major force driving population divergence in sympatric animal radiations (Coyne and Orr 2004), though some evidence suggests that sexual selection and hybridization also might contribute to diversification (Panhuis et al. 2001; Mallet 2007). Trophic specialization driven by competition for food resources has been suggested as a major mechanism explaining the conspicuous diversity of ecologically distinct species in well-known natural model systems such as Darwin’s finches (Schluter and Grant 1984; Schluter et al. 2004). Morphological structures related directly to exploitation of food resources can therefore be expected to reflect differential feeding specializations in adaptive radiations.

Schluter (2000) defined adaptive radiation as evolution of ecological and phenotypic diversity within a rapidly multiplying lineage and put forward criteria to identify cases, including the criterion of “trait utility”. This criterion claims advantages in terms of fitness resulting from adaptations to distinct environmental resources. Adaptive radiations of freshwater fishes are among the most popular model systems for the analysis of speciation processes (Echelle and Kornfield 1984; Coyne and Orr 2004), including the impressive radiations of East Africa’s cichlids (Kocher 2004; Seehausen 2006) and northern lake whitefish (Hudson et al. 2005; Rogers and Bernatchez 2007). Several case studies have demonstrated trait utility in these systems, with focus to trophic morphology of the feeding apparatus (lower and upper jaw, pharyngeal jaws, gill rakers) and body shape (Rüber and Adams 2001; Albertson et al. 2003; Kassam et al. 2003; Amundsen et al. 2004).

“Wallace’s dreamponds”, the Malili Lakes in the central highlands of Sulawesi (Indonesia), harbour lacustrine radiations or endemic lineages of freshwater gastropods, crustaceans, and fish (Kottelat 1990a, b, 1991; von Rintelen and Cai 2009; von Rintelen et al. 2004, 2007; Schubart and Ng 2008; Schubart et al. 2008). The radiation of sailfin silversides (Teleostei: Atheriniformes: *Telmatherinidae*) endemic to ancient graben-lake Matano has recently been suggested to fulfil Schluter’s (2000) criteria of an adaptive radiation (Herder et al. 2006a). This extremely deep (~590 m; Haffner et al. 2001) tropical lake is the hydrological head of this cascading lakes system (Brooks 1950), and is inhabited by two phenotypic groups of sailfin silversides distinguished by shape of their second dorsal and anal fin to “roundfins” and “sharpfins” (Kottelat 1991; Herder et al. 2006b; Gray et al. 2008a, b). Roughly ten *Telmatherina* morphospecies are recognized in the lake (three roundfins, seven sharpfins; Herder et al. 2006b), but a systematic revision of sailfin silversides incorporating recent discoveries remains lacking. Apart from fin shape, species are distinguished mainly by morphometric and meristic character combinations (Kottelat 1991). In certain cases, morphospecies determination incorporates pronounced single characters like puffy lips or a projecting premaxilla (Kottelat 1991; Herder et al. 2006b). Most *Telmatherina* are polymorphic in male coloration (Kottelat 1991; Gray and McKinnon 2006; Herder et al. 2006b), which however appears not to be associated with phenotypic or genetic divergence (Roy et al. 2007a; Herder et al. 2008; Walter et al. 2009).

Both, roundfins and sharpfins, are monophyletic according to nuclear multilocus markers, and constitute together the ancient monophylum “Lake Matano” within the

Malili Lakes telmatherinid radiation (Herder et al. 2006a). In contrast, phylogenetic analyses based on maternally inherited mitochondrial DNA (mtDNA) reveal three clearly distinct groups of haplotypes in Lake Matano's *Telmatherina* (Roy et al. 2004, 2007a, b), one carried by roundfins, and two by sharpfins (Herder et al. 2006a). One of the two haplotype groups of sharpfins is shared with riverine sailfin silversides inhabiting small drainages around Lake Matano, some of which are in contact with lake fish at the interface of lake and streams (Herder et al. 2006a, b; Schwarzer et al. 2008). The phylogenetic discordance of nuclear and mitochondrial markers suggests introgressive hybridization of stream populations into sharpfins, a hypothesis supported by detection of “introgression signal” in nuclear multilocus data (Herder et al. 2006a) and direct evidence for introgression reported in a recent focus study (Schwarzer et al. 2008). In addition to introgressive hybridization into sharpfins, the occurrence of *Telmatherina* with character states intermediate between known morphospecies (Herder et al. 2006a, b; F. H., unpublished data), the shared presence of some morphospecies in both sharpfin mtDNA haplotype clades (Herder et al. 2006a), as well as evidence for substantial but incomplete reproductive isolation among roundfin sailfin silversides based on AFLP analyses and field-gained mating data (Herder et al. 2008) suggest that L. Matano's *Telmatherina* radiation is still in a very dynamic stage of species-flock formation. Size- and morphospecies-assortative mating following alternative adaptations to resource use appears the most likely mechanism triggering and maintaining speciation in roundfin *Telmatherina* (Herder et al. 2008), and may play a crucial role also in the more complex sharpfin flock. However, direct evidence for rejecting the null hypothesis that phenotypic plasticity explains major axes of morphological diversity in sharpfins remains pending.

A recent study focusing on adaptive divergence of L. Matano's *Telmatherina* (Roy et al. 2007b) tested for mtDNA-clade specific differentiation of head morphology and resource use. Roundfins (“clade I” in Roy et al. 2007b) were most distinct compared to both mtDNA clades of sharpfins (“clades II” and “III”), consistent with an offshore pelagic lifestyle in roundfins versus rather inshore benthic or epibenthic ecology in sharpfins (Roy et al. 2007b; see also Herder et al. 2006a, 2008; Herder and Schliewen *in press*). Differentiation was less distinct among sharpfins carrying different mtDNA haplotypes. In other words, the main signal of differentiation identified by Roy et al. 2007b is that between the two major groups of sailfin silversides in L. Matano, roundfins and sharpfins, two groups which are well defined both morphologically and genetically.

Here, we focus on morphological adaptation to resource use within sharpfins. We relate variation in morphological candidate structures to food items actually ingested by individual sharpfins, and address the question if axes of phenotypic trait variation meet patterns of resource use, which in turn would support “trait utility” (Schluter 2000). We combine diet data with fine-scaled analyses of an array of characters discussed as adaptive in radiations of teleost fishes, i.e. shapes of upper and lower oral jaws, lower pharyngeal jaws, body shape, body size, and gill raker expression (Svärdson 1952, 1957; Otten 1983; O'Brien 1987; Liem 1991; Wainwright and Richard 1995; Wainwright 1997; Bernatchez et al. 1999; Wainwright and Shaw 1999; Albertson and Kocher 2001; Rüber and Adams 2001; Kassam et al. 2003). We also explore a novel approach quantifying the relative position and orientation of maxilla, premaxilla, dentary and articular in the mouth structure. “Trait utility” predicts that structures affecting feeding performance differ significantly among groups of individuals sharing similar stomach contents (“trophic groups”), an important component—among the other three of Schluter's criteria—when testing for the adaptive character of potential radiations.

Materials and methods

Material

Sharppin sailfin silversides were collected from locations distributed around the shoreline of Lake Matano in dry season 2002 and rainy season 2004, covering different benthic habitats (see map in Herder et al. 2006b). Specimens were obtained from the upper 10 m of the water column using snorkel- and SCUBA-guided gillnetting during daytime. Fish were marked individually, preserved in 4% formalin and later transferred to 70% ethanol for storage. Given (1) the dependence of sailfin silverside taxonomy on male characters and (2) the considerable effort when aiming to cover diversity of this species flock in a comprehensive analysis incorporating multiple traits, we decided following earlier studies (Roy et al. 2007a, b; Herder et al. 2008) in restricting morphological analyses to males. This excludes sex-specific effects in sexually dimorphic sailfin silversides (Herder et al. 2006a), and might lead to underestimation of differentiation in case of sexual niche differentiation (Ward et al. 2006). All specimens were determined following the available taxonomic concepts (Kottelat 1991, Herder et al. 2006b). Subsequently, random sub-samples were taken from each species-group (total, $n = 125$; *Telmatherina abendanoni*, $n = 27$; *T. opudi*, $n = 29$; *T. sarasinorum*, $n = 38$; *T. wahjui*, $n = 6$; *T. sp.* “elongated”, $n = 9$; *T. sp.* “thicklip”, $n = 16$). Sample sizes depend on the availability of non-deformed (i.e. without artificial bending due to gillnetting or fixation procedures), adult individuals. Sample sizes of *T. wahjui*, *T. sp.* “thicklip” and *T. sp.* “elongated” are lower than average resulting from their rare occurrence in both nature and our sampling. Our strategy allowed covering a wide array of phenotypic variation within the sample size limits of a detailed morphological study, independent of total abundances of phenotypes in the lake. Based on absence of significant differentiation in stomach content composition, samples from different seasons (ANOSIM, $r = 0.005$, $P > 0.3$) and sample sites (ANOSIM, $r = 0.026$, $P > 0.16$) were pooled. As (1) the present study is focused on the interface between morphological variation and trophic resource utilization, not on systematics, and (2) morphospecies-specific analyses do not support unequivocally distinct patterns of prey ingestion (Table 1; Supplemental material S1, S2), the following analyses are based on groups of individuals defined by shared major stomach contents, not on morphospecies assignment (see Supplemental Material S1).

Preparation and stomach content analyses

Standardized pictures of all 125 individuals including a size standard of 8 cm length were taken using a digital camera (Canon PowerShot G1 with macro lens). Subsequently, food

Table 1 Pairwise comparison of stomach contents among sharppin sailfin silversides morphospecies

	<i>T. abendanoni</i>	<i>T. sp.</i> “thicklip”	<i>T. wahjui</i>	<i>T. opudi</i>	<i>T. sarasinorum</i>
<i>T. sp.</i> “elongated”	1.00	0.54	0.04	0.00	0.00
<i>T. sarasinorum</i>	0.01	0.00	0.01	1.00	
<i>T. opudi</i>	0.37	0.13	0.20		
<i>T. wahjui</i>	1.00	0.00			
<i>T. sp.</i> “thicklip”	1.00				

The pairwise P -values of the post hoc test of ANOSIM ($r = 0.1706$, $P < 0.001$) between morphospecies show considerable variation, only some morphospecies show significant differences (bold)

items from the gastrointestinal tract between oesophagus and pylorus were embedded in Gelvatol (Polyvinylalcohol) and the relative surface area of items was estimated for every individual fish (see Herder and Freyhof (2006) for details). Specimens in which the stomach contained no food items were categorized as empty and excluded from further analyses. Contents were present in 100 specimens [*Telmatherina abendanoni* ($n = 21$), *T. opudi* ($n = 24$), *T. sarasinorum* ($n = 33$), *T. wahjui* ($n = 6$), *T. sp.* “elongated” ($n = 7$), *T. sp.* “thicklip” ($n = 9$)], which were chosen for analysis of body shape. All items were determined to the lowest feasible taxonomical level (see Supplemental Material S3).

The network approach of Araújo et al. (2008) was used to test for variation in diet among individuals, including the niche variation (E) ranging from 0 (no individual niche variation) to 1 (strict niche separation among all individuals), and the clustering index (C) measuring the degree of which the population is organized into trophic groups (ranging from $-1 =$ overdispersed diet variation to $0 =$ no clustering to $1 =$ maximal clustering; Araújo et al. 2008; Snowberg and Bolnick 2008). Significance of both indices was tested using a Monte Carlo resampling routine (10,000 replicates) implemented in the program DIETA1 (Araújo et al. 2008). Weighted binary matrices calculated with DIETA1 were then imported into the program Pajek (Batagelj and Mrvar 1998) for visualizing clusters of dominant prey items in a network (see Fig. 1; Araújo et al. 2008).

Supported by strongly discrete clusters with explicit prominent food items (see Figs. 1, 2; Supplemental Material S1), individual fish were grouped according to their dominating (50% majority rule) stomach contents into five “trophic groups”: “fish” (all remains of fish), “egg” (fish eggs), “insect” (terrestrial, mostly winged ants), “mollusc” (aquatic snails, mostly Hydrobiidae), and “shrimp” (freshwater shrimps, genus *Caridina*) (Fig. 2, Supplemental Material S1).

In a next step, 72 individuals were randomly chosen from those containing food items in their stomach (*Telmatherina abendanoni* ($n = 14$), *T. opudi* ($n = 13$), *T. sarasinorum* ($n = 21$), *T. wahjui* ($n = 6$), *T. sp.* “elongated” ($n = 6$), *T. sp.* “thicklip” ($n = 9$)) to be cleared and stained following the slightly modified protocol of Plösch (1991) (standardized digestion temperature 39°C, changing of trypsin solution every fourth day). To quantify position of oral jaw bones in situ, focus pictures were taken from the left lateral head section of each cleared and stained individual after opening the mouth in a standard angle (30°) with a transparent plastic spline. Then, premaxilla and lower jaw bones (articular plus dentary) from the left side, the lower pharyngeal jaw bone and the first gill arch were removed and placed on microscope slides. Under a stereomicroscope, standardized pictures were taken from the exterior lateral side of upper jaw (only premaxilla) and lower jaw, from the dorsal side of the lower pharyngeal jaw, and from the first gill arch, including a size standard of 20 mm length.

Quantification of morphological traits

Based on the pictures obtained, geometric morphometric methods were applied to quantify shape of morphological structures potentially related to trophic ecology. Body shape ($n = 100$) was analyzed using 18 homologous landmarks, following Herder et al. (2006a) (Fig. 3a). Constellation of oral bones ($n = 51$), lower jaw shape ($n = 56$), upper jaw shape ($n = 55$) and lower pharyngeal jaw ($n = 48$) shape were quantified with six to seven landmarks (Fig. 3b–e; see Table 2 for detailed sample sizes), depending on the analyzed trait. Gill rakers on the upper arch were counted ($n = 55$, see Table 2 for detailed sample sizes), and the length and width of the gill rakers in the upper arch were measured from the pictures (Fig. 4, see Supplementary Material S1). Body length was measured from digital

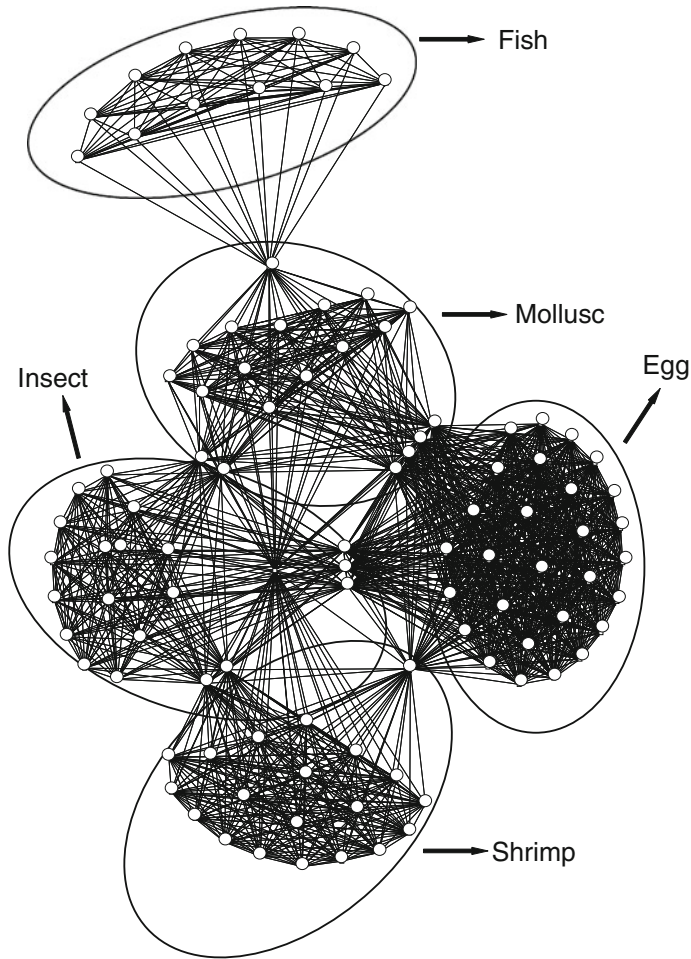


Fig. 1 Binary network of among-individual trophic niche overlap. The weighted trophic network (Araújo et al. 2008) represents dietary overlap among 100 sharpfin individuals. Clustering of individuals is significant (see “Results”), and the five clusters present correspond to trophic groups (surrounded by lines) as defined by the 50% majority rule (Fig. 2)

images using the software *tmorphgen6* included in the IMP software package (Sheets 2002).

Analysis of morphological traits

Morphological traits were analyzed for correlation with food intake, which would be indicative for trophic adaptation. For all traits analyzed by geometric morphometrics, effects of size and position were removed from the data using the “Generalized Procrustes Analysis” procedure (Zelditch et al. 2004) implemented in the IMP software package (Sheets 2002). Principal components (PCs) were calculated from procrustes residuals and reduced to those bearing $\geq 5\%$ of total variance. Variance in shape according to trophic groups was in a first step estimated by a multivariate analysis of variance (MANOVA, with

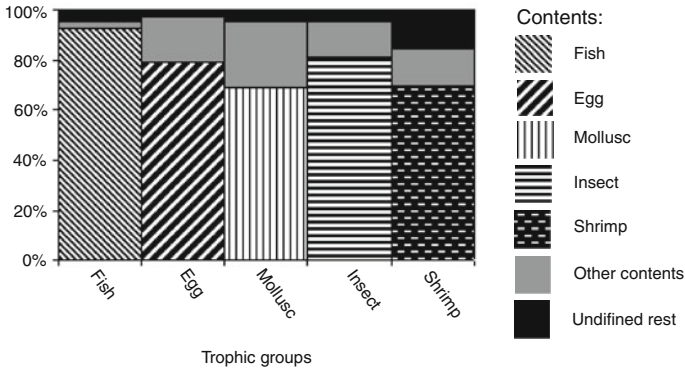


Fig. 2 Stomach contents (in percent) of five trophic groups of sharpfin sailfin silversides ($n_{total} = 100$). See “supplementary material S2” for details and individualized data

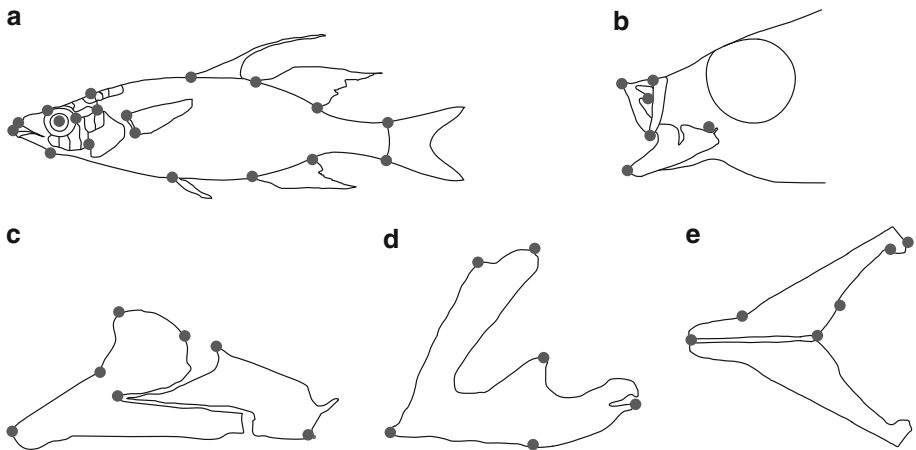
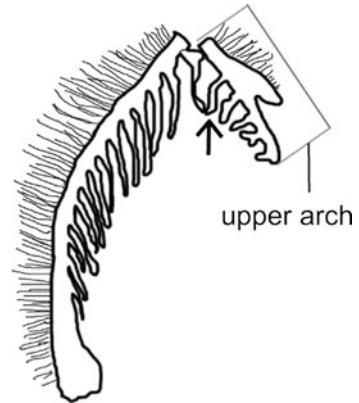


Fig. 3 Landmarks applied to quantify shape variation in the five traits analyzed by geometric morphometric methods. **a** lateral body, **b** jaw bone constellation in situ, **c** articular and dentary (lower jaw), **d** premaxilla (upper jaw), **e** lower pharyngeal jaw

Table 2 Sample sizes according to the six morphological candidate traits analysed

Trait	Trophic groups				
	Fish	Egg	Mollusc	Insect	Shrimp
Body	12	33	20	16	19
Body length	12	33	20	16	19
Lower jaw	8	13	12	10	13
Upper jaw	8	13	12	10	12
Pharyngeal jaw	5	17	7	8	12
Jaw bone constellation	7	16	11	7	10
1st Gill arch	8	13	9	10	13

Fig. 4 First gill arch of *Telmatherina*. The total number of rakers on the upper arch (*marked*) was counted; length and width of the first raker on the upper arch were measured from digital pictures



Hotelling's pairwise test) based on all PCs fulfilling the 5% criterion. Subsequently, each single PC was tested separately for homogeneity of variance among trophic groups, using ANOVAs with Tukey's post hoc tests in case of equal or Welch tests with Dunnett T3 post hoc tests in case of unequal variances. ANOVAs with Dunnett T3 post hoc tests were also applied to test for content-specific segregation in the number of gill rakers on the upper arch, and in the relative width (relation of width to length) of the first three of these gill rakers.

Results

Clustering of stomach contents

Stomach content data show a high degree of among-individual variation. On average, two randomly chosen sharpfin individuals from the present sampling are 79% different ($E = 0.7893$; $P < 0.0001$ given the null hypothesis $E = 0$; see Araújo et al. 2008 and Snowberg and Bolnick 2008). This variation in diet is organized into strongly discrete clusters ($C = 0.5271$; $P < 0.0001$), with major clusters corresponding to the five dominant food items "fish", "egg", "insect", "mollusc" and "shrimp" (Figs. 1, 2). Hence, we consider analyzing trait variation according to these five "trophic groups" justified.

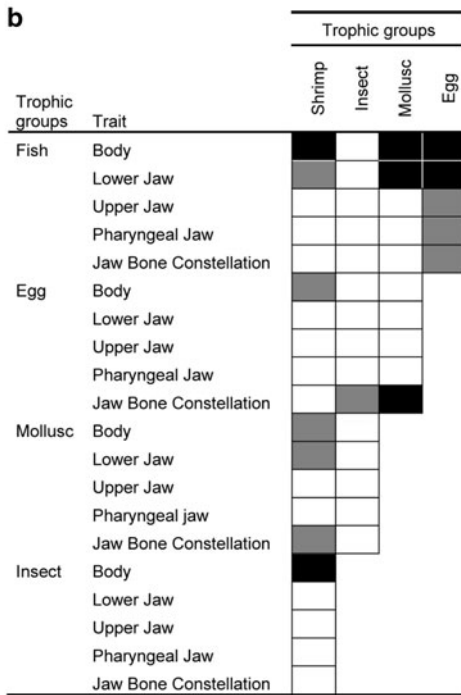
Body shape and jaw bone constellation

Body shape and constellation of oral bones were tested for differentiation among trophic groups determined by stomach content analyses. Significant variation of body shape with major food items is evident (Table 3a), and affects two multivariate axes (Table 4). The first PC distinguishes high-bodied shrimp-feeders with pronounced, fleshy lips from individuals feeding mainly on fish, molluscs or insects (Fig. 5a). PC 5 separates fish-feeders (Fig. 5b), characterized by their slender, fusiform body and elongated caudal peduncle, significantly from all other trophic groups (Fig. 5b). Egg-, insect- and mollusc-feeders are not distinct in body shape, and constitute intermediate ranges between the both extremes, fish- and shrimp-feeders (Fig. 5a, b; Tables 3, 4).

Table 3 Variation in shape of morphological candidate structures, based on principal components (PCs) bearing $\geq 5\%$ of total variance in toto

a

Trait	df1	df2:	F:	p
Body	24	3.1520	2.685	0.000
Lower Jaw	28	1.6370	2.118	0.002
Upper Jaw	24	1.5820	1.410	0.120
Pharyngeal Jaw	24	1.3730	1.060	0.069
Jaw bone constellation	24	1.4770	2.377	0.001



a—One way MANOVAs (Wilk’s lambda test) calculated from morphometric PCs, b—pairwise post hoc test (Hotelling’s test, black— $P < 0.001$; dark grey— $P < 0.05$; white—not significant)

Shape analyses focusing on the in-situ constellation of the feeding apparatus indicate significant differences among egg- feeders and fish-, mollusc- and insect-feeders, as well as among shrimp- and mollusc-feeders (Table 3b; Fig. 5c). However, this signal was only partly supported when comparing trophic groups based on single PCs, with shrimp-feeders distinguished from mollusc-feeders according to mouth width in relation to position of maxilla, indicating a relatively wider mouth in mollusc feeders (PC1, explaining 56% of the total variance, Fig. 5c).

Table 4 Variation in shape of morphological candidate structures, based on single principal components (PCs) fulfilling the criterion of $\geq 5\%$ variance

(a)								
Trait		PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7
Body	$F_{4,95}$	5.198	1.608	0.039	1.248	8.392	0.465	
	P	0.001	0.179	0.997	0.296	0.000	0.761	
Lower jaw	$F_{4,51}$	6.105	4.494	1.18	0.633	2.094	0.702	1.672
	P	0.000	0.003	0.33	0.641	0.932	0.582	0.171
Upper jaw	$F_{4,50}$	2.026	0.454	0.241	4.726	2.094	0.879	
	P	0.105	0.769	0.914	0.003	0.932	0.483	
Jaw bone constellation	$F_{4,47}$	3.509	0.928	0.496	1.476			
	P	0.014	0.456	0.739	0.255			
Pharyngeal jaw	$F_{4,44}$	0.367	0.564	0.428	0.498	4.766	0.369	
	P	0.831	0.690	0.788	0.738	0.003	0.829	

(b)			
Trait		Welch F -test	
		PC 1	PC 3
Jaw bone constellation	$F_{4,47}$	2.429	2.148
	P	0.009	0.110

Results of a—one way ANOVAs, b—Welch tests (in case of unequal variances within the PCs). See Fig. 5 for pairwise post hoc results

Oral jaw shape

Significant differences in lower jaw shape are evident among trophic groups (Tables 3a, b, 4a; Fig. 5d, e). Fish-feeders are clearly distinct (Table 3b; Fig. 5d), as are shrimp-feeders (Table 3b; Fig. 5e). Fish-feeders are characterized by a gracile and elongated lower jaw, contrasted by a short and stout lower jaw of egg- and shrimp-feeders. Shrimp- and mollusc-feeders are distinguished according to shape of the rostral part of the dentary (Fig. 5e): The dentary of shrimp-feeders is more elongated and shallower compared to mollusc-feeding individuals.

In contrast to the lower jaw, MANOVA does not support significant shape differentiation in upper jaw according to diet in toto (Table 3). However, ANOVAs indicate that variation of PC4 is significantly explained by differences between fish-feeders and both, egg- and insect-feeders (Fig. 5f). Intergroup variation is present in width of the dentigerous arm (Fig. 5f), being more thin and elongated in fish-feeders than in egg-feeders.

Shape of pharyngeal jaws, gill rakers, and body size

As in case of the upper jaw, the MANOVA based on the total set of six PCs (Table 3a) does not indicate significant differentiation of lower pharyngeal jaw shape according to trophic groups, whereas ANOVAs reveal significant signal in PC5 (Table 4a; Fig. 5g). Pairwise tests indicate significant differences between fish- and egg- as well as insect-feeders (Fig. 5g)—however, morphological differences are small; they mainly affect the

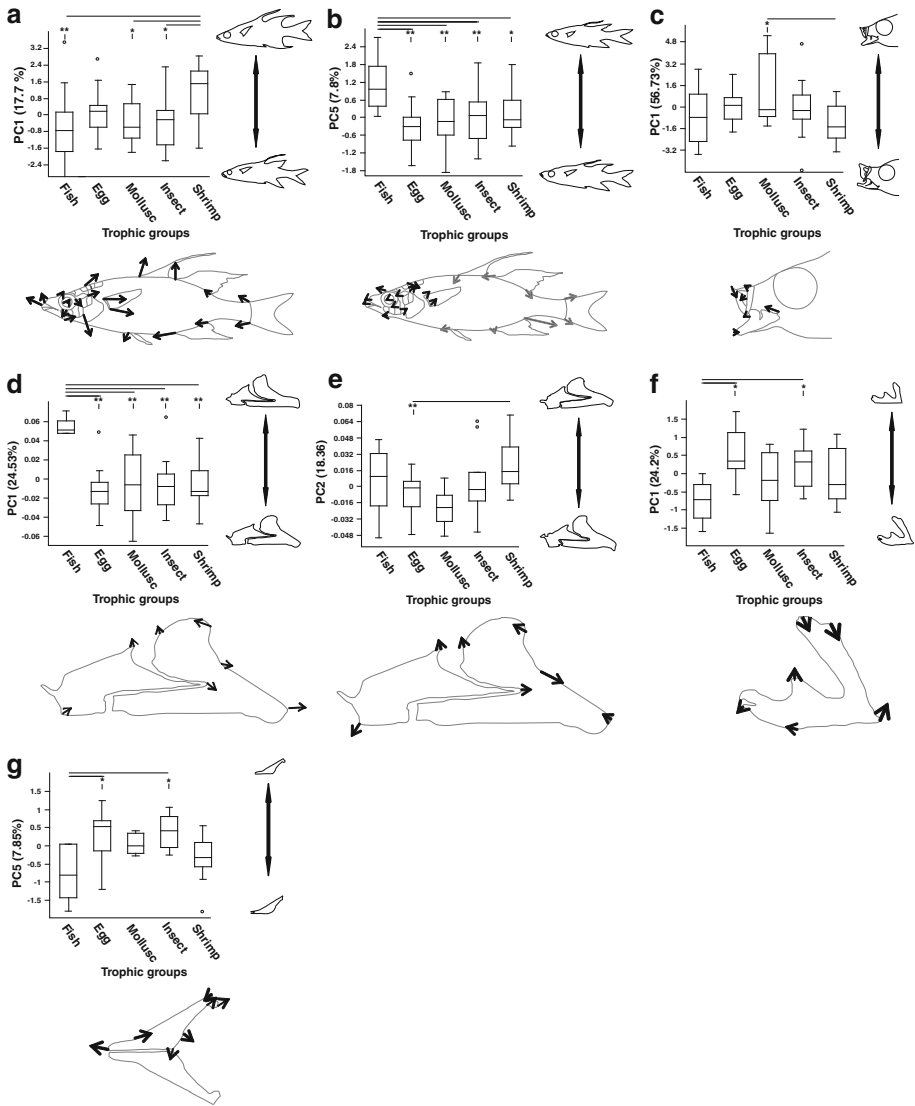


Fig. 5 Major axes of shape variation in candidate traits among trophic groups of sharpfin *Telmatherina*. Boxplots display variation of those principal components (PCs) showing significant (ANOVA; Table 4) variation among groups defined by stomach contents: **a** and **b**: body shape; **c** jaw bone constellation in situ; **d** and **e** lower jaw; **f** upper jaw; **g** lower pharyngeal jaw. Each *box* includes the 25–75% quartiles, median is shown as the *horizontal line* inside the *box*. Minimal and maximal values per boxplot are visualized by the *horizontal lines*, *dots* symbolize outlier. Significant pairwise differentiation (Tukey’s HSD test; * $P < 0.05$; ** $P < 0.001$) is indicated by *lines* above the *boxplots*. *Vector displacements* in pictograms below the *boxplots* indicate the direction of variation in shape for each landmark, with *arrow length* reflecting its contribution to total differentiation

width of the lower pharyngeal jaw in its posterior part, which is wider and shorter in egg- and insect-feeders compared to fish feeders. Mollusc- and shrimp-feeders show intermediate shapes.

Table 5 Variation in gill traits and body length, assessed by one way ANOVAs

Trait	<i>df</i>	<i>F</i>	<i>P</i>
Number of gill rakers total	4,49	2.091	0.096
Number of gill rakers in upper arch	4,49	0.792	0.536
Width/length 1st gill raker	4,49	2.579	0.049
Width/length 2nd gill raker	4,49	0.577	0.680
Width/length 3rd gill raker	4,49	1.102	0.366
Bodylength	4,95	6.189	0.000

See Fig. 6 for pair wise post hoc results

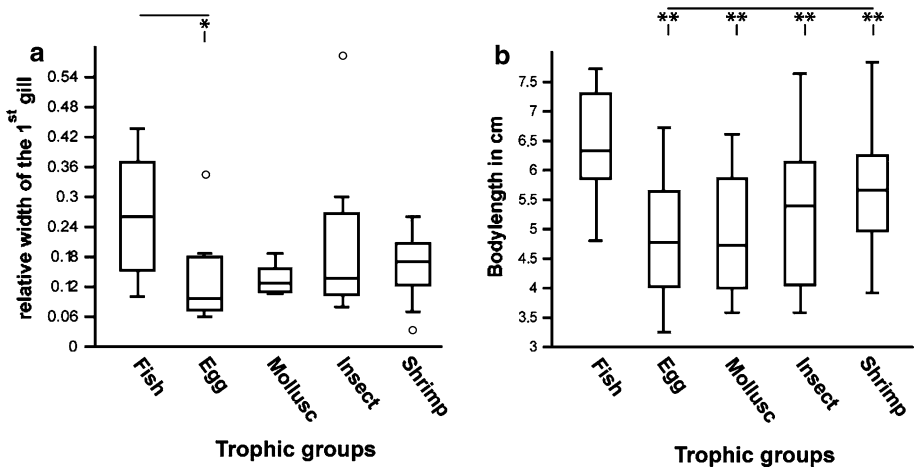


Fig. 6 Relative width of the first gill raker of the upper arch (a), and differentiation in absolute body length (b). Each box includes the 25–75% quartiles, median is shown as the horizontal line inside the box. Horizontal lines visualize minimal and maximal values. Lines above boxplots indicate significant pairwise differentiation (Tukey's HSD test; * $P < 0.05$; ** $P < 0.001$)

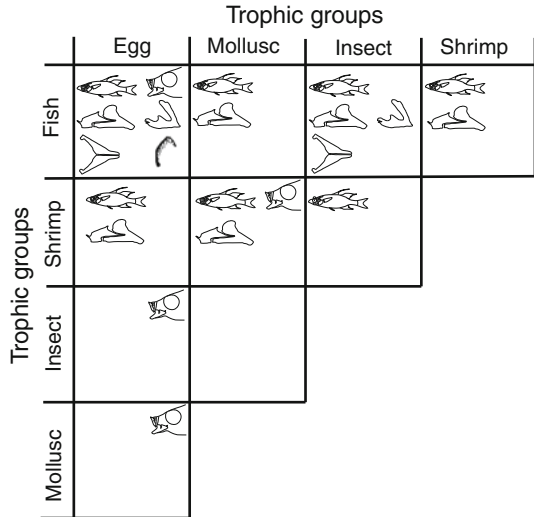
The number of gill rakers on the upper arch ranges from four to seven, and does not vary with diet (Table 5). However, ANOVA based on the trophic groups indicates significant differentiation in the relative width of the first raker (Table 5). It is relatively wider in fish-compared to egg-feeders (Fig. 6). On average, fish-feeders grow significantly larger than egg-, mollusk- or insect-feeders (Table 5; Fig. 6).

Discussion

Significant patterns of adaptation

Our analyses identified significant morphological differentiation among trophic groups of sharpfin sailfin silversides. Pairwise differentiation among these groups covers all seven (fish- vs. egg-feeders) to single traits (jaw bone constellation in egg- versus insect- or mollusk-feeders; body shape in shrimp- versus insect-feeders) (Fig. 7). Insect- versus

Fig. 7 Patterns of significant differentiation in candidate traits among trophic groups of sharpfin sailfin silversides. Symbols indicate significance of differentiation in a certain candidate trait in pairwise comparison of trophic groups (see Tables 3–5 for statistics, and Figs 5, 6 for patterns of trait variation). For size differences see Fig. 6b



mollusc-feeding sharpfins remain the only pairwise combination not distinguished by any trait (Fig. 7).

Fish-feeding sharpfins grow conspicuously large (Fig. 6), and have a fusiform, slender body (Fig. 5b), gracile elongated premaxilla and lower jaw (Fig. 5d, f), an elongated lower pharyngeal jaw (Fig. 5g), and wide gill rakers (Fig. 6). All these traits are characteristic for piscivory in fishes (Liem 1973; Fraser et al. 1999; Waltzek and Wainwright 2003). Though likewise feeding on mobile prey of similar size, shrimp-feeders have a significantly deeper body, shorter and deeper upper and lower jaws, and more gracile gill rakers than fish-feeders. High body depth has been demonstrated to allow for increased turning rates in fishes (Domenici et al. 2008), and might here be an adaptation to predominantly benthic, mobile prey like shrimps. Pronounced, fleshy lips as associated with shrimp-feeding in sharpfins are well known also from benthic feeders in other lacustrine fish radiations (Albertson and Kocher 2006). However, the specific function of this strange lip type remains unknown (Streelman et al. 2007); they have been discussed in context of mechanical sealing of the mouth against a surface (Barlow 2000), or might be linked to enhanced reception abilities of fish feeding on benthic invertebrates (Horstkotte 2005).

In sharpfins, egg-feeding is associated with high body depth, short and strouted upper and lower jaw and comparatively long, gracile gill rakers. Like in shrimp-feeders, high body depth is likely to increase turning rates, which in turn is most likely an adaptation to specialized egg-feeding (Gray et al. 2007, 2008b; Cerwenka et al. in review). Compared to fish-feeders, egg-feeders are distinct in all seven morphological complexes. With respect to insect- and mollusc-feeders, segregation is only evident in jaw bone constellation (Fig. 7), indicating a conspicuously large total mouth width in mollusc-feeders (Fig. 5c). Trophic specialization to egg-feeding, including morphological and behavioural adaptations, has been reported from lacustrine cichlid radiations (Ribbink and Lewis 1981; McKaye and van den Berghe 1997; Ribbink and Ribbink 1997). Correspondingly, the present study suggests morphological adaptations to egg-feeding, fitting expectations derived from alternative egg-feeding strategies in the sharpfin morphospecies *Telmatherina sarasinorum* (Cerwenka et al. in review). However, we found substantial amounts of fish eggs also in two other sharpfin morphospecies (see Supplemental Material S2), suggesting an overall importance of this high-nutrition food item (Hirayama et al. 2005) in sharpfins.

Insect- and mollusc-feeding sharpfins strongly differ from fish- and shrimp-feeders (see above). They are characterized by their less gracile and elongated upper and lower jaw, a deeper body in comparison to fish-feeders, and by absence of fleshy lips occurring in shrimp-feeders (morphospecies *T. sp.* “thicklip”; see Supplemental Material S1). The complete lack of differentiation among insect- and mollusc-feeders (Figs. 5 and 7; Table 3b) appears surprising in light of morphological adaptations to shell-crushing reported from other fish radiations (Hulsey et al. 2005, 2006). However, shells of hydrobioid gastropods ingested by sharpfins are of minute size (Haase and Bouchet 2006), and were recorded mostly unbroken in stomachs. This clearly indicates ingestion of the whole snail without mechanical processing, which most likely explains absence of morphological adaptation to crushing.

In contrast to fish- and shrimp-feeders, morphological similarity of egg-, insect- and mollusc-feeding sharpfins may be explained by widely lacking mobility of all three food categories (ants, accounting for most of the insects, are here assumed to be nearly immobile once in contact with water). Shared combination of short and stout oral jaws, gracile elongated gill rakers, wide lower pharyngeal jaws, and deep bodies appear compatible with the hypothesis of a “suction” mode of food ingestion (Otten 1983; Wainwright 1997; Wainwright and Shaw 1999). These traits clearly contrast with the morphology of predatory foraging in shrimp- and fish-feeding sharpfins.

Multiple axes of differentiation

The complexity of morphological differentiation among trophic groups, covering different morphological structures and complexes, suggests that adaptation is most likely not the result of a recently evolved single “key innovation”. It rather indicates that combinations of quantitative character states might result in increased ability to exploit certain resources. It also suggests that feeding specializations are strong and fine-scaled, most likely a consequence of competition for limited resources in oligotrophic Lake Matano (Haffner et al. 2001).

Restrictions to the interpretation of the degree of differentiation come from a probable lack of independence of several structures analyzed here, i.e. shapes of upper and lower jaw, or jaw bone constellation and oral jaw shape. Adaptations affecting coupled structures or complexes of traits might lead to over-interpretation of the extend of differentiation. However, the prime goal of the present study was to test for the overall presence of morphological adaptation to resource use—the evaluation of morphological dependence is clearly beyond its scope. Nevertheless we consider significantly distinct expression of traits covering body shape, oral jaws, the gill apparatus and pharyngeal jaws as robust indications for fine-scaled trait utility in sharpfins. However, fitness consequences of individual morphology and hence direct evidence for the utility of morphological structures remain to be assessed in forthcoming studies.

Stomach content analyses provide only “snapshots” of an individual’s feeding habits. In consequence, we suppose to rather under- than overestimate differentiation among trophic groups, given feeding opportunism reported from various freshwater fishes (Lowe-McConnell 1964). However, consistent indications for trophic differentiation between round- and sharpfins coming from stomach content and stable isotope data in an earlier study (Roy et al. 2007b; roundfins correspond to mtDNA clade I, sharpfins to clades II and III), suggest rather low levels of variation in stomach content composition of *Telmatherina*. A second factor potentially leading to underestimation of differentiation might be the strict

application of the “majority rule” for defining trophic groups, not considering variation in the remaining food items.

The trophic groups used here to test for segregation of candidate traits with food intake partly coincide with morphospecies concepts (see Supplemental Material S1), a finding not surprising in the light of feeding specialisations reported from some sharpfin morphospecies (Kottelat 1991; Gray et al. 2008b; Cerwenka et al. in review), and indications that natural selection acting on resource use most likely triggers divergence in sympatric roundfins (Herder et al. 2008). However, trophic niches of sharpfin morphospecies widely overlap (see Supplemental Material S2), which is in turn not unexpected in a most likely young, evolving species flock (Herder et al. 2008; Herder and Schliewen in press).

Apart from ecological selection pressure, sexual selection might induce variation in morphological structures related to resource use in fishes (Sakashita 1992). There is robust evidence for sexual selection acting on conspicuous patterns of male coloration in *Telmatherina* (Gray et al. 2008a), which has however been demonstrated not to be associated to morphological or genetic divergence in roundfins (Herder et al. 2008). Lacking indication for sex-specific morphological differences other than those commonly observed in Atheriniformes (including larger fins and conspicuous coloration in sexually active males) suggests that sexual niche differentiation does not play a major role in this system.

A case of adaptive radiation?

The four criteria put forward by Schluter (2000) provide a framework for evaluating the adaptive character of radiations. In case of Lake Matano’s sailfin silversides, the studies available support common ancestry of both, sharpfins and roundfins, as well as monophyly of the lake’s *Telmatherina* in toto (Herder et al. 2006a). Correlation of diverging morphospecies with environmental parameters is evident in roundfins (Herder et al. 2008), but remains to be tested in sharpfins. When comparing sharpfins and roundfins, widely distinct “morphospaces” reflecting variation in body shape (Herder et al. 2006a) support in line with differentiation in skull (Roy et al. 2007b) and trophic (Roy et al. 2007b; Herder et al. 2008; present study) parameters rather pelagic ecology in roundfins vs. benthic ecology in sharpfins. Rapid speciation sensu Schluter (2000) appears likely in L. Matano’s sailfin silversides judging from (1) a distance-based molecular clock approach (0.95–1.9 Myr of sharpfins vs. roundfins; Roy et al. 2007b), (2) the geological age estimates of L. Matano (1–2 Myr; von Rintelen et al. 2004), (3) lacking mtDNA lineage-sorting within both of its endemic clades (Herder et al. 2006a, Roy et al. 2004, 2007b), and (4) indications for incipient speciation in roundfins (Herder et al. 2008). By demonstrating that resource use correlates with fine-scaled patterns of morphological variation, the present study supports the hypothesis that the endemic species flock of L. Matano’s sharpfins fulfils the criterion of “trait utility” (Schluter 2000), which is—among the other criteria—indicative of adaptive radiation.

The most likely, moderately plausible alternative explanation to adaptive radiation of sharpfin sailfin silversides is phenotypic plasticity, the development of different phenotypes from a single genotype (Miner et al. 2005). Indirect evidence favouring adaptive divergence rather than prominent phenotypic plasticity in L. Matano’s sharpfins are (1) morphospecies-specific behaviour and observation of morphospecies-assortative mating (Gray and McKinnon 2006; Gray et al. 2007, 2008a, b; Herder et al. 2008; Cerwenka et al. in review), (2) correlating genotypic and phenotypic variation in sharpfins inhabiting L. Matano’s outlet (Schwarzer et al. 2008), and (3) sympatric speciation detected by AFLP genotyping in the sister clade of sharpfins, L. Matano’s roundfin *Telmatherina* morphospecies (Herder et al. 2008). However, further studies are required to critically test for

population divergence and levels of gene flow—preferably population genetic approaches using nuclear markers that can be linked to morphological character states.

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