Functional morphology of prey capture in stream-dwelling sailfin silversides (Telmatherinidae) based on high-speed video recordings

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Abstract
Understanding how ecology shapes the evolution of morphological traits is a major goal in organismal biology. By quantifying force of motion, hypotheses on the function of fundamental tasks of animals like feeding can be tested. Ray-finned fishes use various feeding strategies, classified into three main feeding modes: suction, ram and manipulation. While manipulation feeders are usually distinct in morphology and feeding behavior, differentiation between suction and ram feeders is often fine-scaled and transitional. Previous studies have identified different feeding modes and biomechanical adaptations on interspecific and intersexual levels in lake-dwelling sailfin silversides, species of a Sulawesi freshwater radiation. Functional feeding morphology of stream-dwelling species remained in contrast unstudied. We hypothesized that different requirements of riverine habitats favor the evolution of alternative functional adaptations in stream-dwelling sailfin silversides. To test this hypothesis, we investigated feeding of two phenotypically distinct riverine species, Telmatherina bonti and Marosatherina ladigesi, and their sexes, by high-speed videos and biomechanical models. The kinematic approaches identify T. bonti as ram feeder and M. ladigesi as suction feeder. Surprisingly, the biomechanical models of the jaw apparatus provide contradicting results: only one out of three studied parameters varies between both species. Contrarily to lake-dwelling Telmatherina, sexes of both species do not differ in feeding biomechanics. We conclude that T. bonti predominantly uses ram feeding while M. ladigesi primarily uses suction feeding as its main hunting strategy. Feeding biomechanics of stream-dwelling sailfin silversides are less distinct compared to lake-dwelling species, likely due to different trophic ecologies or less stable ecological conditions.

Keywords Feeding biomechanics · Feeding mode · High-speed video analysis · Force transmission · Prey capture kinematics · Sulawesi

Introduction
Understanding the connection between ecology and the evolution of morphological traits is a major goal in organismal biology (Sonnefeld et al. 2014; Wainwright & Richard 1995). The quantification of velocity, force and kinematic transmission of movements can be used to test hypotheses on the function of fundamental biological tasks of animals such as feeding, locomotion and respiration (Cooper & Westneat 2009; Westneat 1994, 2004).

The > 30,000 species of ray-finned fishes (Actinopterygii) use a great variety of feeding strategies to capture food items (Camp et al. 2015; Day et al. 2015). Feeding modes can be assigned to three major categories: suction feeding, ram feeding and manipulation (Ferry-Graham et al. 2001a,b; Norton & Brainerd 1993; Porter & Motta 2004). Suction feeding generates a pressure gradient that sucks food items into the mouth by rapid expansion of the oral cavity (Camp et al. 2015; Day et al. 2015; Porter & Motta 2004), and is the most common feeding mode among ray-finned fishes (Camp et al. 2015; Higham et al. 2006b; Westneat & Olsen 2015). This feeding mode is supported by a small maximum gape width, a high jaw opening and a low jaw closing velocity (Day et al. 2015; Higham et al. 2017). It enables efficient feeding on mostly small, elusive or non-elusive prey like
zooplankton, shrimps or insects (Ferry-Graham et al. 2001b; Sonnefeld et al. 2014). In contrast, ram feeding fishes capture their prey by overtaking them in forward locomotion (Ferry-Graham et al. 2001a, b; Norton & Brainerd 1993; Wainwright & Bellwood 2002). They are characterized by a large maximum gape width, a rather low jaw closing velocity and an intermediate transmission of force (Higham et al. 2017; Sonnefeld et al. 2014). Swarms of planktonic prey or single larger elusive organisms, like other fishes, are the typical prey of ram-feeding fishes (Porter & Motta 2004; Sonnefeld et al. 2014; Wainwright & Bellwood 2002).

Finally, manipulation is the direct application of jaws on prey by scraping or biting (Ferry-Graham et al. 2001a, b; Norton & Brainerd 1993). Manipulation feeders typically have a small gape width, and jaws that open and close at low velocity while transmitting high biting forces (Sonnefeld et al. 2014; Wainwright & Bellwood 2002; Wainwright & Richard 1995). The main prey of manipulation feeders is either hard shelled or attached to substrate like mollusks, crustaceans, algae or sponges (Sonnefeld et al. 2014; Wainwright & Bellwood 2002).

While morphology and feeding behavior of manipulation feeders is usually easily distinguishable from the other two major feeding modes because they depend on bite force, the distinction between suction and ram feeders is often more discrete and fine scaled since both feeding modes rely on speed of motion (Wainwright & Bellwood 2002; Wainwright & Richard 1995). Nevertheless, distinction between suction and ram feeding is facilitated when incorporating the extent of forward locomotion of the predator versus the acceleration of prey items through suction pressure (Wainwright & Bellwood 2002; Wainwright et al. 2001). During a specialized suction strike, the prey moves while the predator does not, contrasted by the moving predator that overtakes static prey in a pure ram strike (Norton & Brainerd 1993). However, specialized suction and ram feeding represent ends of a continuum and most fishes use a combination of both modes (Norton & Brainerd 1993; Wainwright & Bellwood 2002; Wainwright et al. 2001).

High-speed videos, i.e. videos recorded at more than 60 frames per second (fps), and biomechanical models are efficient tools for investigating the kinematics of prey capture. High-speed videos enable the precise assessment of speed and prey capture duration, and are extensively used in studies targeting the functional morphology of the feeding apparatus of fishes (e.g. Copus & Gibb 2013; Day et al. 2015; Ferry-Graham et al. 2002; Konow et al. 2013; Van Wassenbergh & De Rechter 2011). Biomechanical models, in contrast, focus on force and kinematic transmission, like those involved in opening and closing of fish jaws. Two widely used models are the simple lever system of the lower jaw and the complex four-bar linkage system of the anterior jaw (Pfaender et al. 2011; Wainwright & Richard 1995; Westneat 1990). Both models represent functional trade-offs between speed and force of jaw motion (Cooper & Westneat 2009; Wainwright & Richard 1995; Westneat 2004). These can be quantified by two kinematic ratios: the lower jaw ratio (LJR) and the maxillary kinematic transmission coefficient (MKT). High LJR and low MKT values indicate a slow but forceful motion, while small LJR and high MKT values indicate a fast but less forceful movement (Cooper & Westneat 2009; Hulsey & García de León, 2005; Hulsey & Wainwright 2002; Parnell et al. 2008; Pfaender et al. 2011; Wainwright & Richard 1995).

The Indonesian island Sulawesi harbors species flocks of sailfin silversides (Telmatherinidae) (Herder & Schliewen 2010; von Rintelen et al. 2012). These serve as a model system for investigating processes underlying adaptive divergence (Herder & Schliewen 2010; Pfaender et al. 2016; Walter et al. 2009). The study of Pfaender et al. (2011) revealed alternative feeding modes among closely related “roundfin” Telmatherina, a lineage endemic to ancient graben-lake Matano. Ranging from ram to suction feeding, the species show substantial biomechanical adaptations according to their respective feeding niche (Pfaender et al. 2011; Wasiłjew et al. 2021). So far, two sailfin silversides have been described from Sulawesi’s rivers and streams: Telmatherina bonti (Weber & Beaufort 1922) and Marosatherina ladigesi (Ahl 1936). Both have substantially different overall body shapes (Kottelat 1990; Sterba 1987; Online Resource 1), and different feeding strategies appear plausible. The fusiform body of T. bonti suggests a ram feeding mode while the deeper, laterally compressed body of M. ladigesi (Online Resource 1) rather indicates a suction feeding mode (Arbour & Lopez-Fernandez 2014, 2016). However, the biotic and abiotic factors of a riverine habitat differ thoroughly from the conditions in a lacustrine habitat (Brinsmead & Fox 2002; King et al. 2021). Theory predicts that the different requirements in comparison to a lacustrine habitat might favor the evolution of alternative functional adaptations in both stream-dwelling sailfin silversides compared to lake-dwelling roundfins (Brinsmead & Fox 2002; Collin & Fumagalli 2011; Theis et al. 2014). Thus, the aim of the present study was to evaluate whether T. bonti and M. ladigesi also use alternative feeding modes and if so, show different biomechanical adaptations compared to the lake-dwelling roundfins.

Here, we test whether the two stream-dwelling sailfin silversides T. bonti and M. ladigesi differ in functional feeding morphology using high-speed video recordings and biomechanical models of the oral jaw apparatus. While M. ladigesi is endemic to karst of south-west Sulawesi (Hadiyat 2007; Nasyrah et al. 2019), T. bonti occurs around the Malili Lakes system in Central Sulawesi (Fig. 1; Herder et al. 2006; Kottelat 1990). Molecular clock analyses estimate the split between the ancestors of both species between 12.9 and
Since *M. ladigesi* and *T. bonti* occupy similar macrohabitats, i.e., clear hillstreams to medium-sized rivers of the Sulawesi highlands (Gray 2007; Hadiaty 2007; Nasyrah et al. 2019; von Rintelen et al. 2012), similar functional adaptations with respect to feeding ecology would appear plausible. However, aquarium observations and their overall different body morphology (Kottelat 1990; Online Resource 1) imply the use of differing feeding modes.

Based on observations (Reckel 2001; Reckel et al. 2002; Reckel & Melzer 2003) and the identified differences in overall body shape (Kottelat 1990; Online Resource 1), we hypothesized that *T. bonti* predominantly use ram feeding whereas *M. ladigesi* primarily use suction feeding. In this case, we would expect both species to show specific functional adaptations towards the respective feeding mode (Day et al. 2015; Higham et al. 2017; Pfaender et al. 2011; Sonnfeld et al. 2014; Wainwright & Richard 1995). We used four estimators to quantify the feeding mechanics of both species: maximum gape width, prey capture velocity, LJR and MKT. We predicted that *T. bonti* has a large gape, intermediate prey capture velocity, low MKT and high LJR, as expected for a ram feeder (Ferry-Graham et al. 2001b; Pfaender et al. 2011; Porter & Motta 2004; Sonnfeld et al. 2014; Wainwright & Richard 1995). Likewise, we assumed that *M. ladigesi* has a smaller gape, high prey capture velocity, high MKT and low LJR, meeting the predicted patterns of a suction feeder (Ferry-Graham et al. 2001b; Higham et al. 2017; Pfaender et al. 2011; Sonnfeld et al. 2014; Wainwright & Richard 1995).
relevant traits. Therefore tested for sexual dimorphism in these ecologically and LJR (Pfaender et al. 2011; Wasiljew et al. 2021). We influence maximum gape width, prey capture velocity, MKT nick & Doebeli 2003; Ronco et al. 2019) and thus, might ing morphology can be affected by ecological factors (Bol- intersexual variation can translate into alternative diet compositions, which likely reduce competition for ecologi- cal resources (Pfaender et al. 2011; Wasiljew et al. 2021). In contrast to ornamental features, which are most likely induced by sexual selection, body size and functional feeding morphology can be affected by ecological factors (Bol- nick & Doebeli 2003; Ronco et al. 2019) and thus, might influence maximum gape width, prey capture velocity, MKT and LJR (Pfaender et al. 2011; Wasiljew et al. 2021). We therefore tested for sexual dimorphism in these ecologically relevant traits.

Materials and methods

Materials and fish keeping

Adult captive bred individuals of T. bonti and M. ladigesi were used for high-speed video analysis. Specimens of T. bonti were bred from offspring that was obtained from field research on Sulawesi (Indonesia) in 2010. Individuals of M. ladigesi were purchased at an aquarium trade center. Fishes were housed and filmed in two individual 100 and 220 L glass aquaria at a water temperature of 25 °C. Observation boxes of 2.4 L were inserted in both aquaria that contained a sheet of scaled paper on the rear cover. Fishes were fed daily ad libitum at 10:00 a.m. with living Artemia salina nauplia within the observation boxes.

High-speed video recording

Recording of high-speed videos was performed daily during feeding with a GoPro Hero7 Black at 120 and 240 frames per second (fps) at a resolution of 960p and 1440p. Two different framerates and resolutions were selected to ensure an optimum quality for distance and velocity measurements. The camera was placed at about 5 cm distance to the aquarium. The A. salina nauplia were inserted into the observation boxes in intervals of about 30 s. Prey captures of respectively 25 male and 25 female specimens of both species were recorded (total n = 100). To reduce measurement error, prey capture events were only used when they happened in an estimated distance of less than 1 cm to the scaled paper and if the specimens were fully visible in lateral view during the complete event (Fig. 2a, b; Ferry-Graham et al. 2001a).

Prey capture kinematics

Video recordings with 120 fps at a resolution of 1440 p were used for the analysis of the maximum gape width. Screenshots of the moment when maximum gape width was achieved were taken with the video editing software Wondershare Filmora Video Editor ver. 9.2.1.10. On the base of these screenshots measurements of the maximum gape width and the standard length of each specimen were performed with tpsUtil ver. 1.76 and tpsDig ver. 2.31 (Rohlf 2015). Specimens of T. bonti (mean: 51.45 mm) were signifi- cantly larger (t test, p < 0.01) than specimens of M. ladigesi (mean: 39.41 mm), following the documented size ranges of both species (Aarn et al. 1998; Kottelat 1990). Gape width was defined as the distance from the tip of the premaxilla to the tip of the dentary (Pfaender et al. 2011). To compare the measured gape width of the video recorded specimens with the maximum gape width, respectively ten male and ten female specimens of both species, which were available from collection material, were photographed with an Olympus E-330 digital camera with their mouth held open.

Video recordings at 240 fps and at a resolution 960 p were used for the analysis of the prey capture time. Time measurements for the duration of the overall prey capture event, such as for the time until the maximum gape width and complete closure was achieved (Motta & Porter 2004), were performed with Wondershare Filmora Video Editor ver. 9.2.1.10.

Feeding biomechanics

Biomechanical analyses were based on specimens of T. bonti and M. ladigesi housed at the LIB fish collection, available from earlier collections, including stream Nuha north of Lake Matano (see Herder et al. 2006).

The biomechanics of the oral jaw apparatus were ana-lyzed using the complex maxillary 4-bar linkage lever system and the simple lower jaw lever system (Fig. 3a, b). Ten male and ten female specimens of T. bonti and M. ladigesi, respectively, were X-rayed with the X-ray scanner Faxitron LX-60 to quantify both lever systems. The four physical links of the maxillary 4-bar linkage system were measured following Pfaender et al. (2011)
Fig. 2  Examples for a kinematic sequence of prey capture of a Telmatherina bonti and b Marosatherina ladigesi in 8 ms steps.

Fig. 3  X-ray images of the head of Telmatherina bonti. Biomechanical models used for the quantification of speed and force of oral jaw motion are visualized in red. a The simple lever system of the lower jaw consisting of three levers: Out-lever, Closing-in-lever and Opening-in-lever. b The complex maxillary 4-bar linkage system consisting of four links: fixed link, input link, output link and coupler link.
using the software packages tpsUtil ver. 1.76 and tpsDig ver. 2.31 (Rohlf 2015). These four links are the fixed link (defined as the distance between the contact point of the neurocranium and nasal to the coronoid process), the input link (the distance between quadrate/articular joint and maxilla/articular joint), the output link (the distance between the maxilla/articular connection and the nasal/maxilla connection) and the coupler link (measured as the length of the nasal) (Hulsey & García de León, 2005; Hulsey & Wainwright 2002; Pfaender et al. 2011; Westneat 1990). To calculate the maxillary kinematic transmission coefficient (MKT), specimens were scanned twice: once with their mouth closed and once with their mouth held open. The MKT is defined as the ratio of the maxillary output rotation to input rotation. Since the maxillary 4-bar linkage has only one degree of freedom, all angles in the system can be calculated at any point of movement if one angle is given (Hulsey & García de León, 2005; Hulsey & Wainwright 2002; Pfaender et al. 2011; Westneat 1990). The starting angle between the fixed and the input link was defined at $33^\circ$ by measuring a subsample of both species for this study. Thus, all angles of the maxillary 4-bar linkage could be calculated using the law of cosines: $\cos(\text{angle}) = (A^2 + B^2 - E^2)/(2AB)$. The input rotation of the lower jaw was determined at $26^\circ$ by subtracting the starting angle from the opening angle of the input link. The output rotation of the maxilla was calculated for every specimen using the maxillary 4-bar linkage model. The MKT of each specimen was then calculated by dividing the output rotation by the input rotation of $26^\circ$. A high MKT indicates a high motion transmission while a low MKT suggests a high force transmission (Cooper & Westneat 2009; Hulsey & García de León, 2005; Hulsey & Wainwright 2002; Parnell et al. 2008; Pfaender et al. 2011).

The simple lower jaw lever system consists of three levers: the Opening in-lever (distance from the jaw joint to the attachment of the interopercular mandibular ligament on the angular bone), the Closing in-lever (distance from the jaw joint to the attachment of the adductor mandibulae on the coronoid process of the articular bone) and the Out-lever (distance from the jaw joint to the anterior tip of the lower jaw) (Wainwright et al. 2004; Wainwright & Richard 1995; Westneat 2004). The measurements of these three links were performed correspondent to the measurements of the maxillary 4-bar linkage to calculate the lower jaw ratio (LJR). The LJR for opening was calculated by dividing the Opening in-lever by the Out-lever. Accordingly, the LJR for closing was calculated by dividing the Closing in-lever by the Out-lever. Contrary to the MKT, High LJRs indicate a forceful and slow movement while low ratios indicate a fast but weak motion of the lower jaw (Pfaender et al. 2011; Wainwright et al. 2004; Wainwright & Richard 1995; Westneat 2004).

### Statistical analyses

Bivariate linear models and a multiple linear regression were performed for the absolute measurements of maximum gape width, prey capture time and standard length. For the bivariate linear models, maximum gape width and prey capture time were paired with standard length, respectively. The resulting residuals of each bivariate linear model and the absolute values of MKT and LJR were used to perform one-way ANOVAs with Tukey’s pairwise tests in the software PAST ver. 3.22 (Hammer et al. 2001) to test for differences between species and sexes.

### Results

#### Maximum gape width

Absolute maximum gape width ranged from 4.3 mm to 7.3 mm in *T. bonti* (mean: 6.1 mm) and from 2.8 mm to 5.7 mm in *M. ladigesi* (mean: 4.2 mm). Specimens of *T. bonti* had a significantly higher absolute gape width ($p < 0.01$) than specimens of *M. ladigesi*, matching the difference in body size. Maximum gape width was linearly correlated with standard length in both species (Fig. 4a; $p < 0.01$). Relative maximum gape width was significantly higher in *T. bonti* compared to *M. ladigesi* (Fig. 5a; $p < 0.01$) and did not differ significantly between the specimens used for recording and the collection specimens used for biomechanical measurements ($p > 0.1$). Sexual dimorphism was significant in *M. ladigesi* but not in *T. bonti*. Male *M. ladigesi* were significantly larger ($p < 0.01$) and had a higher absolute but lower relative maximum gape width than females ($p < 0.05$).

#### Prey capture velocity

Absolute prey capture time ranged from 46 to 108 ms in *T. bonti* (mean: 72 ms) and from 33 ms to 108 ms in *M. ladigesi* (mean: 57 ms). *Marosatherina ladigesi* opened and closed their jaws significantly faster than *T. bonti* ($p < 0.01$). In *M. ladigesi* there was no significant difference between jaw opening and closing time whereas jaw opening in *T. bonti* was significantly faster than jaw closing (Fig. 5c; $p < 0.01$). Overall prey capture time was linearly correlated with standard length (Fig. 4b; $p < 0.01$). In relation to standard length, *M. ladigesi* had a significantly higher prey capture velocity than *T. bonti* (Fig. 5b; $p < 0.01$). Interssexual variation in absolute prey capture velocity was not detectable in either species ($p > 0.05$). In relation to standard length, male *T. bonti* showed a significantly higher relative prey capture...
velocity than females ($p < 0.05$). Contrarily, there was no significant difference between sexes of *M. ladigesi* ($p > 0.1$).

### Feeding biomechanics

The lower jaw ratio (LJR) for opening did not differ significantly between species or sexes (Fig. 5d; mean: 0.14; $p > 0.1$) while the LJR for closing was significantly lower in *T. bonti* (mean: 0.31) compared to *M. ladigesi* (Fig. 5e; mean: 0.5; $p < 0.01$). Significant intersexual differences in LJR for closing were not detectable in both species ($p > 0.1$). *Telmatherina bonti* (mean: 0.98) showed a slightly higher maxillary kinematic transmission (MKT) than *M. ladigesi* (mean: 0.85), but the difference was not significant (Fig. 5f; $p = 0.08$). Both species showed no sexual dimorphism in MKT ($p > 0.1$).

### Discussion

#### Prey capture kinematics provide indications for different feeding modes

**Interspecific differentiation in maximum gape width**

The results of the prey capture kinematics support the hypothesis that feeding modes of *T. bonti* and *M. ladigesi* differ substantially. Relative maximum gape width is significantly lower in *M. ladigesi* compared to *T. bonti*. A small gape is considered advantageous for suction feeders because it enhances the pressure gradient that sucks prey items into the mouth opening (Day et al. 2015). Thus, the low maximum gape width detected in *M. ladigesi* supports the hypothesis that this species primarily uses suction feeding to capture prey items (Day et al. 2015; Sonnefeld et al. 2014; Wainwright et al. 2007). In contrast, the high values measured in *T. bonti* rather suggest ram feeding, where a large gape is considered beneficial as it enables predators to engulf larger prey items, reduces the effect of the bow wave and increases the strike accuracy (Higham et al. 2017; Wainwright & Bellwood 2002). Likewise, the significantly higher maximum gape width of *T. bonti*, compared to *M. ladigesi*, supports the theory of predominant ram feeding in *T. bonti* (Ferry-Graham et al. 2001b; Higham et al. 2017; Sonnefeld et al. 2014). Our hypotheses are supported by the findings of Higham et al. (2017) who identified a correlation between ram speed and maximum gape width in three-spined stickleback populations. Similar findings were also documented in Neotropical cichlids by Arbour & López-Fernández (2014, 2016).

**Sexual dimorphism in maximum gape width within *M. ladigesi***

In intraspecific comparison, we found a higher relative gape width in female *M. ladigesi* compared to conspecific males, whereas this trait is not dimorphic in sexes of *T. bonti*. As the maximum gape width limits the maximum prey size a fish is able to consume (Higham et al. 2007; Wainwright & Bellwood 2002), the larger gape of female *M. ladigesi* might have an effect on their diet composition, enabling them to capture slightly larger prey items than males. Sexual niche differentiation in line with sexual dimorphism in feeding morphology has been rarely documented in fishes (McGee & Wainwright 2013). It was reported for lake-dwelling roundfin sailfin silversides, where *T. antoniae* males have a larger gape and feed to
a higher extent on larger prey organisms than females (Pfaender et al. 2011). Another potential explanation for the sexual dimorphism in *M. ladigesi* might be intrasexual selection, as male *M. ladigesi* tend to bite opponents as part of their competition behavior (Hadiaty 2007). Since a reduced maximum gape width is correlated with an increased bite force, a smaller mouth might be beneficial in intrasexual competition; similar patterns were reported for three-spined sticklebacks (McGee & Wainwright 2013) or blenniid fishes (Rico-Guevara & Hurme 2019). However,
without further details about the biology and ecology of *M. ladigesi*, this hypothesis remains to be tested.

**Interspecific differentiation in prey capture velocity**

The significant difference between the measured values of the prey capture velocity in *M. ladigesi* and *T. bonti* also corroborate the hypothesis of two different feeding modes. Prey capture events of *M. ladigesi* are significantly shorter compared to *T. bonti*. A particularly high opening velocity is considered beneficial for suction feeding because it increases the subambient buccal pressure and thus accelerates the water flowing into the oral cavity (Higham et al. 2006a, b, 2017; Wainwright et al. 2007), while a low prey capture velocity with the associated higher reliance on ram speed is indicative for ram feeding (Higham et al. 2017). The fast prey capture kinematics identified in *M. ladigesi* therefore support the theory of a suction feeding mode chiefly used by this species and match with the general pattern of a suction feeder (Day et al. 2015; Sonnefeld et al. 2014; Wainwright et al. 2007). In contrast, the low prey capture velocity of *T. bonti* supports the hypothesis of a ram feeding mode primarily used by this species and meets with the generally documented prey capture kinematics of ram feeding fishes (Higham et al. 2017; Sonnefeld et al. 2014).

**Intersexual variation in prey capture velocity in *T. bonti***

Prey capture velocity of male *T. bonti* is significantly higher compared to females. Velocity is likely of high adaptive value as it directly affects the efficiency to feed on elusive prey: fast moving jaws, typical for species specialized on elusive prey, result in lower prey capture times compared to fishes feeding on immobile prey (Hulsey & Wainwright 2002; Parnell et al. 2008; Wainwright & Bellwood 2002). This has been documented for example in cichlids and labrid fishes (Arbour et al. 2020; Hulsey & Wainwright 2002; Wainwright et al. 2004). Thus, the lower prey capture time of male *T. bonti* compared to females would suggest a higher proportion of elusive prey in their diet. However, since ecological data for *T. bonti* is restricted to preliminary studies (Bach & Herder, unpublished data), it remains speculative if the intersexual variation in prey capture velocity is associated with dietary differences. The same applies to the hypothesis that a faster moving oral jaw in male *T. bonti* could also serve as display for potential mates or competing males and thus be affected by sexual selection. However, in contrast to maximum gape width, there are, to the best of our knowledge, no reported cases of a positive relationship between prey capture velocity and display in fishes.

**No indications for different feeding modes based on biomechanics**

In contrast to our results of the prey capture kinematics, feeding biomechanics contradict the hypothesis that *T. bonti* and *M. ladigesi* use different feeding modes. Based on previous research (Pfaender et al. 2011), we hypothesized that *T. bonti* has a lower maxillary kinematic transmission (MKT) and higher lower jaw ratio (LJR), resulting in a slower but more powerful jaw motion compared to *M. ladigesi*. However, neither the LJR for opening nor the MKT revealed any significant inter- or intraspecific differences. The only parameter where we found significant differences was the LJR for closing. But in contrast to the raised hypothesis, *M. ladigesi* showed a higher LJR for closing than *T. bonti*, which suggests a more powerful but slower closing lower jaw (Cooper & Westneat 2009; Pfaender et al. 2011; Wainwright & Richard 1995). Based on the assumption that *M. ladigesi* mainly uses suction feeding and *T. bonti* primarily uses ram feeding, this finding is surprising: ram feeders expectedly benefit from a stronger jaw grip to grasp their prey (Sonnefeld et al. 2014; Wainwright & Bellwood 2002). However, these opposing results of the LJR for closing are in accordance with discrepancies in previous studies on cichlids and sailfin silversides (Arbour et al. 2020; Arbour & López-Fernández 2016; Pfaender et al. 2011), which also identified a lower LJR for closing in ram feeding species compared to a higher value in suction feeding species. Thus, the LJR for closing might have also been affected by other parameters than feeding mode, which were not assessable with the present study.

**Different trophic ecologies might explain the opposing biomechanics**

A possible explanation for our supposedly contradicting results of the prey capture kinematics and the feeding biomechanics could lie in the trophic ecology of the focal species. Fishes feeding on elusive prey are expectedly characterized by a high MKT and low LJR, whereas fishes feeding on immobile prey usually show opposite values (Alfaro et al. 2005; Hulsey & Wainwright 2002; Parnell et al. 2008; Wainwright & Richard 1995). The surprisingly high MKT and low LJR for closing in *T. bonti* could therefore indicate a higher proportion of elusive prey in their diet compared to *M. ladigesi*. Although quantitative analyses of trophic ecology are lacking for both species, there are documented observations and preliminary data which support this theory (Andriani 2000; Bach & Herder, unpublished data; Nasyrah et al. 2019, 2020; Reckel 2001; Reckel et al. 2002; Reckel & Melzer 2003). For instance, preliminary ecological data suggests that *T. bonti* mainly feed on aquatic insects, crustaceans and small fishes (Bach & Herder, unpublished data).
which usually show very strong escape responses (Hulsey & García de León, 2005; Hulsey & Wainwright 2002). Thus, T. bonti would benefit from a combination of a high MKT, low LJR and fast moving jaws (Alfaro et al. 2005; Arbour et al. 2020; Hulsey & Wainwright 2002; Parnell et al. 2008; Wainwright & Richard 1995). Contrarily, Reckel et al. (2002) and other authors (Andriani 2000; Nasyrah et al. 2019, 2020; Sterba 1987) reported that M. ladigesi predominantly feeds on terrestrial insects accompanied by aquatic insects and zooplankton. These prey categories generally lack strong escape responses (Pfaender et al. 2011), meaning that a high MKT, low LJR and fast moving jaws would not be advantageous for M. ladigesi. Taken together, potential differences in diet composition might provide a possible explanation for the lacking biomechanical indications for different feeding modes. However, this assumption is tentative as long as no quantitative analysis of trophic ecology has been performed on both studied species.

### Less pronounced biomechanical adaptations could be due to contrasting habitats

The limited biomechanical differentiation identified in the present study is in contrast to the substantial biomechanical adaptations to alternative feeding profiles revealed in roundfin Telmatherina (Pfaender et al. 2011), with significant inter- and intraspecific differences in MKT and LJR between the suction feeding T. antoniae and the ram feeding T. prog-natha (Online Resource 2; see also Fig. 7 in Pfaender et al. (2011) for detailed kinematic and biomechanical results). This discrepancy in biomechanics between lacustrine and riverine sailfins silversides might be explained by the contrasting conditions of stream and lake habitats (Brinsmead & Fox 2002; King et al. 2021). Besides of the continuous flow and close integration with terrestrial ecosystems, stream environments are more variable, less isolated and affected by a higher frequency of catastrophic events compared to the generally more stable lake environments (Brinsmead & Fox 2002; King et al. 2021; McLaughlin & Grant 1994). The less pronounced biomechanical adaptations of T. bonti and M. ladigesi with respect to feeding mode might therefore be the result of less stable environmental conditions.

### Conclusions

In summary, prey capture kinematics suggest that T. bonti is predominantly a ram feeder, whereas M. ladigesi is primarily a suction feeder. Sexual niche partitioning provides a possible explanation for the identified sexual dimorphism in T. bonti and M. ladigesi. Sexual selection might also affect the intersexual variation in maximum gape width but appears less likely for the differentiation in prey capture velocity. The results of the biomechanical analyses contradict the prey capture kinematics as well as previous findings detected in the related roundfin radiation. In contrast to the lacustrine sailfin silversides, T. bonti and M. ladigesi do not show substantial biomechanical differences according to their respective feeding mode. We conclude that this lack of differentiation might be explainable by the more variable conditions of a flowing habitat and by different diet compositions of both species. However, it has to be kept in mind that ecological data for T. bonti and M. ladigesi is based on limited sample sizes and raw observations. It therefore has to be corroborated by future research and additional ecological data on both investigated species. Investigating additional biomechanical systems and parameters used to quantify force and kinematic transmission in the jaw of fishes, such as the opercular linkage, hyoid link-age, maximum jaw protrusion and the suction index (Anker 1974; Hulsey et al. 2005; Muller 1987; Wainwright et al. 2007; Westneat 1990) would be interesting to critically test the limited biomechanical differentiation identified in the present study.

### Supplementary Information
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### Author contributions
BDW: performed the high-speed video recordings and collected the data. FH, JP and BDW: designed the study, BDW and JP: analysed the data. BW: aided morphological analyses. BDW: and FH: wrote the manuscript, with contributions from all other authors. All authors gave final approval for publication.

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### Data availability statement
The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

### Declarations

#### Conflict of interest
The authors have no financial interest to declare. Benjamin Wipfler is a member of the editorial board of Zoomorphol-ogy.

#### Ethical approval
No approval of research ethics committees was required to accomplish the goals of this study because no experiments on living animals were conducted. Living fishes were only filmed during the regular daily feeding procedure.
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