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RESEARCH ARTICLE

Sexual dimorphism in the feeding mechanism of threespine stickleback

Matthew D. McGee* and Peter C. Wainwright
Department of Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA
*Author for correspondence (mcgee.matthew@gmail.com)

SUMMARY

Sexual dimorphism is common in nature and has the potential to increase intraspecific variation in performance and patterns of resource use. We sought to determine whether anadromous threespine stickleback, *Gasterosteus aculeatus*, exhibit sexual dimorphism in feeding kinematics. We filmed four males and four females consuming live prey in a total of 51 sequences filmed at 500 Hz, then tested for differences in cranial kinematics using a combination of principal component analysis and linear mixed models. We document, for the first time in fishes, divergence between males and females in both the timing of key movements and the magnitude of excursions reached by the hyoid, jaws and neurocranium during prey capture. Some of the largest differences are in jaw protrusion, with males exhibiting faster time to peak jaw protrusion but females exhibiting greater maximum jaw protrusion. Measurements of morphological jaw protrusion on cleared and stained specimens significantly predict jaw protrusion in kinematics. This morphological divergence could reflect ecological divergence between the sexes, or the demands of nest building and territory defense compromising male feeding performance. Remarkably, the morphological jaw protrusion divergence in anadromous males and females is similar to jaw protrusion divergence between ecomorphs in a benthic–limnetic species pair, with limnetics exhibiting female-like patterns of protrusion and benthics exhibiting male-like patterns. These results suggest that sexual dimorphism in feeding functional morphology exists in nature and may have played an important role in the radiation of threespine stickleback.

Key words: *Gasterosteus aculeatus*, suction feeding, jaw protrusion.

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INTRODUCTION

Sexual dimorphism – phenotypic divergence between the sexes – is a common and often substantial form of intraspecific phenotypic variation. For example, the West Indies island radiations of *Anolis* lizards exhibit sexual dimorphism in size, shape and habitat preference, and sexual dimorphism substantially increases morphospace occupation within each radiation (Schoener, 1967; Butler et al., 2000). Many studies have examined sexual dimorphism in various traits, including body size, trophic morphology, locomotor ability and color (Nagamine and Knight, 1980; Hedrick and Temeles, 1989; Shine, 1989; Price and Birch, 1996; Berwaerts et al., 2006; Albert and Crampton, 2009), but the consequences of morphological sexual dimorphism for functional dimorphism have rarely been addressed, particularly in the context of sex-specific behaviors impairing performance in non-sex-specific behaviors.

Some evidence exists that sexual dimorphism occurs in traits closely linked to movement and activity performance. Adult male rainbow trout, *Oncorhynchus mykiss*, exhibit double the cardiac power output of females, in part as a consequence of an increase in heart mass (Franklin and Davie, 1992). In *Pararge* butterflies, males produce lift more effectively than females, as a result of increased wing beat frequency and stroke amplitude (Berwaerts et al., 2006). However, *Archilochus* hummingbirds show the opposite pattern, with shorter-winged males exhibiting decreased hovering ability relative to females (Chai et al., 1996).

In contrast to recent work on sexual dimorphism in locomotor kinematics, dimorphism in feeding kinematics has received little attention. However, if individuals exhibit sexual dimorphism in diet, habit or behaviors performed with the trophic apparatus, selection could favor divergence in feeding kinematics. For example, if habitat occupation differs between the sexes (*sensu* Reimchen and Nosil, 2004), selection may favor kinematic specializations on food items unique to each habitat. Conversely, behaviors such as territory defense, display or brood care may place demands on the trophic apparatus that compromise feeding performance; for example, enlargement of the buccal cavity in mouth-brooding male cardinalfishes could compromise suction-feeding ability (Barnett and Bellwood, 2005; Wainwright et al., 2007). However, despite extensive study of the kinematics of prey capture (Wainwright et al., 2007; Higham, 2007) and divergence in diet and feeding morphology between the sexes (Vincent et al., 2004; Barnett and Bellwood, 2005; Barnett et al., 2006; Hoey et al., 2012), there appear to be no examples of sexual dimorphism in feeding kinematics.

The threespine stickleback, *Gasterosteus aculeatus*, offers an excellent system for examining dimorphic feeding kinematics. Stickleback are known to exhibit sexual dimorphism in body shape and trophic morphology (Caldecutt and Adams, 1998; Kitano et al., 2007; Aguirre et al., 2008; Aguirre and Akinpelu, 2010; Leinonen et al., 2011). Additionally, males exhibit sex-specific behaviors involving the trophic apparatus (Stanley and Wootton, 1986). During the breeding season, male threespine stickleback construct nests from benthic debris, which they collect with the oral jaws. Once the nest is complete, male stickleback defend their territory from other males and egg predators *via* bites delivered with the oral jaws. Therefore, males use their feeding apparatus not only for prey capture and processing but also for parental care and male–male competition. However, stickleback females exhibit none of these behaviors and use the trophic apparatus primarily in feeding and respiration. The multiple competing demands on the trophic apparatus of male stickleback may alter the kinematics of prey capture and any underlying morphological traits relative to females.

In this study, we sought to determine whether male and female threespine stickleback exhibit divergent prey-capture motions of the oral jaws, neurocranium and hyoid. We predicted that males would exhibit kinematic patterns that were slower and/or less effective at prey capture than females, likely due to the influence of male-specific behaviors like nest building and/or territory defense. We also sought to determine whether kinematic differences between the sexes have a morphological basis and, if so, whether intersexual divergence in an ancestral population resembles interpopulation divergence in derived freshwater populations.

MATERIALS AND METHODS

Collections and filming

We collected adult anadromous threespine stickleback (*G. aculeatus*, Linnaeus 1758) from Cheney Outlet in Bodega Bay, Sonoma County, CA, USA, using unbaited minnow traps. Fish were transported to the University of California, Davis and maintained in 100 l aquaria at 16°C. Fish were fed *ad libitum* with freeze-dried chironomid larvae. A total of four fish showing red nuptial coloration and four fish showing no nuptial coloration were selected for filming; they were placed individually into 20 l aquaria, acclimated, and starved 24 h prior to filming to ensure a strong feeding response. Stickleback, like many teleost fishes, capture their prey in milliseconds (Grobecker and Pietsch, 1979), so we opted to film fish using high speed video. We used a NAC Memrecam ci digital system (Tokyo, Japan) set at 500 frames s^{-1}. Fish were filmed laterally while consuming live cladoceran prey (*Daphnia* sp.) introduced singly *via* pipette. Only sequences that appeared to be in squared lateral view, as determined by the orientation of the fish's open mouth, were processed further. We collected sequences from each fish until a minimum of eight lateral full-effort strikes were recorded. Afterwards, fish were killed with an overdose of MS-222 and placed in a solution of 95% ethanol.

Genetic determination of sex

Tissue samples from epaxial muscle posterior to the pectoral girdle and from the pectoral fins were removed from the ethanol-preserved fish. Genomic DNA was extracted from these samples, and genotypes were obtained for the *Idh* (isocitrate dehydrogenase) gene using established methods (Peichel et al., 2004). The *Idh* locus was previously shown to exhibit sex-based polymorphism in wild East Pacific stickleback populations, and *Idh* was found to co-segregate with the sex determining locus in 98.5% and 99.4% of individuals in genetic mapping populations derived from these fish (Peichel et al., 2004). Among the stickleback specimens we investigated, four *Idh* homozygotes (females) and four *Idh* heterozygotes (males) were found. Genetically determined sex always agreed with phenotypically determined sex. For example, all fish displaying red nuptial coloration (a male courtship ornament) were genotyped as *Idh* heterozygotes.

Morphological measurements

After tissue sample removal, fish were fixed in formalin, cleared, and bone-stained with Alizarin Red. We measured standard length (SL) in each fish, as well as a set of variables associated with maximum jaw protrusion and hyoid depression, which exhibited some measure of divergence in our kinematic analysis. Standard length was measured using calipers, while jaw protrusion and hyoid variables were measured with an ocular micrometer under a dissecting microscope. We measured the distance from the anteriormost portion of the orbit to the tip of the premaxilla when the fish's mouth was closed (Motta, 1988; Barnett et al., 2006). The same distance was measured again after elevating the neurocranium and opening the mouth to elicit a posture similar to the position of the head at peak gape during prey capture. We calculated morphological jaw protrusion by subtracting the premaxilla–orbit distance with the mouth closed from the premaxilla–orbit distance with the mouth open. For hyoid depression, we measured the distance from the ventral-most portion of the orbit to the ventral tip of the hyoid bone while the fish's jaws remained closed. We then measured this same distance when the fish's neurocranium was elevated and the jaws opened, and calculated morphological hyoid depression by subtracting this distance with the mouth open from the distance between the same two landmarks with the mouth closed. To evaluate the extent of variation in jaw protrusion between populations, we also measured standard length and morphological jaw protrusion on a group of 10 male and 10 female anadromous stickleback from Jakle's Lagoon, San Juan Island, WA, USA, as well as previously collected limnetic and benthic fish from Paxton Lake, BC, Canada, including both males and females, with 29 limnetic and 28 benthic fish in total.

Digitizing sequences

Kinematic sequences were analyzed using a custom-written modification of the DLTdv3 package in MATLAB (Hedrick, 2008; Holzman et al., 2012). A total of 11 landmarks (Fig. 1) were tracked from the beginning of mouth opening until the prey item was captured and the mouth closed. These landmarks were used to calculate a series of 12 kinematic variables (Table 1) that describe maximum excursions and timings of major movements.

Maximum gape was defined as 95% of the maximum distance between two landmarks on the anteriormost points of the upper and lower jaw, respectively. We defined maximum jaw protrusion as the maximum distance between the anteriormost point of the upper jaw and a stable landmark on the skull. Maximum hyoid depression was defined in a similar manner, as the maximum distance between the ventralmost visible extent of the hyoid complex and the same stable skull landmark described above. Maximum cranial and lower jaw rotation were defined as the maximum change in the angle of either two points on the skull or two points covering the extent of the lower jaw, respectively, relative to two stable points on the body.

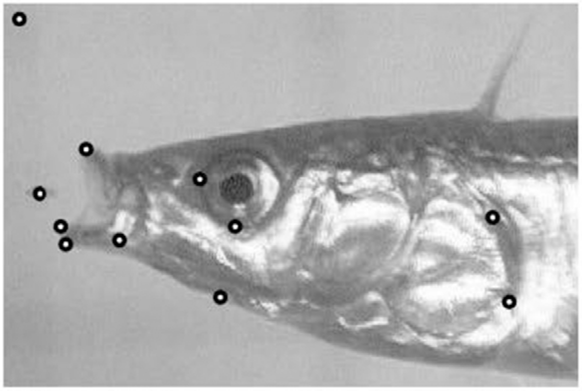

Fig. 1. The 11 landmarks used for calculating kinematic variables. Two points track gape width, two track lower jaw rotation, two track body movement and angle, two track head movement and angle, one tracks the hyoid, one tracks the prey, and a final point tracks the background.

Table 1. Principal component loadings and results from mixed-model analysis of kinematic variables

	PC1 loading	*P*-value	Female	Male
Excursions				
Gape	0.063	0.130	5.0 mm	5.5 mm
Jaw protrusion	0.481	0.001**	2.1 mm	1.5 mm
Hyoid depression	0.335	0.007**	1.7 mm	1.3 mm
Cranial rotation	0.444	0.013*	14.0 deg	9.1 deg
Lower jaw rotation	0.497	0.005**	30.8 deg	24.1 deg
Strike distance	0.456	0.021*	13.5 mm	11.8 mm
Timings				
Gape	–0.431	0.115	18 ms	10 ms
Jaw protrusion	–0.405	0.032*	30 ms	18 ms
Hyoid depression	–0.397	0.096	30 ms	22 ms
Cranial rotation	–0.359	0.747	34 ms	30 ms
Lower jaw rotation	–0.439	0.067	18 ms	10 ms
Time to prey capture	–0.414	0.028*	20 ms	10 ms

The female and male values were calculated using the fixed effect of standard length (for a 60 mm fish) and the fixed effect of sex from a mixed-effect model for each kinematic trait.

P-values for fixed effects were obtained from Markov Chain Monte Carlo (MCMC) simulation (see Materials and methods).

$^*P<0.05$, $^{**}P<0.01$.

Time to peak gape was defined as the time between 20% and 95% of maximum gape (Day et al., 2005; Higham et al., 2006). This convention avoids the confounding effects of a highly variable slow opening phase and the asymptotic approach to peak gape, allowing a measure of the speed of movement during the rapid expansion phase of suction feeding (Sanford and Wainwright, 2002). Other timings, including time to peak jaw protrusion, hyoid depression, cranial rotation and jaw rotation, were defined as the time between 20% and 95% of each variable's maximum value. Strike distance was defined as the distance between the midpoint of two landmarks indicating anteriormost points of the upper and lower jaw and the position of the prey at 20% of peak gape. Time to prey capture was defined as the time between 20% of peak gape and the time when the prey item passed between the two anteriormost points of the upper and lower jaw.

To ensure that camera motion did not affect kinematic results, the position of every landmark was referenced to a fixed background point in the sequence. To ensure that only high effort strikes were analyzed, we excluded the sequence from further analysis if it contained a maximum gape less than 75% of the maximum gape recorded from all sequences of that individual. After removal of these sequences, we analyzed a total of 51 videos, with five to eight sequences per individual.

Kinematic analysis

We performed a principal component analysis (PCA) on the correlation matrix of the six timing variables and another PCA on the correlation matrix of the six excursion variables. PCA takes correlation between variables into account, which is particularly important in kinematic studies because variables, especially those reflecting timing, are often highly correlated with each other. To determine how many principal components to interpret, we used a broken-stick model implemented in the R package 'vegan' to determine whether each principal component axis contained more variation than would be expected by chance (Jackson, 1993).

Another difficulty with kinematic analysis is that sequences obtained from the same individual cannot be treated as independent, so we used linear mixed models in our comparisons of kinematics in the two sexes. Each retained principal component axis was regressed on sex as a fixed effect and individual fish as a random effect. Body size is known to affect strike kinematics in fishes (Richard and Wainwright, 1995), so we also performed mixed-model analysis as described above, adding standard length as an additional fixed effect.

Mixed-model analysis does not allow for traditional significance calculations, so we used Markov Chain Monte Carlo (MCMC) methods to simulate the underlying distributions for fixed effects and generated *P*-values using the 'pvals.fnc()' function in the 'languageR' package; 10,000 MCMC samples were generated for each analysis. We then examined the loadings of individual kinematic variables on principal component axes that showed a significant effect of sex in our MCMC analysis. We also used a mixed-model approach similar to that described above to analyze the 12 individual kinematic variables. In addition, we calculated two speed variables, jaw-protrusion speed and prey-capture speed, by dividing the appropriate excursion variable by the relevant timing variable.

Morphological analysis

Morphological data analysis was handled using a mixed-model approach similar to that described above, with kinematic maximum jaw protrusion treated as a dependent variable, morphological jaw protrusion and standard length treated as fixed effects, and individual fish treated as a random effect. For analyses of hyoid depression morphology and its relationship to kinematics, kinematic maximum hyoid depression was treated as a dependent variable, morphological hyoid depression and standard length as fixed effects, and individual fish as a random effect. For analysis of population variation in morphological jaw protrusion, we corrected for the effects of size using a regression of morphological jaw protrusion on standard length. We then compared the residuals using a Wilcoxon rank-sum test. The same procedure was followed when analyzing the limnetic and benthic fish.

RESULTS

For both the timing and the excursion PCA, only the first principal component was found to contain more variation than expected by chance; the other components were discarded. The first principal component of excursion explained 44.7% of total variation and the first principal component of timing explained 81.3% of total variation. A plot of excursion PC1 *versus* timing PC1 shows that

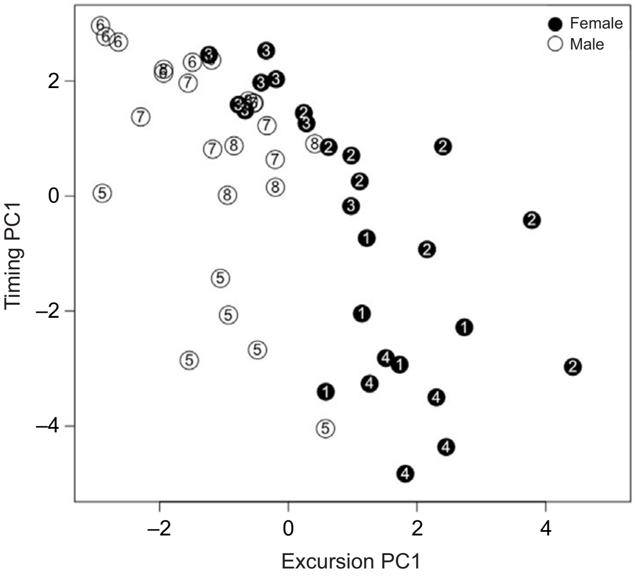

Fig. 2. The first principal component (PC) of the six excursion variables *versus* the first principal component of the six timing variables. Numbers within points indicate sequences from a given individual.

the sexes exhibit little overlap (Fig. 2). Mixed-model MCMC simulation indicated that sex was a significant predictor of timing ($P<0.0002$) and excursion ($P<0.0494$) kinematics. Standard length was not a significant predictor of strike kinematics, nor did it affect the significance of the effect of sex for either comparison. This was likely because our males and females occupied a similar and narrow size range ($P=0.49$, Wilcoxon rank-sum test, Table 2).

On the first principal component of timing, all six timing variables exhibited similarly strong loadings (Table 1), indicating that males exhibited slightly faster strikes than females. In contrast, only five of the six variables loaded strongly on the first principal component of excursion (Table 1). Individual kinematic variables associated with the first principal component showed a significant effect of sex (Table 1). Maximum jaw protrusion had both the smallest P value (0.0004) and the largest effect size of sex (Table 1). Two individual kinematic timing variables, time to peak jaw protrusion and time to prey capture, showed a significant effect of sex (Table 1), but a mixed-model analysis of jaw protrusion speed and speed of prey capture indicated no significant effect of sex ($P=0.31$ and $P=0.35$, respectively).

Morphological jaw protrusion was significantly related to kinematic jaw protrusion ($P<0.0018$) and to log-transformed standard length ($P<0.025$). However, morphological hyoid depression was not a significant predictor of kinematic hyoid depression. A Wilcoxon rank-sum test indicated that morphological jaw protrusion differed between males and females in the second anadromous (WA) population ($P<0.0002$, Table 2) and between mixed-sex benthic and limnetic populations ($P<0.0012$, Table 2).

DISCUSSION

Sexual dimorphism in trophic structures is known in several fish groups (Feduccia and Slaughter, 1974; Barnett and Bellwood, 2005; Albert and Crampton, 2009; Hoey et al., 2012) and is suspected in others, but our findings are the first to demonstrate sexual dimorphism in feeding kinematics. It is particularly interesting that one of the major differences between male and female stickleback is in jaw protrusion, a trait that has long been thought to impact various aspects of feeding ability (Schaeffer and Rosen, 1961; Motta, 1984) and was recently shown to play a major role in determining suction-feeding performance (Holzman et al., 2008; Holzman et al., 2012). Below we discuss our results and their implications for the feeding biomechanics and ecology of anadromous stickleback.

Sexual dimorphism in kinematic patterns

The sexually dimorphic first principal component of excursion was most strongly correlated with strike distance and head elevation, followed by jaw protrusion, jaw rotation and excursion of the hyoid. The distribution of strikes along this axis suggests that males strike closer to the prey item and exhibit less skull kinesis during the strike. Closer strikes risk alerting visually sensitive prey prior to strike initiation (Holzman et al., 2012). Male stickleback may initiate strikes at a closer distance to the prey in order to compensate for decreased jaw protrusion. Decreased cranial elevation and jaw rotation may also result in male stickleback being unable to expand their buccal cavity as much as female stickleback, potentially impacting the hydrodynamic force males can exert on prey and the volume of water they ingest. Kinematic timing also differs between males and females. Stickleback males usually reach their maximum excursions faster than females, with jaw protrusion occurring 11 ms earlier. However, these faster timings likely reflect the fact that it takes males less time to reach their maximum excursions because male maximum excursions are less than female maximum excursions, given that speed variables do not exhibit sexual dimorphism.

Kinematic differences do not always map closely to morphological measurements of manipulated excursions made on cleared and stained specimens, but our mixed-model approach

Table 2. Basic statistics for standard length and jaw protrusion between and among populations

	Female	Male	*P*-value
Standard length			
Anadromous (CA)	62.5±3.4	60.9±2.3	*P*=0.49
Anadromous (WA)	53.1±2.7	50.5±3.3	*P*=0.07
Jaw protrusion, size-corrected residuals			
Anadromous (CA)	0.19±0.09	–0.19±0.13	*P*<0.03*
Anadromous (WA)	0.23±0.12	–0.23±0.15	*P*<0.0002***
	Limnetic	**Benthic**	***P*-value**
Standard length	43.3±4.2	50±6.8	*P*<0.00004***
Jaw protrusion, size-corrected residuals	0.09±0.24	–0.09±0.14	*P*<0.0015**

Female, male, limnetic and benthic data are means ± s.d.
P-values were obtained from a rank-sum test. **P*<0.05; ***P*<0.01, ****P*<0.001.

indicates that morphological jaw protrusion is a significant predictor of that individual's maximum jaw protrusion during a strike. Morphological hyoid depression is not a significant predictor of kinematic maximum jaw depression, though kinematic hyoid depression is significantly different between the sexes. This is likely because hyoid depression during feeding was not perfectly replicated by the method we used when measuring hyoid depression on cleared and stained specimens, or because life-like hyoid depression is harder to achieve in a cleared and stained specimen than life-like jaw protrusion. The presence of morphological jaw protrusion as a significant predictor of kinematic jaw protrusion suggests that, in this case, sexual dimorphism in morphology is driving sexual dimorphism in feeding kinematics. Sexual dimorphism in morphological jaw protrusion exhibits strikingly similar patterns in the California and Washington populations (Table2), suggesting that this divergence is likely widespread in anadromous East Pacific stickleback populations.

Ecology of jaw protrusion

In teleosts, differences in jaw protrusion are often associated with ecological and functional divergence (Motta, 1984). Osse suggests that highly protrusible jaws should be less effective at grasping prey because the formation of the mouth into a protrusible tube reduces the length of the toothed jaw edge (Osse, 1985). In a comparison of two Lake Victoria haplochromine cichlids, one of the characteristics distinguishing a generalist species from a biting specialist was reduced jaw protrusion in the biter (Otten, 1982). More recent work also supports an association between increased jaw protrusion and the capture of evasive, mid-water prey (Waltzek and Wainwright, 2003; Holzman and Wainwright, 2009).

Reduced maximum jaw protrusion and shorter strike distance in males may decrease foraging efficiency when feeding on visually sensitive evasive prey, but if reduced maximum protrusion correlates with increased bite force on the prey, foraging success on alternative prey types may improve. Many benthic prey items are relatively non-evasive, relying instead on armor, clinging and burrowing (Benson, 1981; Heinis et al., 1994; Limén et al., 2005). Decreased excursion of the premaxilla may increase the fish's ability to manipulate and bite prey using the oral jaws.

In Enos Lake, benthic fish routinely bite prey items and drag them up in the water column for consumption (Bentzen and McPhail, 1984). Interestingly, in the same study, male limnetic stickleback fed on benthic prey items when placed in aquaria, but female limnetics avoided benthic foraging even in conditions of high prey abundance, suggesting that some stickleback populations may have the capacity for sex-specific foraging behavior. In another British Columbia lake, stickleback exhibited sexual dimorphism in foraging area, with females and males occupying open-water and littoral habitat, respectively (Reimchen and Nosil, 2004). Our study supports these previous results indicating 'male-like' benthics and 'female-like' limnetics, and suggest that some of the sexual divergence in habitat use seen in freshwater populations may have originated with the ancestral colonizing anadromous form.

Kinematics in the light of reproductive behavior

While both sexes use the trophic apparatus for feeding and indirectly in respiration, male stickleback use their jaws differently from females during the breeding season. Male stickleback use the oral jaws to grip and move benthic objects for assembly into a nest (Van Iersel, 1953). A more robust, less kinetic skull may help male stickleback grip benthic objects and assemble a nest more efficiently, even if this robustness comes at the cost of reduced jaw protrusion.

After the nest is complete, male stickleback defend their territories from rival males and egg predators. Defense is typically accomplished by biting invaders until they or the defender is evicted from the area. If correlated with increased bite force, reduced jaw protrusion may help stickleback males deliver more powerful bites and more effectively defend their territory. This situation may be analogous to several lizard systems including Caribbean *Anolis*, where male lizards have larger heads than females and exhibit a corresponding increase in bite force (Herrel et al., 2007).

Sexual dimorphism in stickleback adaptive radiation

If male stickleback enjoy an advantage in benthic foraging and female stickleback exhibit greater success on evasive limnetic prey, sexual dimorphism in this system may help facilitate rapid adaptive radiation into benthic and limnetic ecomorphs (Albert et al., 2008). The pattern of jaw protrusion divergence in limnetic and benthic fish mirrors that of ancestral anadromous males and females. Limnetic fish from Paxton Lake exhibit a 'female-like' pattern of jaw protrusion, despite the population samples including both males and females. Benthics, conversely, exhibit a 'male-like' pattern of reduced jaw protrusion in both males and females. In this case, the evolution of sexual dimorphism increases the range of ecomorphological population variation. If a sexually dimorphic anadromous population invades a new habitat that favors only one prey-capture strategy, the population should adapt more quickly because it already contains ecologically relevant variation for selection to act on. This process would likely resemble models for the evolution of sexual dimorphism (Bolnick and Doebeli, 2003), but in reverse, possibly through movement of a sex-linked allele to the autosomes or *via* a change in one or more sex-limited modifier alleles (Rice, 1984). The presence of sexual dimorphism in anadromous stickleback may help explain why stickleback evolve rapidly when anadromous populations invade new freshwater habitats (Albert et al., 2008; Bell et al., 2004).

Conclusion

Our study shows that anadromous threespine stickleback exhibit sexual dimorphism in feeding kinematics. This variation has implications for feeding performance and could be driven by sexual divergence in resource use, as well as by the demands of nest building and/or territory defense in males. Sexually dimorphic feeding kinematics are likely much more common in natural systems than has previously been reported, particularly when a species exhibits sex-specific reproductive behavior with the trophic apparatus.

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REFERENCES

Aguirre, W. E. and Akinpelu, O. (2010). Sexual dimorphism of head morphology in three-spined stickleback *Gasterosteus aculeatus. J. Fish Biol.* **77**, 802-821.

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

Albert, J. S. and Crampton, W. G. R. (2009). A new species of electric knifefish, genus *Compsaraia* (Gymnotiformes: Apteronotidae) from the Amazon River, with extreme sexual dimorphism in snout and jaw length. *Syst. Biodivers.* **7**, 81-92.

Albert, A. Y. K., Sawaya, S., Vines, T. H., Knecht, A. K., Miller, C. T., Summers, B. R., Balabhadra, S., Kingsley, D. M. and Schluter, D. (2008). The genetics of adaptive shape shift in stickleback: pleiotropy and effect size. *Evolution* **62**, 76-85.

Barnett, A. and Bellwood, D. R. (2005). Sexual dimorphism in the buccal cavity of paternal mouthbrooding cardinalfishes (Pisces: Apogonidae). *Mar. Biol.* **148**, 205-212.

Barnett, A., Bellwood, D. R. and Hoey, A. S. (2006). Trophic ecomorphology of cardinalfish. *Mar. Ecol. Prog. Ser.* **322**, 248-257.

Bell, M. A., Aguirre, W. E. and Buck, N. J. (2004). Twelve years of contemporary armor evolution in a threespine stickleback population. *Evolution* **58**, 814-824.

Benson, R. H. (1981). Form, function, and architecture of ostracode shells. *Annu. Rev. Earth Planet. Sci.* **9**, 59-80.

Bentzen, P. and McPhail, J. D. (1984). Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): specialization for alternative trophic niches in the Enos Lake species pair. *Can. J. Zool.* **62**, 2280-2286.

Berwaerts, K., Aerts, P. and Van Dyck, H. (2006). On the sex-specific mechanisms of butterfly flight: flight performance relative to flight morphology, wing kinematics, and sex in *Pararge aegeria*. *Biol. J. Linn. Soc. Lond.* **89**, 675-687.

Bolnick, D. I. and Doebeli, M. (2003). Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. *Evolution* **57**, 2433-2449.

Butler, M. A., Schoener, T. W. and Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution* **54**, 259-272.

Caldecutt, W. J. and Adams, D. C. (1998). Morphometrics of trophic osteology in the threespine stickleback, *Gasterosteus aculeatus*. *Copeia* **1998**, 827-838.

Chai, P., Harrykissoon, R. and Dudley, R. (1996). Hummingbird hovering performance in hyperoxic heliox: effects of body mass and sex. *J. Exp. Biol.* **199**, 2745-2755.

Day, S. W., Higham, T. E., Cheer, A. Y. and Wainwright, P. C. (2005). Spatial and temporal patterns of water flow generated by suction-feeding bluegill sunfish *Lepomis macrochirus* resolved by particle image velocimetry. *J. Exp. Biol.* **208**, 2661-2671.

Feduccia, A. and Slaughter, B. H. (1974). Sexual dimorphism in skates (Rajidae) and its possible role in differential niche utilization. *Evolution* **28**, 164-168.

Franklin, C. E. and Davie, P. S. (1992). Sexual maturity can double heart mass and cardiac power output in male rainbow trout. *J. Exp. Biol.* **171**, 139-148.

Grobecker, D. B. and Pietsch, T. W. (1979). High-speed cinematographic evidence for ultrafast feeding in antennariid anglerfishes. *Science* **205**, 1161-1162.

Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001.

Hedrick, A. V. and Temeles, E. J. (1989). The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends Ecol. Evol.* **4**, 136-138.

Heinis, F., Sweerts, J. P. and Loopik, E. (1994). Micro-environment of chironomid larvae in the littoral and profundal zones of Lake Maarsseveen I, The Netherlands. *Arch. Hydrobiol.* **130**, 53-67.

Herrel, A., McBrayer, L. D. and Larson, P. M. (2007). Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biol. J. Linn. Soc. Lond.* **91**, 111-119.

Higham, T. E. (2007). The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. *Integr. Comp. Biol.* **47**, 82-95.

Higham, T. E., Day, S. W. and Wainwright, P. C. (2006). The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes. *J. Exp. Biol.* **209**, 3281-3287.

Hoey, A. S., Bellwood, D. R. and Barnett, A. (2012). To feed or to breed: morphological constraints of mouthbrooding in coral reef cardinalfishes. *Proc. Biol. Sci.* **279**, 2426-2432.

Holzman, R. and Wainwright, P. C. (2009). How to surprise a copepod: strike kinematics reduce hydrodynamic disturbance and increase stealth of suction-feeding fish. *Limnol. Oceanogr.* **54**, 2201-2212.

Holzman, R., Day, S. W., Mehta, R. S. and Wainwright, P. C. (2008). Jaw protrusion enhances forces exerted on prey by suction feeding fishes. *J. R. Soc. Interface* **5**, 1445-1457.

Holzman, R., Collar, D. C., Mehta, R. S. and Wainwright, P. C. (2012). An integrative modeling approach to elucidate suction-feeding performance. *J. Exp. Biol.* **215**, 1-13.

Jackson, D. A. (1993). Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. *Ecology* **74**, 2204-2214.

Kitano, J., Mori, S. and Peichel, C. L. (2007). Sexual dimorphism in the external morphology of the threespine stickleback (*Gasterosteus aculeatus*). *Copeia* **2007**, 336-349.

Leinonen, T., Cano, J. M. and Merilä, J. (2011). Genetic basis of sexual dimorphism in the threespine stickleback *Gasterosteus aculeatus*. *Heredity* **106**, 218-227.

Limén, H., van Overdijk, C. D. A. and MacIsaac, H. J. B. (2005). Food partitioning between the amphipods *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyalella azteca* as revealed by stable isotopes. *J. Great Lakes Res.* **31**, 97-104.

Motta, P. J. (1984). Mechanics and functions of jaw protrusion in teleost fishes: a review. *Copeia* **1984**, 1-18.

Motta, P. J. (1988). Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environ. Biol. Fishes* **22**, 39-67.

Nagamine, C. M. and Knight, A. W. (1980). Development, maturation, and function of some sexually dimorphic structures of the Malaysian prawn *Macrobrachium rosenbergii* (De Man) (Decapoda, Palaemonidae). *Crustacea* **39**, 141-152.

Osse, J. W. M. (1985). Jaw protrusion, an optimization of the feeding apparatus of teleosts? *Acta Biotheor.* **34**, 219-232.

Otten, E. (1982). The jaw mechanism during growth of a generalized haplochromis species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **33**, 55-98.

Peichel, C. L., Ross, J. A., Matson, C. K., Dickson, M., Grimwood, J., Schmutz, J., Myers, R. M., Mori, S., Schluter, D. and Kingsley, D. M. (2004). The master sex-determination locus in threespine sticklebacks is on a nascent Y chromosome. *Curr. Biol.* **14**, 1416-1424.

Price, T. and Birch, G. L. (1996). Repeated evolution of sexual color dimorphism in passerine birds. *Auk* **113**, 842-848.

Reimchen, T. E. and Nosil, P. (2004). Variable predation regimes predict the evolution of sexual dimorphism in a population of threespine stickleback. *Evolution* **58**, 1274-1281.

Rice, W. R. (1984). Sex chromosomes and the evolution of sexual dimorphism. *Evolution* **38**, 735-742.

Richard, B. A. and Wainwright, P. C. (1995). Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *J. Exp. Biol.* **198**, 419-433.

Sanford, C. P. J. and Wainwright, P. C. (2002). Use of sonomicrometry demonstrates the link between prey capture kinematics and suction pressure in largemouth bass. *J. Exp. Biol.* **205**, 3445-3457.

Schaeffer, B. and Rosen, D. E. (1961). Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Am. Zool.* **1**, 187-204.

Schoener, T. W. (1967). The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* **155**, 474-477.

Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* **64**, 419-461.

Stanley, B. V. and Wootton, R. J. (1986). Effects of ration and male density on the territoriality and nest-building of male three-spined sticklebacks (*Gasterosteus aculeatus* L.). *Anim. Behav.* **34**, 527-535.

Van Iersel, J. A. A. (1953). An analysis of the parental behavior of the male three-spined stickleback (*Gasterosteus aculeatus*). *Behaviour* **Suppl. 3**, 1-159.

Vincent, S. E., Herrel, A. and Irschick, D. J. (2004). Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). *J. Zool.* **264**, 53-59.

Wainwright, P. C., Carroll, A. M., Collar, D. C., Day, S. W., Higham, T. E. and Holzman, R. A. (2007). Suction feeding mechanics, performance, and diversity in fishes. *Integr. Comp. Biol.* **47**, 96-106.

Waltzek, T. B. and Wainwright, P. C. (2003). Functional morphology of extreme jaw protrusion in Neotropical cichlids. *J. Morphol.* **257**, 96-106.