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Adaptive speciation and sexual dimorphism contribute to diversity in form and function in the adaptive radiation of Lake Matano's sympatric roundfin sailfin silversides

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Telmatherina;
Telmatherinidae.

Abstract

The utility of traits involved in resource exploitation is a central criterion for the adaptive character of radiations. Here, we test for differentiation in morphology, jaw mechanics and nutrition among species and sexes of Lake Matano's sympatric 'roundfin' sailfin silversides. The three incipient fish species differ significant in several candidate traits for adaptation following ecological selection pressure, corresponding to contrasting jaw mechanics and distinct patterns in food resource use. These findings are consistent with functional adaptation and suggest divergence following alternative modes of feeding specialization. Further, intersexual resource partitioning and corresponding adaptation in jaw mechanics is evident in two of the three incipient species, demonstrating that sexual dimorphism contributes to the ecomorphological and trophic diversity of the emerging radiation. This is, to the best of our knowledge, the first study reporting interspecific as well as intersexual adaptation by alternative modes of form and function in an evolving fish species flock.

Introduction

Ecological speciation theory predicts divergent evolution of traits affecting exploitation of limited resources (Rundle & Nosil, 2005; Schluter, 2009). Adaptive radiations restricted to habitat islands serve as prime model systems for the analysis of speciation processes (Grant & Grant, 2002; Dieckmann *et al.*, 2004; Schliewen & Klee, 2004), and strict criteria have been proposed for recognizing such radiations (Schluter, 2000). One of the criteria commonly applied for evaluating the adaptive character of radiations is 'trait utility' (Schluter, 2000), claiming ecological relevance of characters evolving in such species flocks. Trait utility predicts in turn bi- or multimodal morphological variation in feeding-relevant traits that lead to alternative advantageous utilities for the resource exploitation. It has been demonstrated in several animal radiations, including gill raker number in subarctic whitefish (Kahilainen *et al.*, 2007), alternative cryptic coloration in *Timema cristinae* walking stick insects (Nosil & Crespi, 2006) or biting forces in Darwin's finches (Schluter, 2000; Herrel *et al.*, 2005). In teleost fishes, a variety of candidate traits have been related to feeding adaptations, including oral and pharyngeal jaws, gill rakers, body shape, gape width and body size (Liem, 1973, 1991; Schluter, 1995; Wainwright & Richard, 1995; Rüber & Adams, 2001; Kassam *et al.*, 2003; Amundsen *et al.*, 2004; Salzburger, 2009; Elmer *et al.*, 2010). Sexual dimorphism can forward niche divergence in adaptive radiations (Butler *et al.*, 2007) as revealed, for example, in sticklebacks (Aguirre *et al.*, 2008) or *Anolis* lizards (Butler *et al.*, 2007).

Variation in morphological traits can affect the biomechanics of candidate structures directly involved in food intake and hence also the exploitation of distinct trophic niches. Therefore, the link between morphological variation and its functional consequences is of major importance for the understanding of adaptation to trophic resource use. Models are available for calculating

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the biomechanic potential of the teleost anterior jaw apparatus for a complex (maxillary kinematic transmission; Westneat, 1990) or simple (Wainwright & Richard, 1995) lever system. These models have successfully been applied for inferring predominant patterns of trophic resource use in cichlids, labrids and damselfish (Aerts & Verraes, 1984; Westneat, 1990, 2004; Muller, 1996; Wainwright *et al.*, 2004; Hulsey & De Leon, 2005; Parnell *et al.*, 2008; Cooper & Westneat, 2009).

Here, we test for interspecific as well as intersexual adaptation to resource use in a small and incipient radiation of freshwater fishes endemic to an ancient lake. Lake Matano in the central highlands of the Indonesian island Sulawesi is an extremely deep (> 590 m) and stable tropical lake (Crowe *et al.*, 2008). It is widely isolated from the remaining lakes of 'Wallace's dream-ponds', i.e. the Malili Lakes, a hot spot of endemism and adaptive radiation (e.g. Herder *et al.*, 2006a; Schwarzer *et al.*, 2008; von Rintelen *et al.*, 2010, 2011; see von Rintelen *et al.*, 2011 for an overview). Lake Matano's sailfin silversides (Atheriniformes: Telmatherinidae: *Telmatherina*; Kottelat, 1991) consist of the two major clades 'sharpfins' and 'roundfins', characterized by shapes of their second dorsal and anal fins (Herder *et al.*, 2006a,b). Sharpfins show fine-scaled morphological adaptations to resource use covering body shape and size, upper and lower oral jaws, the gill apparatus and pharyngeal jaws (Pfaender *et al.*, 2010). The sharpfin clade is heavily introgressed by stream populations (Herder *et al.*, 2006a; Schwarzer *et al.*, 2008), which has until recently led to some incongruence between studies based on mitochondrial markers alone and those incorporating nuclear markers (Herder *et al.*, 2006a; Roy *et al.*, 2007; see Herder & Schliewen, 2010 for details). In contrast, the three roundfin morphospecies (Fig. 1), the focus group of the present work, are monophyletic based on both marker systems (Herder *et al.*, 2006a). Roundfins provide an example for incipient sympatric speciation following ecological selection pressure (Herder *et al.*, 2008; Walter *et al.*, 2009a,b), as derived from morphospecies-specific differences in habitat use and feeding ecology, paired with strong indications for assortative mating and correspondingly substantial but incomplete reproductive isolation in sympatry. However, functional consequences of the variation detected in the feeding apparatus and the contribution of sexual dimorphism to the ecomorphological and biomechanical diversity of this small incipient radiation were not considered so far.

Here, we combine analyses focusing separately on skull, body and gill traits with biomechanical models of the jaw apparatus (Fig. 2) and individual stomach content data for exploring two hypotheses. First, we test for signature of adaptation among the three incipient morphospecies in characters relevant to feeding ecology, as predicted in the case of 'trait utility' sensu Schluter (2000). Then, we ask whether sexual dimorphism may account for additional complexity in terms of trait variation and function, which appears likely but remains rarely tested in adaptive radiations (Butler *et al.*, 2007). Linking trait variation to its function and utility, this study contributes to the discussion on mechanisms driving speciation without geographic isolation as well

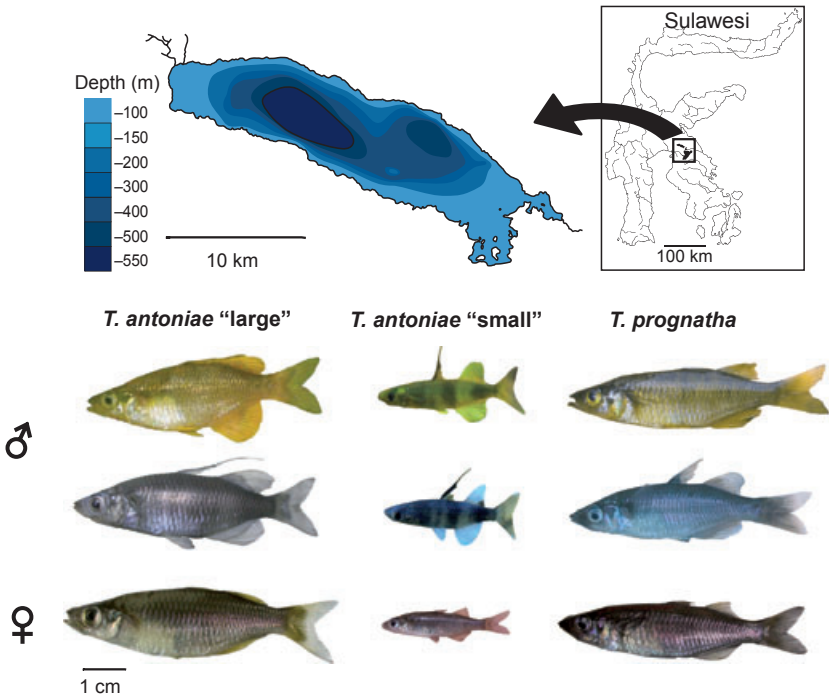

Fig. 1 Lake Matano and its three endemic roundfin morphospecies. Displayed are adult, reproducing males and females; relative specimen size corresponds to natural size. © map by T. von Rintelen, modified (with permission).

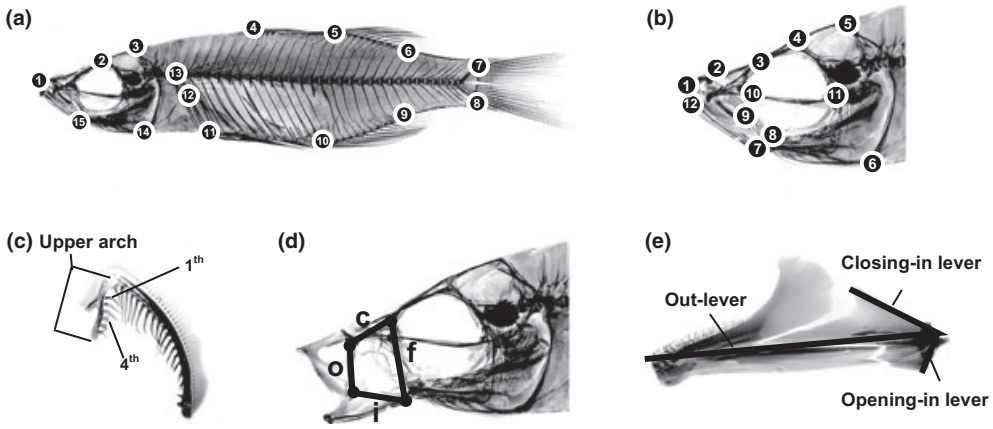

Fig. 2 Morphological traits used for quantifying form and function in roundfin Telmatherina. (a) Body shape is described by 15 landmarks: 1 = anterior tip of premaxilla; 2 = nasal/neurocranium joint; 3 = posterior dorsal tip of neurocranium; 4 = anterior insertion first dorsal fin; 5–6 = insertions second dorsal fin; 7–8 = first and last spline caudal peduncle; 9–10 = insertions of anal fin; 11 = anterior insertion ventral fin; 12–13 = insertions of pectoral fin; 14 = preopercular corner; 15 = posterior ventral end of articular. (b) Head shape analysis based on 12 landmarks: 1 = anterior tip of premaxilla; 2 = nasal/maxilla joint; 3 = nasal/neurocranium joint; 4 = dorsal neurocranium process; 5 = posterior dorsal point of neurocranium; 6 = preopercular corner; 7 = posterior ventral end of articular; 8 = quadrate/articular joint; 10–11 = most anterior-ventral and posterior-ventral point of eye socket; 12 = anterior tip of dentary. (c) Gill traits: number of upper and lower arch gill rakers were counted, and the length of the first and fourth gill rakers was measured from the starting point on the upper arch to the tip. (d) The maxillary 4-bar linkage of the teleost jaws. Complex lever system, with the rotation of the maxilla depending on a given input of lower jaw depression. f = fixed link between nasal/neurocranium joint and quadrate/articular joint; i = input link between quadrate/articular joint and maxilla/articular joint; o = output link as length of the maxilla between maxilla/articular joint and maxilla/nasal joint; c = coupler link between nasal/neurocranium joint and maxilla/nasal joint. (e) The lower jaw constitutes a simple lever system with three levers: out-lever, closing-in-lever and opening-in-lever.

as to debates on the contribution of intersexual differentiation to ecomorphological diversity in adaptive radiations.

Material and methods

Material

Roundfin *Telmatherina* were caught in the dry season 2002 and rainy season 2004 from six locations distributed around the shoreline of Lake Matano (see Herder *et al.*, 2008 for sampling coordinates). Specimens were obtained from up to 10 m depth using snorkel- and SCUBA-guided gillnetting during daytime. Fish were marked individually, preserved in 4% formalin and later transferred to 70% ethanol for storage. In contrast to previous studies (Herder *et al.*, 2008), the present study considered both roundfin sailfin silversides sexes to a similar amount of individuals from the rainy and dry seasons. Thus, 25 males and 25 females of each morphospecies were used (total $n = 150$). Based on the a priori knowledge that body depth and snout shape are the major components distinguishing the three roundfin morphospecies (Herder *et al.*, 2008), shapes of body and head were analysed separately in detail. Accordingly, two high-resolution X-ray pictures were taken from each individual with the mouth closed using a Faxitron LX-60, either focusing on the head or including the whole body.

Stomach content analyses

The gastrointestinal tract ('stomach') of every specimen was dissected, and food items between the oesophagus and pylorus were embedded in Gelvatol (Polyvinylalcohol) or stored in an eppendorf tube in 70% ethanol. Then, food items were identified to the lowest feasible taxonomical level, and the relative volumetric proportion of each food item was estimated in per cent for every individual fish (see Herder & Freyhof, 2006 for details). In total, 120 of 150 stomachs examined contained food items (*T. antoniae* 'small' n♀=22, n♂=20; *T. antoniae* 'large' n♀=16, n♂=19; *T. prognatha* n♀=22, n♂=21). Specimen without stomach contents were categorized as empty and excluded from further analyses. Stomach content data were analysed in two ways. First, Schoener's index (Schoener, 1970) of niche overlap was calculated for estimating trophic niche overlap among the three morphospecies. Second, non-parametric analyses of similarity (ANOSIM, based on 10000 permutations) were calculated to test for the effects of sampling location or season, and for morphospecies or sexual differences in food composition using the program PAST (Hammer *et al.*, 2001).

Comparative analyses of body and head shape

Coordinate data of homologous landmarks were generated from X-ray pictures of the whole body (15

landmarks; Fig. 2a) and the head section (12 anatomical landmarks; Fig. 2b), using the program tpsDig (Rohlf, 2003). A GLS procrustes superimposition (Zelditch *et al.*, 2004) was calculated using the program COORDGEN (included in the IMP software package; Sheets, 2002) to reduce the effects of size and position. The procrustes residuals were then used (i) to calculate principal components (PCs) to extract major axes in shape variation and (ii) in a canonical variates analysis (CVA). Both analyses were carried out in PAST.

Standard length and gill raker morphology

Standard length was measured to the nearest of 0.01 mm for each fish using a digital calliper, from tip of snout to the caudal margin of the hypuralia. Then, the first gill arch of the right side was removed from every fish and x-rayed in standardized orientation including a standard. From these pictures, numbers of gill rakers of the upper (epibranchial) arch and lower (ceratobranchial) arch (see Fig. 2c) were counted and the length of the first and fourth rakers of the upper arch was measured (see Fig. 2c) using the software IMAGE J 1.36. (Rasband, 1997). Gill raker length was related to the length of the upper arch. Finally, PCs were calculated from combined meristic and morphometric gill raker data.

Functional morphology

The biomechanical ability of the feeding apparatus was calculated for a complex and a simple lever system (Fig. 2d,e) in order to test for differentiation among morphospecies and sexes.

In this study, the maxillary 4-bar linkage (Fig. 2d) was used (Westneat, 1990) as a complex lever system. The output of the maxillary 4-bar linkage movement is the protrusion and retraction of the premaxilla during the jaws opening and closing, driven on the maxilla rotation. The maxillary kinematic transmission coefficient (MKT) is defined as the ratio of output rotation to input rotation of the maxilla (Westneat, 1990) and is thus equivalent to the transmission of the input motion of the lower jaw to the maxilla.

One immobile and three mobile links constitute the maxillary 4-bar linkage (Westneat, 1990). During the jaws opening and closing, the mobile links rotate on the fixed link (f in Fig. 2d), measured as the distance between the contact point of neurocranium and nasal to the coronoid process. Through the lower jaw depression, the input link (i in Fig. 2d), measured as the distance between quadrate/articular joint and maxilla/articular connection, transmits the input motion into the linkage. The followed movement of the output link (o in Fig. 2d), measured as the distance between maxilla/articular connection and the nasal/maxilla connection, is coupled to the coupler link (c in Fig. 2d) motion. Therefore, the coupler link is represented by the distance between the posterior nasal begin and the nasal/maxilla connection (c in Fig. 2d).

All link distances were measured in this study from digital X-ray images (see Fig. 2c). Because of the fact that a 4-bar linkage has only one degree of freedom during the movement (Muller, 1996), all angles in the linkage can be calculated at any point of movement as long as one angle is known. In this study, a starting angle of 40° (average angle, measured in a subsample of all morphospecies) between fixed and input links (see Westneat, 1990; Hulsey & De Leon, 2005 for details) was used. Based on the starting angle, all angles in the maxillary 4-bar linkage were calculated. The diagonal distance between the contact point of neurocranium and nasal connection and maxilla/articular coronoid process was estimated because of the known length of empirical measured fixed and input link and the starting angle (see Hulsey & De Leon, 2005 for details).

The MKT was then calculated by dividing the output rotation of the output link (maxilla) by the input rotation (30°; defined through the same procedure used for the starting angle). Calculations of the maxillary 4-bar linkage were made using spreadsheet routines.

The lower jaw lever ratio (LJR) was calculated as the ratio of closing-in-lever to out-lever (Fig. 2e) following Wainwright & Richard (1995). High in-lever/out-lever ratios indicate specialization to slow but forceful closing, as predicted for fish species feeding on immobile prey; the opposite is associated with fast but weak closing, as expected for species feeding on mobile prey (Wainwright & Richard, 1995). Maximum gape width was modelled as the mouth width between tips of premaxilla and dentary. Therefore, the following lengths were measured in addition to the length of the maxillary 4-bar linkage: (i) length of the lower jaw from the articular joint to dentary tip, (ii) ascending arm of premaxilla, (iii) mouth length and (iv) closed mouth width.

Statistical analyses

Each single PC was tested separately for homogeneity of variance among trophic groups, using one-way ANOVAS with Tukey's *post hoc* tests. The same strategy was used to test for morphospecies- and sex-specific variation in estimators for trait function (MKT, LJR, maximum gape width and linkages PC1-3) and in standard length.

Results

Trophic niches vary among morphospecies and sexes

Analyses of stomach contents show clear differences among both morphospecies and sexes. The three roundfin sailfin silversides morphospecies differ significantly in the composition of their stomach contents (ANOSIM:

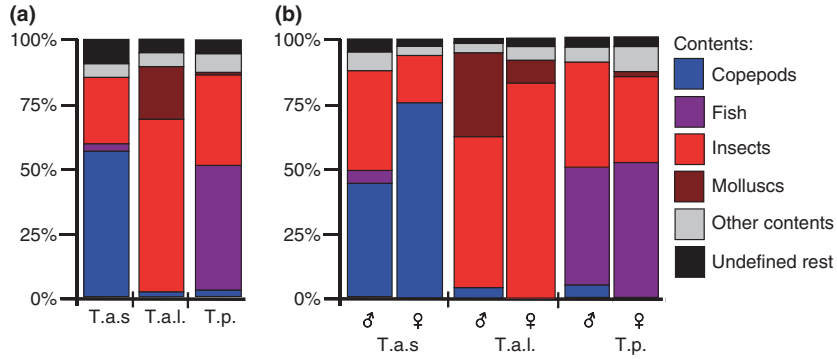

Fig. 3 Stomach content data for (a) morphospecies (sexes pooled) and (b) morphospecies separated by gender (N_{Total} = 120).

R = 0.3036, P < 0.001; Tukey's *post hoc* all P < 0.001). Fish is almost exclusively found in the stomachs of *T. prognatha,* copepods in *T. antoniae* 'small', and molluscs in *T. antoniae* 'large'. The food item 'insects' is present in all three morphospecies but dominates in *T. antoniae* 'large' (Fig. 3a). Trophic niche overlap is higher between *T. prognatha* and *T. antoniae* 'large' (0.48) than between *T. antoniae* 'small' and the other two morphospecies (0.37 with *T. prognatha*, 0.34 with *T. antoniae 'large'*). Intersexual differences in stomach content composition within morphospecies are evident in case of *T. antoniae* 'large' (ANOSIM: R = 0.069, P < 0.05; Tukey's *post hoc* P < 0.05) and 'small' (ANOSIM: R = 0.081, P < 0.05; Tukey's *post hoc* P < 0.05). The stomach of *T. antoniae* 'large' males contained molluscs to a large amount (32.5%), whereas females predominantly fed on insects (66.42%; Fig. 3b) and *T. antoniae* 'small' males feed to a larger amount on insects (40.79%) than the females (25.86%).

In *T.* antoniae 'small', a seasonal effect in food composition is evident (ANOSIM: R = 0.378, P < 0.001, Tukey's *post hoc* P < 0.001). The major food item changes from insects in the rainy season to copepods in the dry season. Stomach contents did not vary significantly among sampling locations (ANOSIM: R = 0.0315; P = 0.05).

Shape variation in head, body and gill raker traits

Shapes of body and head (Fig. 2a,b) show not only significant species-specific (Table 1a), but also sex-specific differences (Table 1a, see Appendix for CVA results). *Telmatherina antoniae* 'large' are characterized by deeper body, superior mouth position and a greater head height compared with both other morphospecies (Table 1b; Fig. 4a,d). Body shapes of *T. antoniae* 'small' and *T. prognatha* are, in contrast, both more slender and fusiform (Fig. 4a). Significant body shape differences between these two morphospecies are mainly affected by the position of fin insertions, which are more anterior in *T. antoniae* 'small' and thus result in an elongated caudal peduncle in *T. prognatha* (Table 1b; Fig. 4b). Head shape of *T. antoniae* 'small' differs significantly (Table 1b) in eye size, eye position and operculum shape from both other roundfins (Fig. 4c). The eye socket is larger and located further caudal in *T. antoniae* 'small' compared with *T. antoniae* 'large' and *T. prognatha*; likewise, its operculum is more elongated (Fig. 4c). Mouth position in *T. antoniae* 'small' and *T. prognatha* is terminal, whereas the mouth is orientated rather dorsal in *T. antoniae* 'large'; this is associated with changes in the maxillar and nasal position as well as in the length of the retracted premaxilla ascending arm (Fig. 4d).

Sexual dimorphism is present in all three morphospecies (Table 1a,c). In *T. antoniae* 'large' and 'small', males have significantly deeper bodies than females (Fig. 4a). A similar tendency is (though not significant) noticeable in *T. prognatha*, which, however, shows intersexual differences in head shape (Table 1c; Fig. 4e): females are characterized by a more posterior orientated contact of nasal and neurocranium, their eye is orientated more anterior, and their joint of maxilla and articular is orientated more superior compared with males (Fig. 4e).

Telmatherina antoniae 'small' differ significantly in gill raker traits from the two other morphospecies in having fever but longer rakers on the upper arch and lower arch (Table 1b; Fig. 5). No significant differences in gill raker traits are found between *T. antoniae* 'large' and *T. prognatha*, both characterized by shorter gill rakers (Fig. 5a). Sexual dimorphism is not evident in any of the three morphospecies according to gill raker traits.

As expected, *T. antoniae* 'small' are clearly distinguished by body size (Table 2a,b; Fig. 6). The present data also support sexual dimorphism in body size in *T. antoniae* 'large', with males being significantly larger than females (Table 2c; Fig. 6). The three morphospecies differ significantly in their absolute maximum gape width (the distance between the jaws when the mouth is opened to its maximum) (Table 2b). *Telmatherina prognatha* has the widest gape, followed by *T. antoniae* 'large' and *T. antoniae* 'small' (Table 2a; Fig. 6). Sexual dimorphism is significant in this character in both *T. antoniae* morphospecies, with males having a larger absolute maximum mouth opening than females (Fig. 6; Table 2c).

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Table 1 Variation in body, head and gill raker traits of roundfin sailfin silversides morphospecies. Displayed are single principal components (PCs) explaining ≥ 5% of the total variance. (a) one-way ANOVAS (significant results in boldface); (b) *Post hoc* test results between morphospecies (Tukey's HSD test); (c) *Post hoc* test results between sexes (Tukey's HSD test). Significant trait variation among morphospecies and sexes is displayed in Figs 4 and 5.

(a)	PC1	PC2	PC3	PC4	PC5	PC6
Morphospecies						
Body						
$F_{2,111}$	163.3	0.3	17.0	1.4	0.5	
P	**< 0.001**	**< 0.000**	**< 0.000**	**< 0.000**	**0.613**	
Head						
$F_{2,108}$	294.1	37.15	4.032	0.8926	6.58	2.4
P	**< 0.001**	**< 0.001**	**< 0.05**	**< 0.001**	**< 0.001**	0.095
Gill						
$F_{2,82}$	23.5	3.3	5.113	0.8		
P	**< 0.001**	**< 0.05**	**< 0.05**	0.441		
Sexes						
Body						
$F_{5,108}$	106.4	2.0	10.9	1.4	1.2	
P	**< 0.001**	0.078	**< 0.001**	0.222	0.293	
Head						
$F_{5,105}$	122.0	16.7	8.6	0.7	4.6	3.6
P	**< 0.001**	**< 0.001**	**< 0.001**	0.6207	**< 0.001**	**< 0.05**
Gill						
$F_{5,75}$	8.7	2.441	2.599	0.8		
P	**< 0.001**	**< 0.05**	**< 0.05**	0.502		

(b)	*T.p.*					*T.a.*l.				
	PC					PC				
Trait	1	2	3	4	5	1	2	3	4	5
*T.a.*s.										
Body	0.065	0.678	**< 0.001**	0.223	0.982	**< 0.001**	0.914	**< 0.001**	0.851	0.742
Head	**< 0.001**	0.0645	0.0828	0.951	0.190	**< 0.001**	**< 0.001**	0.095	0.424	0.146
Gill	**< 0.001**	0.141	**< 0.05**	0.876		**< 0.001**	**< 0.05**	0.565	0.395	
*T.a.*l.										
Body	**< 0.001**	0.900	0.0588	0.500	0.628					
Head	**< 0.001**	**< 0.001**	**< 0.05**	0.609	**0.001**					
Gill	0.840	0.727	0.105	0.694						

(c)	*T.p.*						*T.a.*l.						*T.a.*s.		
	♀			♂			♀			♂			♀		
PC	Body	Head	Gill	Body	Head	Gill	Body	Head	Gill	Body	Head	Gill	Body	Head	Gill
*T.a.*s.															
♂															
1	0.854	**< 0.001**	**< 0.05**	0.770	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.05**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.05**	0.788	1.000
2	0.865	0.907	0.068	0.083	0.098	0.977	0.664	**< 0.001**	0.891	0.515	**< 0.001**	0.479	0.086	0.976	1.000
3	**< 0.001**	**< 0.001**	0.306	**< 0.001**	0.396	0.891	**< 0.001**	0.642	**< 0.05**	**< 0.05**	0.375	**< 0.05**	0.136	1.000	0.630
4	0.866	0.999	0.784	0.988	0.994	0.689	0.972	1.000	0.749	0.767	1.000	1.000	1.000	0.803	0.972
5	0.971	0.858		0.870	0.862		0.726	0.059		0.424	0.491		0.234	0.481	
6		1.000			0.094			0.839			0.719			0.991	
♀															
1	0.095	**< 0.001**	**< 0.05**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.05**	**< 0.001**	**< 0.001**	**< 0.001**			
2	0.631	0.999	0.075	1.000	0.412	0.982	0.841	**< 0.001**	0.904	0.930	**< 0.05**	0.502			
3	**< 0.001**	**< 0.001**	0.995	0.046	0.482	0.997	0.340	0.729	0.738	0.937	0.460	0.572			
4	0.727	0.951	0.995	0.945	0.983	0.982	0.996	0.635	0.991	0.603	0.780	0.978			
5	0.698	**< 0.05**		0.880	0.988		0.962	0.900		0.999	1.000				
6		0.939			**< 0.05**			0.471			0.966				

Table 1 (*Continued*).

	T.p.						*T.a.*l.						*T.a.*s.		
	♀			♂			♀			♂			♀		
PC	Body	Head	Gill	Body	Head	Gill	Body	Head	Gill	Body	Head	Gill	Body	Head	Gill
*T.a.*l.															
♂															
1	**< 0.001**	**< 0.05**	0.570	**< 0.001**	**0.030**	0.999	**< 0.001**	0.049	0.802						
2	0.991	**< 0.05**	0.912	0.926	**< 0.001**	0.897	1.000	0.405	0.979						
3	**< 0.05**	**< 0.001**	0.874	0.951	1	0.284	0.890	0.998	1.000						
4	1.000	0.406	0.805	0.9825	0.9913	0.713	0.2947	1.000	0.771						
5	0.882	**< 0.05**		0.975	0.989		0.997	0.892							
6		0.513			**< 0.05**			0.105							
♀															
1	**< 0.001**	**< 0.001**	0.999	**< 0.001**	**< 0.001**	0.948									
2	0.999	**< 0.001**	0.517	0.835	**< 0.001**	0.999									
3	0.120	**< 0.001**	0.957	1.000	0.999	0.432									
4	0.406	0.985	1.00	0.7216	0.961	1.00									
5	0.989	**< 0.05**		1.000	0.539										
6		0.952			0.69										
T.p.															
♂															
1	0.137	0.932	0.799												
2	0.622	0.598	0.315												
3	0.073	**< 0.001**	0.912												
4	0.996	1.000	1.00												
5	0.999	0.205													
6		0.191													

T.p., *T. prognatha*; *T.a.*s., *T. antoniae* 'small'; *T.a.*l., *T. antoniae* 'large'.

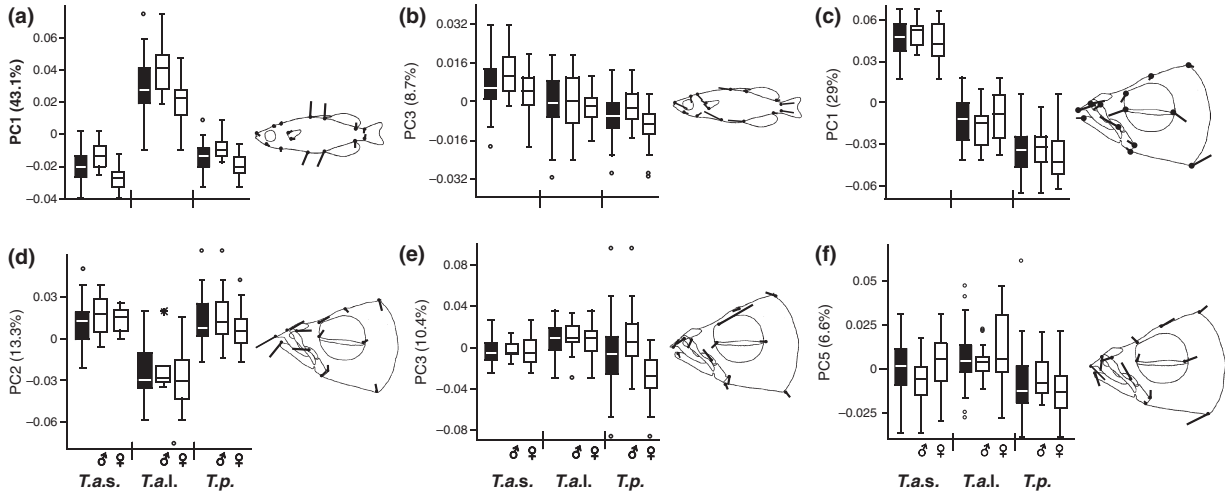

Fig. 4 Significant axes of shape variation (ANOVA; Table 1) in roundfin sailfin silversides: (a) and (b): body shape; (c–f) head shape. Black boxes indicate morphospecies-specific data (males and females pooled). Each box includes the 25–75% quartiles; median is shown as the horizontal line inside the box. Minimal and maximal values per boxplot are visualized by the horizontal lines; dots symbolize outlier. Vector displacements in pictograms beside the boxplots indicate the direction of variation in shape for each landmark; line length reflects its contribution to total differentiation.

Similar to the results of the absolute gape width (Table 2; Fig. 6), all three morphospecies are significantly distinct according to their relative gape width (controlled for body size; Table 3a,b; Fig. 7a). Relative maximum gape width (RMGW) is largest in *T. prognatha* and smallest in *T. antoniae* 'small' (Fig. 7a). Both *T. antoniae*

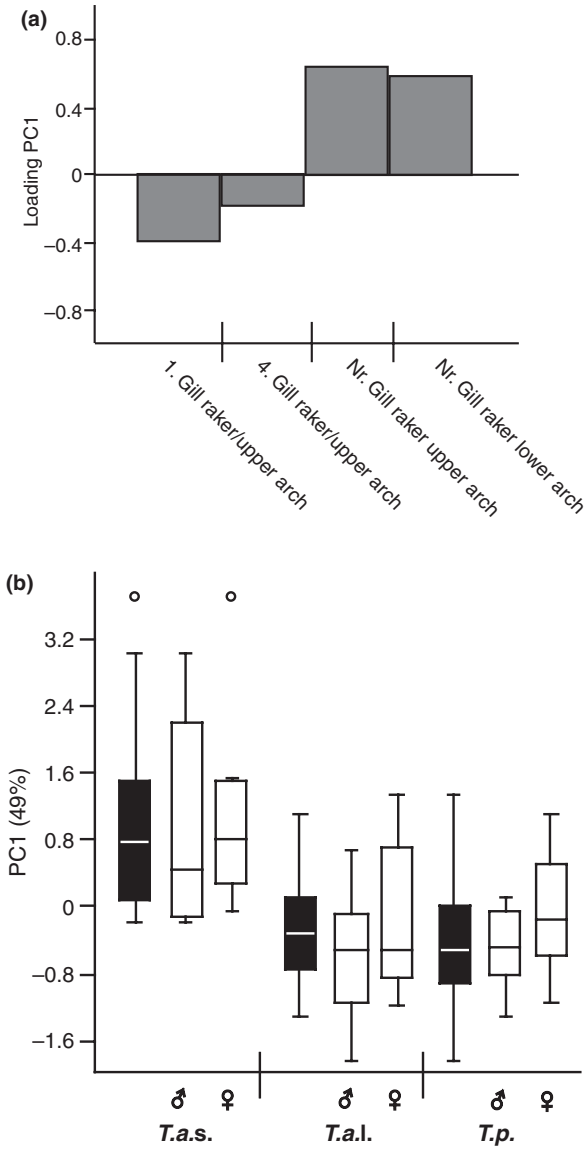

Fig. 5 First principal component (PC) of gill traits with significant differences among roundfin morphospecies and sexes. (a) loadings of the first PC; (b) Boxplot of the respective residuals. Black boxes indicate morphospecies-specific data (males and females pooled). Each box includes the 25–75% quartiles; median is shown as the horizontal line inside the box. Minimal and maximal values per boxplot are visualized by the horizontal lines; dots are outlier.

Table 2 Standard length (Sl) and absolute maximum gape width (AMGW) variation in roundfin sailfin silversides. (a) one-way ANOVAS (significant results in boldface); (b) *Post hoc* test results between morphospecies (Tukey's HSD test); (c) *Post hoc* test results between sexes (Tukey's HSD test). See Fig. 6 for variation details.

(a) Trait	d.f.	*F*	*P*
Morphospecies			
Standard length (SL)	2,104	394.0	**< 0.001**
Absolute maximum gape width (AMGW)	2,104	96.0	**< 0.001**
Sexes			
Standard length (SL)	5,101	183.2	**< 0.001**
Absolute maximum gape width (AMGW)	5,101	55.5	**< 0.001**

(b)	*T.p.*	*T.a.*l.
*T.a.*s.		
Sl	**< 0.001**	**< 0.001**
AMGW	**< 0.001**	**< 0.001**
*T.a.*l.		
Sl	0.151	
AMGW	**< 0.001**	

(c)	*T.p.*		*T.a.*l.		*T.a.*s.
Trait	♀	♂	♀	♂	♀
*T.a.*s.					
♂					
Sl	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	0.9988
AMGW	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.05**
♀					
Sl	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	
AMGW	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	
*T.a.*l.					
♂					
Sl	0.546	0.9979	**< 0.05**		
AMGW	0.998	0.803	**< 0.001**		
♀					
Sl	0.434	**< 0.05**			
AMGW	**< 0.001**	**< 0.001**			
T.p.					
♂					
Sl	0.284				
AMGW	0.957				

T.p., *T. prognatha*; *T.a.*s., *T. antoniae* 'small'; *T.a.*l., *T. antoniae* 'large'.

morphospecies show significant deviation of maximum relative gape width between sexes (Table 2c, Fig. 7a).

Maxillary kinematic transmission and lower jaw closing ratio

Maxillary kinematic transmission and the LJR were used to test for functional consequences of morphological differences in the jaw apparatus of the three morphospecies. Maxillary KTs are significantly higher in *T. antoniae* 'small' (mean: 0.74) and 'large' (mean: 0.69) than in *T. prognatha* (mean: 0.44) (Table 3; Fig. 7b). Likewise, *T. prognatha* show significantly LJR (mean: 0.25) compared with *T. antoniae* 'small' (mean: 0.29) and *T. antoniae* 'large' (mean: 0.29) (Fig. 7c; Table 3b). *Telmatherina antoniae* 'large' and *T. prognatha* show intersexual differences in MKT (Table 3c, Fig. 7b); in case of *T. prognatha,* also the LJR differs between males and females (Table 3c; Fig. 7c).

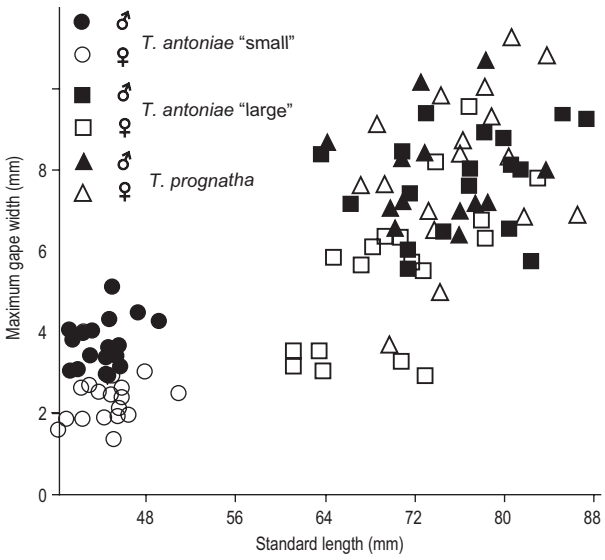

Fig. 6 Distribution of absolute maximum gape width relative to body length in roundfin sailfin silversides.

Proportional changes in the elements of the maxillary 4-bar linkage

Different proportions of maxillary 4-bar linkage components can lead to similar MKT values (Hulsey & Wainwright, 2002; Wainwright *et al.*, 2004). Analyses of the maxillary 4-bar linkage proportions identified significant differences among roundfins (Table 3a), with all three morphospecies being separated significantly by different proportion of the links involved (Table 3b; Fig. 8). In *T. prognatha*, the coupler and the output links (Fig. 2c) are longer and the fixed and the input links are shorter compared with *T. antoniae* 'large' and 'small'; these two differ in turn in all four levers (Fig. 8a,b). *Telmatherina antoniae* 'small' show a longer output and fixed link and shorter input and coupler link than both other morphospecies (Fig. 8a).

Male and female *T. antoniae* 'large' and *T. prognatha* differ significantly in proportion of the maxillary 4-bar linkage (Fig. 8; Table 3c). Male *T. prognatha* have a relatively longer output and coupler link than females (Fig. 8a), whereas male *T. antoniae* 'large' show in proportion a longer fixed and output link than females (Fig. 8b).

Discussion

Alternative modes of resource use arising from disruptive selection pressure are most likely shaping adaptive speciation and the formation of species flocks (Dieckmann *et al.*, 2004; Schluter, 2009). Feeding specializations are well documented in the radiations of various animals such as walking sticks (Nosil & Crespi, 2006; Nosil, 2007), Darwin's finches (e.g. Foster *et al.*, 2008; Herrel *et al.*, 2009, 2010) and teleost fishes (Liem, 1973, 1991; Wainwright & Richard, 1995; Rüber & Adams, 2001; Kassam *et al.*, 2003; Amundsen *et al.*, 2004; Matthews *et al.*, 2010), but the specific function of traits involved as well as the contribution of sexual dimorphism to trophic diversification has rarely been studied (Butler *et al.*, 2007).

Here, we combine morphometric and biomechanical approaches with individual nutrition data to test for adaptation to trophic resource use and the contribution of sexual dimorphism to ecomorphological diversification in the incipient radiation of Lake Matano's roundfin sailfin silversides. We find significant morphological adaptation to alternative feeding modes, including feeding mechanics, and corresponding trophic resource partitioning among species and sexes. This is, to the best of our knowledge, the first study reporting interspecific as well as intersexual adaptation by alternative modes of form and function in an evolving fish species flock.

Ecomorphological adaptations to distinct trophic niches

In teleost fishes, trophic specialization to alternative kinds of prey is commonly reflected by ecomorphological traits favouring either ram feeding, suction feeding, or biting (Liem, 1980). Consistent with previous results (Herder *et al.*, 2008), the present study clearly assigned the three roundfin morphospecies to three distinct trophic niches (Fig. 3a): predominantly piscivore *T. prognatha*, zooplanktivore and insectivore *T. antoniae* 'small' and predominantly insectivore and molluscivore *T. antoniae* 'large'. As predicted for ram feeding predators (Webb, 1978, 1984; Eklöv & Persson, 1995; Wainwright & Richard, 1995; Sibbing & Nagelkerke, 2001; Svanbäck & Eklöv, 2002; Amundsen *et al.*, 2004), *T. prognatha* is characterized by a torpedo-shaped body with a flat head, terminal mouth position, an elongated caudal peduncle (Fig. 4a,d; Herder *et al.*, 2008) and short gill rakers (Fig. 5a). The biomechanics of the feeding apparatus further support the hypothesis of adaptation to ram feeding: *T. prognatha* show a speed-modified closing of gracile elongated jaws with weak kinematic transmission through the maxillary 4-bar linkage (Fig. 7a,b) (Westneat, 1990, 1995; Wainwright *et al.*, 2004; Hulsey & De Leon, 2005).

Similar to *T. prognatha*, open-water-dwelling *T. antoniae* 'small' have a fusiform and slender body, which remains, however, significantly smaller and is characterized by a substantially shorter caudal peduncle and larger eyes (Figs 4b and 6; Herder *et al.*, 2008). This is combined with long and gracile gill rakers (Fig. 5), a trait typically facilitating zooplankton feeding in pelagic species (Van der Meer & Anker, 1984; Fernald, 1988; Walker, 1997; Wainwright, 1999; Sibbing & Nagelkerke, 2001; Svanbäck & Eklöv, 2002). Body shapes of *T. antoniae* 'small' and *T. prognatha* are sharply contrasted by *T. antoniae* 'large'. These grow as large as *T. prognatha*

Table 3 Roundfin sailfin silversides variation in maxilla kinematic transmission (MKT), lower jaw ratio (LJR) and maximum gape width relative to the distance between nasal/neurocranium joint and articular joint (relative MGW) and single principal components (PCs; explaining ≥ 5% of the total variance) of the maxillary four-bar linkage proportions. (a) one-way ANOVAs (significant results in boldface); (b) *Post hoc* test results between morphospecies (Tukey's HSD test); (c) *Post hoc* test results between sexes (Tukey's HSD test). Variation in the traits mentioned here are shown in Figs 7 and 8.

(a) Trait	d.f.	*F*	*P*
Morphospecies			
Maxillary KT (MKT)	2,107	27.4	**< 0.001**
Closing in-/out-lever ratio (LKT)	2,107	16.0	**< 0.001**
Maximum gape width (MGW)	2,107	21.0	**< 0.001**
PC1 linkages	2,108	38.2	**< 0.001**
PC2 linkages	2,108	10.7	**< 0.001**
PC3 linkages	2,108	1.9	0.154
Sexes			
Maxillary KT (MKT)	5,104	20.7	**< 0.001**
Closing in-/out-lever ratio (LKT)	5,104	8.9	**< 0.001**
Maximum gape width (MGW)	5,104	21.4	**< 0.001**
PC1 linkages	5,105	24.05	**< 0.001**
PC2 linkages	5,105	10.0	**< 0.001**
PC3 linkages	5,105	6.2	**< 0.001**

(b)	*T.p.*			*T.a.*l.		
	MKT	LR	MGW	MKT	LR	MGW
*T.a.*s.	**< 0.001**	**< 0.001**	**< 0.001**	0.913	0.265	**< 0.05**
*T.a.*l.	**< 0.001**	**< 0.001**	**< 0.05**			
T.p.				**< 0.001**	**< 0.001**	0.998
*T.a.*s.	**< 0.05**	0.978	0.235	**< 0.001**	**< 0.001**	0.235
	1	2	3	1	2	3
		PC-4-bar			PC-4-bar	

(c)	*T.p.*						*T.a.*l.						*T.a.*s.		
	♀			♂			♀			♂			♀		
	MKT	LR	MGW	MKT	LR	MGW	MKT	LR	MGW	MKT	LR	MGW	MKT	LR	MGW
*T.a.*s.															
♂	**< 0.001**	0.740	**< 0.001**	**< 0.05**	0.867	**< 0.001**	0.126	**< 0.05**	**< 0.05**	0.916	**< 0.05**	**< 0.001**	0.9903	0.2644	**< 0.001**
♀	**< 0.001**	**< 0.001**	**< 0.05**	**< 0.001**	**< 0.001**	**< 0.05**	0.651	0.872	0.559	0.5934	1.000	**< 0.05**			
*T.a.*l.															
♂	**< 0.001**	**< 0.001**	1.000	**< 0.05**	**< 0.05**	**0.998**	**< 0.04**	0.968	**< 0.05**				0.116	0.923	1.000
♀	**< 0.001**	**< 0.05**	**< 0.001**	0.689	**< 0.05**	**< 0.001**				0.416	**< 0.05**	**< 0.05**	0.984	**< 0.05**	**< 0.05**
T.p.															
♂	**< 0.001**	1.000	1.000				**< 0.05**	**< 0.05**	**< 0.05**	0.591	1.000	0.887	**< 0.001**	0.845	0.967
♀				**< 0.001**	**< 0.05**	**0.054**	**< 0.001**	**< 0.001**	1.000	**< 0.001**	**< 0.05**	**< 0.05**	**< 0.001**	0.099	**< 0.05**
*T.a.*s.															
♂	**< 0.001**	0.556	0.215	**< 0.001**	0.275	0.991	0.157	**< 0.001**	0.187	**< 0.001**	0.384	0.544	0.504	0.929	0.727
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
		PC-4-bar			PC-4-bar			PC-4-bar			PC-4-bar			PC-4-bar	

T.p., *T. prognatha*; *T.a.s.*, *T. antoniae* 'small'; *T.a.*l., *T. antoniae* 'large'.

(Fig. 6, Herder *et al.*, 2008) but have a substantially deeper body (Fig. 4a). Their mouth position is superior, opposed by a terminal mouth position in *T. antoniae* 'small' and *T. prognatha* (Fig. 4d); similar to *T. prognatha*, the gill rakers are short (Fig. 5). Together, these traits are commonly occurring in fish species specialized to feeding immobile prey in littoral zones or on the water surface (Webb, 1984; Amundsen, 1988; Walker, 1997; Sibbing & Nagelkerke, 2001).

Characteristic for a suction feeding mode, and predicted for species specialized on 'picking' zooplankton or immobile benthic prey (Westneat, 1990; Hulsey &

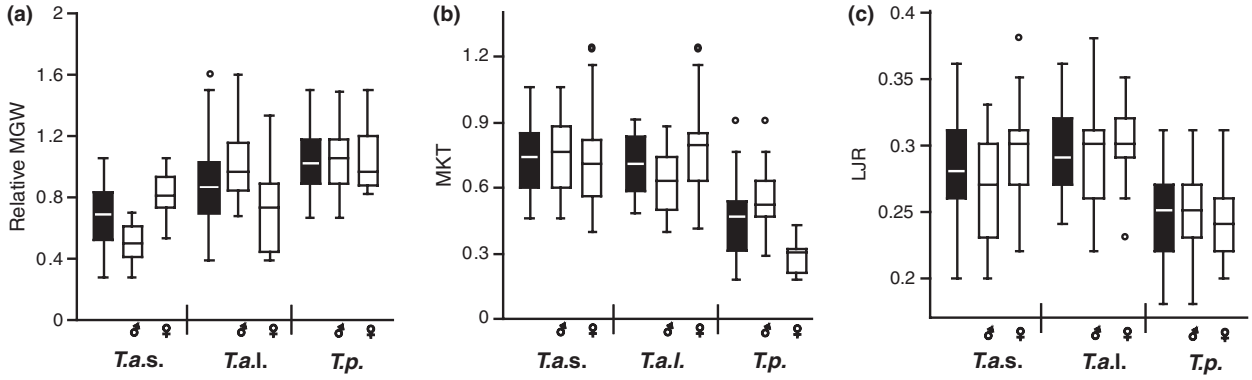

Fig. 7 Differentiation among roundfin morphospecies and sexes according to (a) maximum gape width relative to the fixed link (distance between nasal/neurocranium joint and quadrate/articular joint; relative MGW), (b) maxillary kinematic transmission, (c) lower jaw closing ratio; Black boxes indicate morphospecies-specific data (males and females pooled). 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 are outlier.

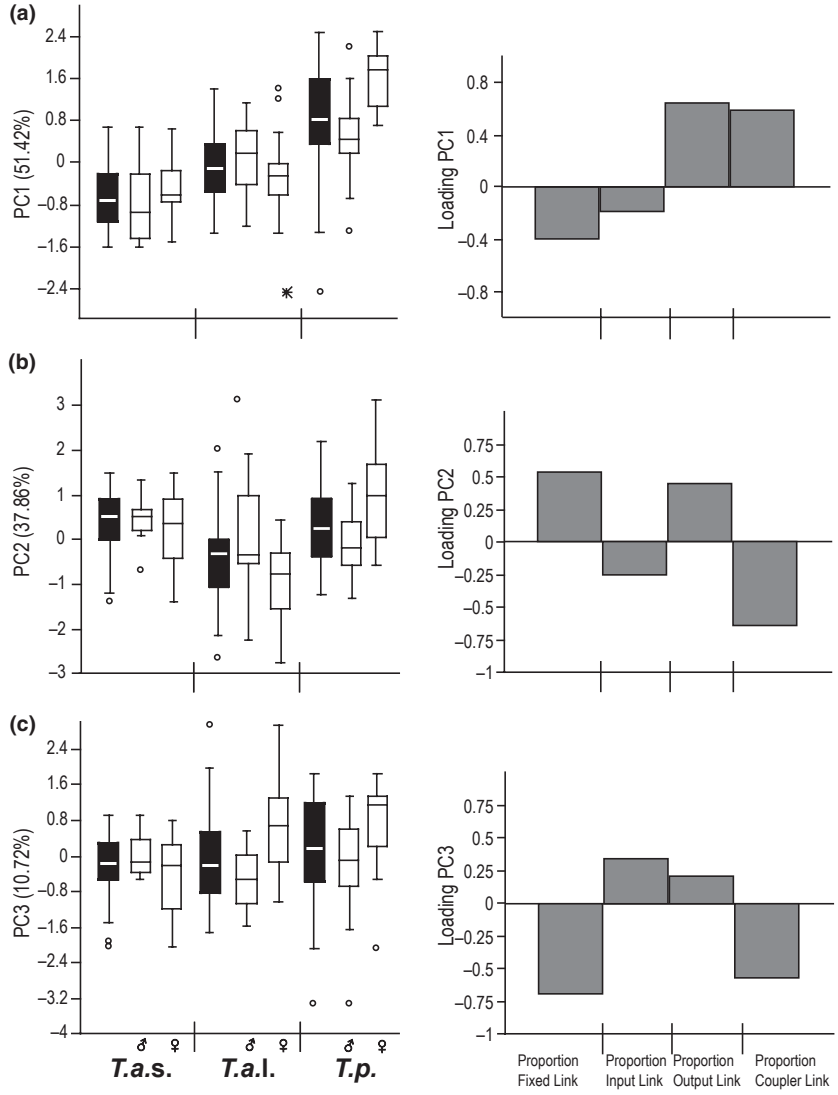

Fig. 8 Significant differentiation among morphospecies and sexes according to maxillary 4-bar linkage components proportions. Histograms display axis loadings of the first three principal components. Black boxes indicate morphospecies-specific data (males and females pooled). Each box includes the 25–75% quartiles; median is shown as the horizontal line inside the box. Minimal and maximal values per boxplot are visualized by the horizontal lines; dots are outlier.

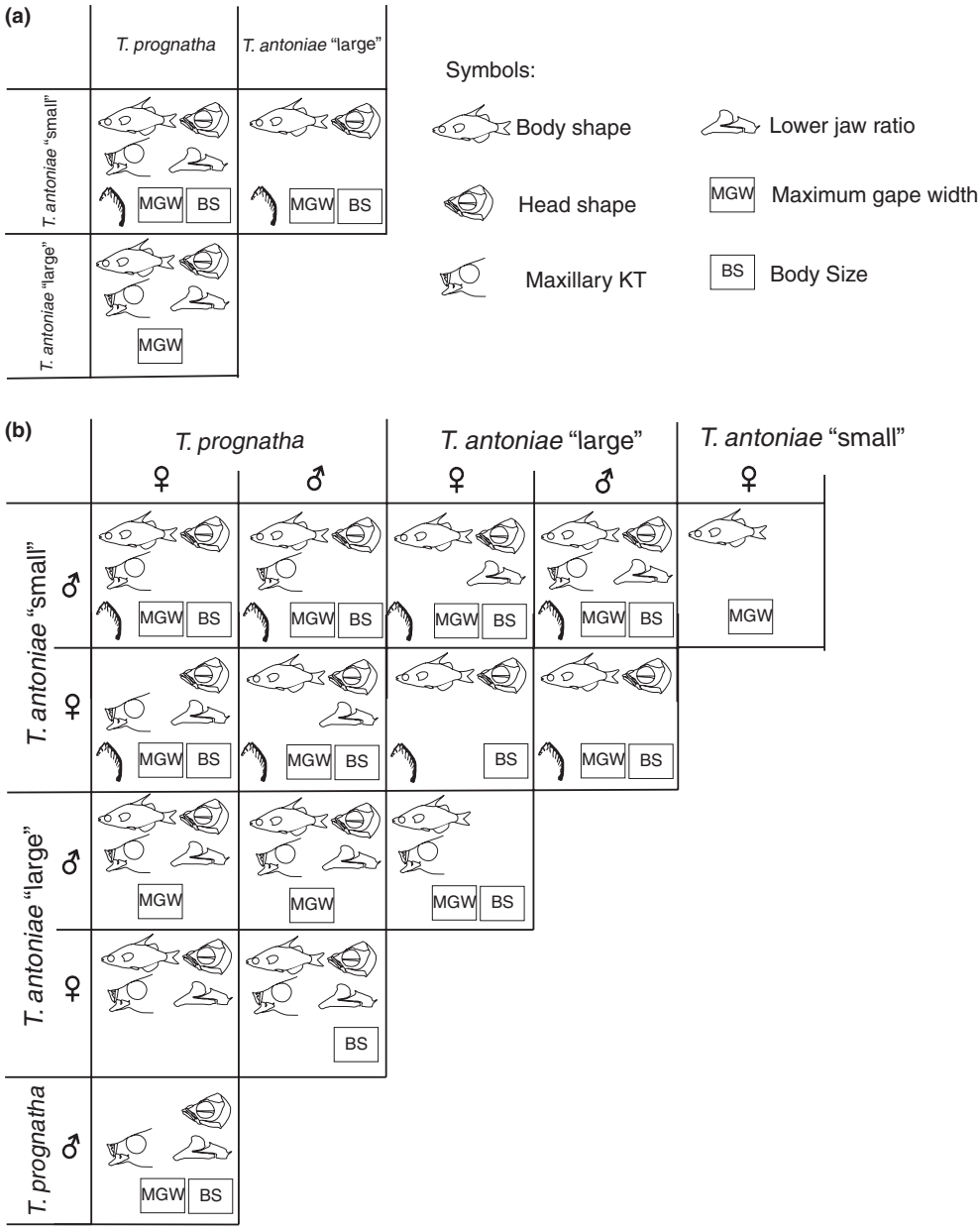

Fig. 9 Significant morphological and biomechanical differentiation among (a) morphospecies and (b) sexes of roundfin *Telmatherina*. Significant differences according to pairwise comparison in candidate traits are displayed by the presence of symbols (see Tables 1–3 for statistics and Figs 4,5,7 and 8 for the patterns of trait variation; for size differences in gape width and body, see Fig. 6 and Tables 2–3).

Wainwright, 2002; Wainwright *et al.*, 2004), *T. antoniae* 'small' and 'large' both show conspicuously high MKT values (Fig. 7b), reflecting high motion of the maxilla and thus a speed-modified linkage. However, similar MKTs arise from clearly different morphological designs of the maxillary 4-bar linkage (Fig. 8a and b), supporting the hypothesis of 'many to one mapping' (Hulsey & Wainwright, 2002; Parnell *et al.*, 2008): different shapes of the oral jaws can lead to similar MKT values.

Lower jaw ratios clearly oppose the MKT results (Fig. 7b) in both *T. antoniae* 'large' and 'small'. The high motion transmission through the maxillary 4-bar linkage, combined with low velocity of the lower jaw closing ratio, is indicative for efficient suction feeding, with small and rather short oral jaws (Westneat, 2006). *Telmatherina antoniae* 'large' and 'small' are thus less distinct than *T. prognatha* but are, nevertheless, clearly distinguished in oral jaw mechanics, size and gape width (Fig. 9a).

Taken together, morphology and feeding mechanics can explain the interspecific trophic specializations observed in roundfins.

Ecomorphological and functional consequences of sexual dimorphism

Sexual dimorphism affecting the feeding ecology is widespread in different groups of animals, such as in seabirds (Selander, 1966; Hulscher & Ens, 1992; Durell *et al.*, 1993; Weimerskirch *et al.*, 2006; Van De Pol *et al.*, 2010), Darwin's finches (Herrel *et al.*, 2010) or snakes (Brooks *et al.*, 2009; Brischoux *et al.*, 2011). Studies on sexual dimorphism in adaptive radiations mostly focus either on size (reviewed in Blanckenhorn, 2005) or on the relevance of shape variation for mating or breeding behaviour (e.g. Herler *et al.*, 2010), although the contribution of sexual dimorphism to ecomorphological and functional diversification remains largely unexplored (Butler *et al.*, 2007). Disruptive ecological and disruptive sexual selection are both expected to contribute to divergence forcing adaptive radiation, especially when mating preferences are coupled to ecologically relevant traits (see Maan & Seehausen, 2011 for a review).

In roundfin sailfin silversides, sexual dimorphism affects the morphology of the feeding apparatus in all three morphospecies (Tables 2c and 3c; Figs 6, 7 and 8) but is less pronounced than interspecific differences in form and function (Figs 4–8). Results of the stomach content analyses show a significant diet dissimilarity among male and female *T. antoniae* 'small' and 'large' (Fig. 3b). In both morphospecies, differences in the nutrition can be explained by fine-scaled changes in the feeding apparatus morphology. In case of *T. antoniae* 'small', males show a larger relative and absolute gape width than females (Figs 6 and 7a). Conspicuously, this comes along with increased amounts of insect prey in males compared with females (Fig. 3b), a nutrition clearly benefiting from larger mouth width compared with the ingestion of zooplankton (Wainwright & Richard, 1995). A slow but more powerful closing of the male jaw is evident in *T. antoniae* 'large' through a lower MKT (Fig. 7b; Table 3c). This might be advantageous for the picking on small molluscs (Wainwright, 1999), which are found in a significant larger amount in the stomach of male *T. antoniae* 'large' compared with females.

Surprisingly, the pronounced differences in the ecomorphology and biomechanic function of the feeding apparatus in *T. prognatha* (Fig. 9b) are not reflected by trophic resource partitioning among sexes. This may have different reasons. Trophic niche differentiation might be restricted to certain periods of increased competition, a phenomenon revealed, for example, in cichlids (Binning *et al.*, 2009). As our sampling contains fish obtained in different seasons, and tests for seasonal effects remained nonsignificant, this hypothesis appears rather unlikely. Sexual selection affecting traits relevant to trophic ecology, a phenomenon not uncommon in fish (e.g. in gobies Chen *et al.*, 1995), might provide an alternative explanation for sexual dimorphism without significant trophic niche shift. Taken together, the present study revealed fine-scaled intersexual ecomorphological and functional differentiation in roundfins, which most likely emerged following both ecological and sexual selection pressure.

The utility of alternative trait compositions

Interspecific as well as intersexual differences in biomechanical abilities arising from morphological variation in trophic key characters have been demonstrated in, for example, the bill shape in birds (Badyaev *et al.*, 2008; Herrel *et al.*, 2010) or the jaw apparatus in teleost fishes (e.g. Westneat, 1994; Wainwright, 1995; Cooper & Westneat, 2009). In evolving radiations, alternative 'utilities' of traits affecting resource use likely reflect divergent ecological selection and have been proposed as a central criterion for recognizing the adaptive character of radiations (Schluter, 2000). The present study links traits characterizing morphospecies of Lake Matano's incipient roundfin sailfin silverside radiation to their functional consequences and ecological relevance and shows that males and females also differ substantially in form, function and diet.

The analyses targeting interspecific ecomorphological and biomechanical variation support two alternative modes of feeding ecology in roundfins. A trait composition indicative of ram feeding coincides with fish as dominant stomach content in *T. prognatha*, whereas the two other morphospecies are both suction feeders, differing, however, substantially in body size and accordingly also in absolute gape width (Fig. 9a). This and contrary patterns of habitat use, living predominantly either inshore (*T. antoniae* 'large') or offshore (*T. antoniae* 'small'; Herder *et al.*, 2008), can be considered as adaptations to different feeding specializations. Alternative mechanics of the jaw apparatus strongly suggest that traits distinguishing the morphospecies translate into alternative modes of foraging adaptation and thus reflect distinct 'utilities' for resource exploitation. Therefore, roundfin sailfin silversides are here suggested to satisfy Schluter's (2000) criterion of 'trait utility' indicative of adaptive radiation. Importantly, the signature of adaptation is also significant among sexes, adding another component to the complexity of this emerging fish radiation.

The present study explicitly focused on traits related to trophic resource use. Adaptive divergence might also be expected to affect other characters and functions like cryptic coloration and defensive morphology (Schluter, 2000; Vamosi, 2002; Nosil & Crespi, 2006). Although there are no apparent indications for alternative crypsis

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in roundfin *Telmatherina*, significantly differing body depths and adult sizes likely affect predation risk (Hambright, 1991; Magnhagen & Heibo, 2004). The performance of morphological traits in terms of predation might provide complementary or in part alternative explanations to the present interpretations, hypotheses requiring further investigations.

Specialization to ram vs. suction feeding is not uncommon in fish radiations (Norton & Brainerd, 1993; Wainwright *et al.*, 2001). However, several other teleost radiations like labrids, damselfish or cichlids contain additional specializations (Liem, 1980, 1991; Albertson, 2008; Konow *et al.*, 2008). Roundfins are less species rich and show accordingly less biomechanical diversity in the feeding apparatus than these groups. The diet spectrum available in oligotrophic L. Matano, competitors from other fish radiations emerging in the lake, developmental constraints in atheriniform compared with perciform fishes and the young age of the radiation may provide possible explanations.

Conclusions

Ecomorphological variation detected among morphospecies and sexes translates into alternative modes of feeding mechanics in the roundfins species flock. Ecological selection pressure favouring alternative modes of resource use can explain the substantial interspecific differences, whereas the less pronounced but still significant intersexual differentiation detected is likely shaped by both ecological and sexual selection pressure. Functional adaptation is indicative of adaptive radiation with respect to morphospecies and satisfies the criterion of 'trait utility' sensu Schluter (Schluter, 2000). Morphological differentiation among males and females is fine scaled compared with patterns among morphospecies but, nevertheless, contributes to ecofunctional diversity in all three morphospecies. However, intersexual differentiation in resource use only occurs in *T. antoniae* 'small' and 'large'; sexual selection directly affecting traits involved in feeding mechanics may provide possible explanations for the absence of clear ecological differences despite functional divergence among male and female *T. prognatha*. In conclusion, our results suggest that resource partitioning in this incipient radiation can be explained by adaptation to resource use in trophic-relevant traits and sexual dimorphism can contribute to the emerging adaptive radiations ecomorphological and trophic diversity.

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References

Aerts, P. & Verraes, W. 1984. Theoretical analysis of a planar four bar linkage in the teleostean skull. The use of mathematics in biomechanics. *Ann. Soc. R. Zool. Belg.* **114**: 273–290.

Aguirre, W.E., Ellis, K.E., Kusenda, M. & Bell, M.A. 2008. Phenotypic variation and sexual dimorphism in anadromous threespine stickleback: implications for postglacial adaptive radiation. *Biol. J. Linn. Soc.* **95**: 465–478.

Albertson, R.C. 2008. Morphological divergence predicts habitat partitioning in a Lake Malawi cichlid species complex. *Copeia* **3**: 689–698.

Amundsen, P.-A. 1988. Habitat and food segregation of two sympatric populations of whitefish (*Coregonus lavaretus* L.s.l.) in lake Stuorajavri, northern Norway. *Nordic J. Freshw. Res.* **64**: 67–73.

Amundsen, P.-A., Bøhn, T. & Vågå, G. 2004. Gill raker morphology and feeding ecology of two sympatric morphs of European whitefish (*Coregonus lavaretus*). *Ann. Zool. Fenn.* **41**: 291–300.

Badyaev, A.V., Young, R.L., Oh, K.P. & Addison, C. 2008. Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. *Evolution* **62**: 1951–1964.

Binning, S.A., Chapman, L.J. & Cosandey-Godin, A. 2009. Specialized morphology for a generalist diet: evidence for Liem's Paradox in a cichlid fish. *J. Fish Biol.* **75**: 1683–1699.

Blanckenhorn, W.U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology* **111**: 977–1016.

Brischoux, F., Bonnet, X., Cherel, Y. & Shine, R. 2011. Isotopic signatures, foraging habitats and trophic relationships between fish and seasnakes on the coral reefs of New Caledonia. *Coral Reefs* **30**: 155–165.

Brooks, S.E., Allison, E.H., Gill, J.A. & Reynolds, J.D. 2009. Reproductive and trophic ecology of an assemblage of aquatic and semi-aquatic snakes in Tonle Sap, Cambodia. *Copeia* **2009**: 7–20.

Butler, M.A., Sawyer, S.A. & Losos, J.B. 2007. Sexual dimorphism and adaptive radiation in Anolis lizards. *Nature* **447**: 202–205.

Chen, I.-S., Shao, K.-T. & Fang, L.-S. 1995. A new species of freshwater goby *Schismatogobius ampluvinculus* (Pisces: Gobiidae) from southeastern Taiwan. *Zool. Stud.* **34**: 202–205.

Cooper, W.J. & Westneat, M.W. 2009. Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. *BMC Evol. Biol.* **9**: 24.

Crowe, S.A., O'Neill, A.H., Katsev, S., Hehanussa, P., Haffner, G.D., Sundby, B. *et al.* 2008. The biogeochemistry of tropical lakes: a case study from Lake Matano, Indonesia. *Limnol. Oceanogr.* **53**: 319–331.

Dieckmann, U., Doebeli, M., Metz, J.A.J. & Tautz, D. 2004. *Adaptive Speciation*. Cambridge University Press, Cambridge.

Durell, S.E.A. Le V. Dit, Goss-Custard, J.D. & Caldow, R.W.G. 1993. Sex-related differences in diet and feeding method in the oystercatcher *Haematopus ostralegus*. *J. Anim. Ecol.* **62**: 205–215.

Eklöv, P. & Persson, L. 1995. Species-specific antipredator capacities and prey refuges – interactions between piscivorous perch (*Perca-Fluviatilis*) and juvenile perch and roach (*Rutilus-rutilus*). *Behav. Ecol. Sociobiol.* **37**: 169–178.

Elmer, K.R., Fan, S., Gunter, H.M., Jones, J.C., Boekhoff, S., Kuraku, S. *et al.* 2010. Rapid evolution and selection inferred from the transcriptomes of sympatric crater lake cichlid fishes. *Mol. Ecol.* **19**: 197–211.

Fernald, R.D. 1988. Aquatic adaptations in fish eyes. In: *Sensory Biology of Aquatic Animals* (J. Atema, R.R. Fay, N.N. Popper & W.N. Tavolga, eds), pp. 435–466. Springer Verlag, New York.

Foster, D., Podos, J. & Hendry, A.P. 2008. A geometric morphometric appraisal of beak shape in Darwin's finches. *J. Evol. Biol.* **21**: 263–275.

Grant, P.R. & Grant, B.R. 2002. Adaptive radiation of Darwin's finches. *Am. Sci.* **90**: 130–139.

Hambright, K.D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Trans. Am. Fish. Soc.* **120**: 500–508.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **4**: 9.

Herder, F. & Freyhof, J. 2006. Resource partitioning in a tropical stream fish assemblage. *J. Fish Biol.* **69**: 571–589.

Herder, F. & Schliewen, U.K. 2010. Beyond sympatric speciation: radiation of sailfin silverside fishes in the Malili Lakes (Sulawesi). In: *Evolution in Action – Adaptive Radiations and the Origins of Biodiversity* (M. Glaubrecht, ed.), pp. 465–483. Springer, Heidelberg.

Herder, F., Nolte, A., Pfaender, J., Schwarzer, J., Hadiaty, R.K. & Schliewen, U.K. 2006a. Adaptive radiation and hybridization in Wallace's Dreamponds: evidence from sailfin silversides in the Malili Lakes of Sulawesi. *Proc. Biol. Sci.* **275**: 2178–2195.

Herder, F., Schwarzer, J., Pfaender, J., Hadiaty, R.K. & Schliewen, U.K. 2006b. Preliminary checklist of sailfin silversides (Pisces: Telmatherinidae) in the Malili Lakes of Sulawesi (Indonesia), with a synopsis of systematics and threats. *Ver. Ges. Ichthyol.* **5**: 139–163.

Herder, F., Pfaender, J. & Schliewen, U.K. 2008. Adaptive sympatric speciation of polychromatic ''roundfin'' sailfin silverside fish in Lake Matano (Sulawesi). *Evolution* **62**: 2178–2195.

Herler, J., Kerschbaumer, M., Mitteroecker, P., Postl, L. & Sturmbauer, C. 2010. Sexual dimorphism and population divergence in the Lake Tanganyika cichlid fish genus Tropheus. *Front. Zool.* **7**: 4.

Herrel, A., Podos, J., Huber, S.K. & Hendry, A.P. 2005. Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. *Funct. Ecol.* **19**: 43–48.

Herrel, A., Podos, J., Vanhooydonck, B. & Hendry, A.P. 2009. Force–velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation? *Funct. Ecol.* **23**: 119–125.

Herrel, A., Soons, J., Aerts, P., Dirckx, J., Boone, M., Jacobs, P. *et al.* 2010. Adaptation and function of the bills of Darwin's finches: divergence by feeding type and sex. *EMU* **110**: 39–47.

Hulscher, J.B. & Ens, B.J. 1992. Is the bill of the male Oystercatcher a better tool for attacking mussels than the bill of the female? *Neth. J. Zool.* **42**: 85–100.

Hulsey, C.D. & De Leon, F.J.G. 2005. Cichlid jaw mechanics: linking morphology to feeding specialization. *Funct. Ecol.* **19**: 487–494.

Hulsey, C.D. & Wainwright, P.C. 2002. Projecting mechanics into morphospace: disparity in the feeding system of labrid fishes. *Proc. R.Soc.B Biol. Sci.* **269**: 317–326.

Kahilainen, K.K., Malinen, T., Tuomaala, A., Alajaervi, E., Tolonen, A. & Lehtonen, H. 2007. Empirical evaluation of phenotype-environment correlation and trait utility with allopatric and sympatric whitefish, *Coregonus lavaretus* (L.), populations in subarctic lakes. *Biol. J. Linn. Soc.* **92**: 561–572.

Kassam, D.D., Adams, D.C., Ambali, A.J.D. & Yamaoka, K. 2003. Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. *Anim. Biol.* **53**: 59–70.

Konow, N., Bellwood, D.R., Wainwright, P.C. & Kerr, A.M. 2008. Evolution of novel jaw joints promote trophic diversity in coral reef fishes. *Biol. J. Linn. Soc.* **93**: 545–555.

Kottelat, M. 1991. Sailfin silversides (Pisces: Telmatherinidae) of Lake Matano, Sulawesi, Indonesia, with descriptions of six new species. *Ichthyol. Explor. Freshwaters* **1**: 321–344.

Liem, K.F. 1973. Evolutionary strategies and morphological innovations – cichlid pharyngeal jaws. *Syst. Zool.* **22**: 425–441.

Liem, K.F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* **20**: 283–293.

Liem, K.F. 1991. Functional morphology. In: *Cichlid Fishes: Behaviour, Ecology and Evolution* (K.F. Liem, ed.), pp. 129–150. Chapman & Hall, New York.

Maan, M.E. & Seehausen, O. 2011. Ecology, sexual selection and speciation. *Ecol. Lett.* **14**: 591–602.

Magnhagen, C. & Heibo, E. 2004. Growth in length and in body depth in young-of-the-year perch with different predation risk. *J. Fish Biol.* **64**: 612–624.

Matthews, B., Marchinko, K.B., Bolnick, D.I. & Mazumder, A. 2010. Specialization of trophic position and habitat use by sticklebacks in an adaptive radiation. *Ecology* **91**: 1025–1034.

Van der Meer, H.J. & Anker, G.C. 1984. Retinal resolving power and sensitivity of the photopic system in seven haplochromine species (Teleostei, Cichlidae). *Nord. J. Fresh. Res.* **34**: 197–209.

Muller, M. 1996. A novel classification of planar 4-bar linkages and its application to the mechanical analysis of animal systems. *Philos. Trans. R Soc. Lond. B Biol. Sci.* **351**: 689–720.

Norton, S.F. & Brainerd, E.L. 1993. Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**: 11–29.

Nosil, P. 2007. Divergent host-plant adaptation and reproductive isolation between ecotypes of *Timema cristinae* walking-sticks. *Am. Nat.* **169**: 151–162.

Nosil, P. & Crespi, B.J. 2006. Experimental evidence that predation promotes divergence in adaptive radiation. *Proc. Natl. Acad. Sci. USA* **103**: 9090–9095.

Parnell, N.F., Hulsey, C.D. & Streelman, J.T. 2008. Hybridization produces novelty when the mapping of form to function is many to one. *BMC Evol. Biol.* **8**: 122.

Pfaender, J., Schliewen, U.K. & Herder, F. 2010. Phenotypic traits meet patterns of resource use in the radiation of ''sharpfin'' sailfin silverside fish in Lake Matano. *Evol. Ecol.* **24**: 957–974.

Rasband, W.S. 1997. *Image J*. U. S. National Institutes of Health, Bethesda, MD, USA.

von Rintelen, K., Glaubrecht, M., Schubart, C.D., Wessel, A. & von Rintelen, T. 2010. Adaptive radiation and ecological diversification of Sulawesi'S Ancient lake shrimps. *Evolution* **64**: 3287–3299.

von Rintelen, T., von Rintelen, K., Glaubrecht, M., Schubart, C.D. & Herder, F. 2011. Aquatic biodiversity hotspots in Wallacea – the species flocks in the ancient lakes of Sulawesi, Indonesia. In: *Biotic Evolution and Environmental Change in Southeast Asia* (D.J. Gower, K.G. Johnson, J.E. Richardson, B.R. Rosen, L. Rüber & S.T. Williams, eds). Cambridge University Press, Cambridge (in press).

Rohlf, J. 2003. *TpsDig, Digitize Landmarks And Outlines, Version 1.39*. Department of Ecology and Evolution, Sate University of New York at Stony Brook, Stony Brook.

Roy, D., Paterson, G., Hamilton, P.B., Heath, D.D. & Haffner, G.D. 2007. Resource-based adaptive divergence in the freshwater fish *Telmatherina* from Lake Matano, Indonesia. *Mol. Ecol.* **16**: 35–48.

Rüber, L. & Adams, D.C. 2001. Evolutionary convergence of body shape and trophic morphology in cichlids from Lake Tanganyika. *J. Evol. Biol.* **14**: 325–332.

Rundle, H.D. & Nosil, P. 2005. Ecological speciation. *Ecol. Lett.* **8**: 336–352.

Salzburger, W. 2009. The interaction of sexually and naturally selected traits in the adaptive radiations of cichlid fishes. *Mol. Ecol.* **18**: 169–185.

Schliewen, U.K. & Klee, B. 2004. Reticulate sympatric speciation in Cameroonian crater lake cichlids. *Front. Zool.* **1**: 1–12.

Schluter, D. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. *Ecology* **76**: 82–90.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, New York, Oxford.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. *Science* **323**: 737–741.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of Lizards in patchy habitats. *Ecology* **51**: 408–418.

Schwarzer, J., Herder, F., Misof, B., Hadiaty, R.K. & Schliewen, U.K. 2008. Gene flow at the margin of Lake Matano's adaptive sailfin silverside radiation: Telmatherinidae of River Petea in Sulawesi. *Hydrobiologia* **615**: 201–213.

Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* **68**: 113–151.

Sheets, H.D. 2002. *IMP-Integrated Morphometrics Package*. Department of Physics, Canisius College, Buffalo, New York.

Sibbing, F.A. & Nagelkerke, L.A.J. 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Rev. Fish. Biol. Fish.* **10**: 393–437.

Svanbäck, R. & Eklöv, P. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia* **131**: 61–70.

Vamosi, S.M. 2002. Predation sharpens the adaptive peaks: survival trade-offs in sympatric sticklebacks. *Ann. Zool. Fenn.* **39**: 237–248.

Van De Pol, M., Brouwer, L., Ens, B.J., Oosterbeek, K. & Tinbergen, J.M. 2010. Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution* **64**: 836–851.

Wainwright, P.C. 1995. Functional morphology as a tool in ecological research. In: *Ecological Morphology* (P.C. Wainwright & S.M. Reilly, eds), pp. 42–59. The University of Chicago Press, Chicago.

Wainwright, P.C. 1999. Ecomorphology of prey capture in fishes. In: *Advances in Ichthyological Research* (E. Saksena, ed.), pp. 375–387. Jiwaji University Press, Gwalior, India.

Wainwright, P.C. & Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. *Environ. Biol. Fish.* **44**: 97–113.

Wainwright, P.C., Ferry-Graham, L.A., Waltzek, T.B., Carroll, A.M., Hulsey, C.D. & Grubich, J.R. 2001. Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**: 3039–3051.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., Grubich, J.R. & Hoey, A.S. 2004. A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc.* **82**: 1–25.

Walker, J.A. 1997. Ecological morphology of lacustrine three-spine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. *Biol. J. Linn. Soc.* **61**: 3–50.

Walter, R.P., Haffner, G.D. & Heath, D.D. 2009a. Dispersal and population genetic structure of *Telmatherina antoniae*, an endemic freshwater Sailfin silverside from Sulawesi, Indonesia. *J. Evol. Biol.* **22**: 314–323.

Walter, R.P., Haffner, G.D. & Heath, D.D. 2009b. No barriers to gene flow among sympatric polychromatic 'small' *Telmatherina antoniae* from Lake Matano, Indonesia. *J. Fish Biol.* **74**: 1804–1815.

Webb, P.W. 1978. Fast-start performance and body form in seven species of teleost fish. *J. Exp. Biol.* **74**: 211–226.

Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**: 107–120.

Weimerskirch, H., Le, C.M., Ropert-Coudert, Y., Kato, A. & Marsac, F. 2006. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. *Oecologia* **146**: 681–691.

Westneat, M.W. 1990. Feeding mechanics of teleost fishes (Labridae, Perciformes) – a test of 4-bar linkage models. *J. Morphol.* **205**: 269–295.

Westneat, M.W. 1994. Transmission of force and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorphology* **114**: 103–118.

Westneat, M.W. 1995. Feeding, function, and phylogeny – analysis of historical biomechanics in labrid fishes using comparative methods. *Syst. Biol.* **44**: 361–383.

Westneat, M.W. 2004. Evolution of levers and linkages in the feeding mechanisms of fishes. *Integr. Comp. Biol.* **44**: 378–389.

Westneat, M.W. 2006. Skull biomechanics and suction feeding in fishes. *Fish Biomech.* **23**: 29–75.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D. & Fink, W.L. 2004. *Geometric Morphometrics for Biologists*. Academic Press, London.

Appendix

Results of the canonical analysis of variance (Table A1) are similar to the findings of the PCA and one-way ANOVA (Table 1; Fig. 4); however, a separate pairwise comparison within the morphospecies is necessary to identify intersexual variation in body shape (Tables A1 and A2).

Table A1 Canonical analysis of variance for body shape and head shape of roundfin sailfin silversides morphospecies. (a) Wilks'lambda test (significant results in boldface); (b) *Post hoc* test results between morphospecies (Hotelling's pairwise test); (c) *Post hoc* test results between sexes (Hotelling's pairwise test).

(a) Trait	d.f.1	d.f.2	*F*	*P*
Morphospecies				
Body	48	176	14.86	**< 0.001**
Head	40	178	28.88	**< 0.001**
Sexes				
Body	130	413.9	6.627	**< 0.001**
Head	100	424.2	9.366	**< 0.001**

(b)	*T.p.*	*T.a.*l.
*T.a.*s.		
Body	**< 0.001**	**< 0.001**
Head	**< 0.001**	**< 0.001**
*T.a.*l.		
Body	**< 0.001**	
Head	**< 0.001**	

(c)	*T.p.*		*T.a.*l.		*T.a.*s.
Trait	♀	♂	♀	♂	♀
*T.a.*s.					
♂					
Body	**< 0.05**	**< 0.05**	**< 0.05**	**< 0.05**	0.126
Head	**< 0.05**	**< 0.001**	**< 0.001**	**< 0.001**	0.164
♀					
Body	0.064	**< 0.05**	**< 0.05**	**< 0.05**	
Head	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	
*T.a.*l.					
♂					
Body	**< 0.05**	**< 0.05**	0.107		
Head	**< 0.05**	**< 0.05**	0.088		
♀					
Body	**< 0.05**	**< 0.05**			
Head	**< 0.05**	**< 0.001**			
T.p.					
♂					
Body	0.489				
Head	**< 0.05**				

T.p., T. prognatha; *T.a.*s., *T. antoniae* 'small'; *T.a.*l., *T. antoniae* 'large'.

Table A2 Intersexual pairwise comparison of body shape variation. Wilks' lambda test and Hotelling's pairwise *post hoc* test results between sexes (significant results in boldface).

	Trait	d.f.1	d.f.2	*F*	*P*	Hotelling's test
*T.a.*s.	Body	26	10	5.647	**< 0.05**	**< 0.001**
*T.a.*l.	Body	30	8	3.535	**< 0.05**	**< 0.001**
T.p.	Body	27	10	2.648	0.344	

T.p., T. prognatha; *T.a.*s., *T. antoniae* 'small'; *T.a.*l., *T. antoniae* 'large'.

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