

Rapid Divergence of Predator Functional Traits Affects Prey Composition in Aquatic Communities

Dominik W. Schmid,^{1,*}† Matthew D. McGee,^{2,‡} Rebecca J. Best,^{1,§} Ole Seehausen,^{2,3} and Blake Matthews^{1,*}

1. Department of Aquatic Ecology, Center for Ecology, Evolution, and Biogeochemistry, Swiss Federal Institute of Aquatic Science and Technology (Eawag), Kastanienbaum, Switzerland; 2. Department of Fish Ecology and Evolution, Center for Ecology, Evolution, and Biogeochemistry, Eawag, Kastanienbaum, Switzerland; 3. Division of Aquatic Ecology and Macroevolution, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

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ABSTRACT: Identifying traits that underlie variation in individual performance of consumers (i.e., trait utility) can help reveal the ecological causes of population divergence and the subsequent consequences for species interactions and community structure. Here, we document a case of rapid divergence (over the past 100 generations, or ~150 years) in foraging traits and feeding efficiency between a lake and stream population pair of threespine stickleback. Building on predictions from functional trait models of fish feeding, we analyzed foraging experiments with a Bayesian path analysis and elucidated the traits explaining variation in foraging performance and the species composition of ingested prey. Despite extensive previous research on the divergence of foraging traits among populations and ecotypes of stickleback, our results provide novel experimental evidence of trait utility for jaw protrusion, gill raker length, and gill raker spacing when foraging on a natural zooplankton assemblage. Furthermore, we discuss how these traits might contribute to the differential effects of lake and stream stickleback on their prey communities, observed in both laboratory and mesocosm conditions. More generally, our results illustrate how the rapid divergence of functional foraging traits of consumers can impact the biomass, species composition, and trophic structure of prey communities.

Keywords: trait utility, jaw protrusion, foraging performance, prey preference, rapid population divergence, *Gasterosteus aculeatus*.

Introduction

Adaptive divergence of consumer populations often involves the rapid evolution of multiple foraging traits, which can underlie both individual performance of consumers and the effect of consumers on their prey communities (Matthews et al. 2011; Schoener 2011; Thompson 2013). There is growing evidence that contemporary phenotypic evolution can affect not only population dynamics (Kokko and López-Sepulcre 2007; Smallegange and Coulson 2013) and interactions among pairs of species (Becks et al. 2010; Hiltunen and Becks 2014) but also the composition and structure of species-rich communities (Harmon et al. 2009; Weber et al. 2017; terHorst et al. 2018). Because of these wide-reaching effects, a sound understanding of the traits underlying variation in individual performance—trait utility—is critical for understanding the interaction between evolving organisms and their environments (Schluter 2000; Thompson 2013).

The complex relationships among multiple traits, individual performance, and environmental context often make it difficult to establish the links between trait evolution and the trait-mediated impacts of organisms on ecosystems. Evidence for trait utility is typically obtained from phenotype by environment correlations (Schluter 2000), functional trait models (Wainwright and Richard 1995), and experimental manipulation of trait variation (Wainwright and Shaw 1999). However, even for well-studied organisms, it is often challenging to identify the heritable traits responsible for effects on individual performance and subsequently for effects on prey communities and ecosystem dynamics (Matthews et al. 2011).

* Corresponding authors; email: d.w.schmid@qmul.ac.uk, blake.matthews@eawag.ch.

† Present address: School of Biological and Chemical Sciences, Queen Mary University of London, London, United Kingdom; and Department of Evolutionary Ecology, Max Planck Institute for Evolutionary Biology, Plön, Germany.

‡ Present address: School of Biological Sciences, Monash University, Melbourne, Victoria, Australia.

§ Present address: School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, Arizona.

ORCID: Schmid, <http://orcid.org/0000-0001-8908-3882>; Best, <http://orcid.org/0000-0003-2103-064X>; Seehausen, <http://orcid.org/0000-0001-6598-1434>; Matthews, <http://orcid.org/0000-0001-9089-704X>.

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The threespine stickleback (*Gasterosteus aculeatus*) is a particularly useful starting point for integrative analyses of the community consequences of consumer trait evolution. Previous work with stickleback has studied trait utility for a limited set of traits, including body size (Schluter 1993), gill raker characteristics (Robinson 2000), and jaw kinematics (McGee et al. 2013; Higham et al. 2017) as well as the heritability (Schluter et al. 2004; Berner et al. 2010, 2011) and plasticity (Day et al. 1994; Wund et al. 2012; Laskowski and Bell 2013; Lucek et al. 2014b) of these traits in a variety of environmental contexts. A separate body of work has also investigated the ecosystem effects of closely related stickleback species (Harmon et al. 2009; Des Roches et al. 2013), lineages (Best et al. 2017), and ecotypes (Matthews et al. 2016; Brunner et al. 2017). Yet there remains a critical gap between the two approaches. Whereas organism-focused studies of trait utility work to mechanistically link morphology with the capture of specific prey items (McGee et al. 2013; Higham et al. 2017), ecosystem-focused studies test for impacts of consumer trait distributions on whole seminatural communities in mesocosm experiments (e.g., Harmon et al. 2009). A missing link between these two approaches is a solid understanding of variation, over time and space, in the community context of trait utility—more specifically, how natural variation in prey communities can influence the trait evolution of consumers and how this, in turn, may shape prey communities and feed back to affect consumer trait evolution (Holt 1995; Schoener 2011; Hendry 2016; Matthews et al. 2016).

Here, we investigate how an unusually rapid case of adaptive population divergence, occurring over the past 150 years between a lake and a stream population of threespine stickleback (Marques et al. 2016), has led to divergence in several foraging traits—traits that could mediate both individual feeding performance and community-wide effects on prey species. Trait divergence between pairs of lake and stream stickleback populations is both widespread and common, although the nature and extent of divergence varies among population pairs, likely due to the environmental contrasts between lakes and streams and the influence of both adaptive and nonadaptive processes (Raeymaekers et al. 2017; Stuart et al. 2017). Foraging trait divergence between pairs is often characterized by lake populations having more and longer gill rakers than stream populations (Kaeuffer et al. 2011; Lucek et al. 2013; Stuart et al. 2017). This might reflect adaptations to foraging in open-water habitats (where zooplankton are more prevalent), compared with feeding on larger invertebrates and insects in streams (Kaeuffer et al. 2011; Lucek et al. 2012). However, there is a lack of experimental evidence for the utility of these and other functional foraging traits, and this limits our ability to make inferences about the underlying ecological drivers

of natural selection. Gill rakers can aid planktivorous fish retain prey during selective filter feeding (Zaret 1980) and are often divergent in their structure (e.g., number, length, spacing) between limnetic and benthic ecotypes of postglacial freshwater fish (e.g., rainbow trout [Budy et al. 2005], white fish [Roesch et al. 2013], alewives [Post et al. 2008], stickleback [Bentzen and McPhail 1984; Schluter 1996]). However, in addition to gill rakers, foraging traits involved in prey pursuit and capture rather than retention can also affect foraging efficiency of planktivorous fish (Holzman et al. 2011; Higham et al. 2017). Jaw protrusion, for instance, influences the striking distance and directional suction potential of predator attacks (Wainwright et al. 2007; Holzman et al. 2008; Holzman and Wainwright 2009), while displacement advantage (the ratio of output to input displacement) constrains the opening velocity of the lower jaw (Barel 1983; Westneat 1994). Collectively, these traits might underlie not only individual performance and feeding efficiency (reducing prey biomass) but also prey selection (altering prey community composition and size structure). Furthermore, the prey species of plankton communities vary widely in their vulnerability to predation, with the more evasive species being more predatory (e.g., cyclopoid copepods) than the less evasive species (e.g., many herbivorous cladocerans). As a result, rapid evolution of stickleback foraging traits that govern feeding efficiency and preference (i.e., between copepods and cladocerans) could play a role in shaping both the species composition and the trophic structure of prey communities.

In this study, we combine detailed individual morphology with foraging experiments using a natural lacustrine zooplankton community as prey for stickleback. We chose stickleback individuals from a recently diverged pair of lake and stream ecotypes, which we raised under common laboratory conditions. Our results reveal novel evidence for the utility of jaw protrusion and gill rakers (width and length)—heritable foraging traits associated with the capture of zooplankton prey by stickleback. We further show that several foraging traits are divergent in this lake-stream pair and investigate the link between these traits and the differential foraging efficiency and diet composition of stickleback when feeding on a natural zooplankton assemblage. To establish the link from foraging traits through performance to environmental impacts, we then compare the biomass reduction of different zooplankton prey species from our laboratory foraging experiments with changes in biomass of the same species in a previous mesocosm experiment using the same lake and stream ecotypes (Matthews et al. 2016). Overall, we illustrate how diverging multivariate phenotypes interact with the natural variability in prey community composition to determine both differential performance and community-wide effects of these lake and stream ecotypes.

Material and Methods

Sample Collection

Parental threespine stickleback (*Gasterosteus aculeatus*) ecotypes were caught from the southeastern shores of Lake Constance (lake ecotype; 47°29'55"N, 9°33'25"E) and several kilometers upstream at Aubach in Oberriet (stream ecotype; 47°19'38"N, 9°34'24"E) in both 2013 and 2014 (fig. 1A). From these parents we bred cohorts of lake (2013: three families; 2014: 30 families) and stream (2013: five families; 2014: four families) fish. All juveniles were reared on *Artemia* and zooplankton for the first 2 months and later fed bloodworms (*Chironomidae* spp. larvae) daily and live zooplankton biweekly. These fish were adults (~1 and 2 years old) at the time of the foraging experiment in 2015. To compare morphology between these laboratory fish and wild stickleback, we also captured adult fish from the same populations in 2015. Fish collections, husbandry, and experimental procedures were according to fishing permits obtained from the canton of Saint Gallen and animal care permits obtained from the veterinary office of the canton of Lucerne.

Experimental Procedure and Behavioral Measures

For all foraging experiments we used a complete randomized block design of multiple trials, each with factorial combinations of age (1+; 2+) and ecotype (lake; stream), replicated 22 times ($N = 88$ fish used for foraging trials). Within each trial we used a single sex where possible and tried to minimize size differences between individuals. Prior to each trial the fish were not fed for 24 h. We initially placed the fish into 10-L tanks (20 cm × 20 cm × 30 cm) behind a partition and allowed the fish to acclimate for 5 min (see fig. A1; figs. A1, A2 are available online). During this time, a sample of live zooplankton (500 mL), collected on the same day from Lake Lucerne, was added and allowed to disperse on the other side of the partition. An additional random 500-mL sample of zooplankton was preserved for quantification of initial composition. The zooplankton composition of Lake Lucerne is comparable to that of Lake Constance and includes a combination of both herbivorous (e.g., *Daphnia longispina*, *Daphnia galeata* [mean ± SE: 0.69 ± 0.01 mm], *Bosmina longirostris* [mean ± SE: 0.42 ± 0.01 mm]) and omnivorous (e.g., *Eudiaptomus gracilis* [mean ± SE: 0.51 ± 0.01 mm], *Cyclops vicinus* [mean ± SE: 0.54 ± 0.01 mm]) taxa. In this community context, the predatory zooplankton tend to be more evasive than the herbivores because they are copepods with superior escape responses (Yen et al. 2015).

For each trial, we started all replicates simultaneously by raising the partition in each of the four tanks and allowing the fish to feed freely for 8 min. We video recorded each fish (GoPro Hero 3 Silver). Later, the playback of those

videos and the software JWatcher 1.0 (<http://www.jwatcher.ucla.edu/>) was used to quantify the total number of strikes, the time spent between strikes (i.e., search time), and the time until the first strike (i.e., latency time). The researcher analyzing these videos (D. W. Schmid) was blind to the identity (ecotype) of each fish. At the end of each trial, stickleback were sacrificed with an overdose of MS-222. Both gut contents and the estimated initial zooplankton samples were inspected to quantify prey species composition, abundance, and size via a dissecting microscope (Leica; fig. A2). Using the zooplankton counts from the initial sample and the final gut, we computed an index of prey electivity (Vanderploeg and Scavia 1979): $E^* = (W_i - n^{-1})(W_i - n^{-1})^{-1}$, where n is the number of different prey types available and $W_i = (r_i p_i^{-1})(r_i p_i^{-1})^{-1}$, with r_i and p_i indicating the number of prey type i in the gut and initial environment, respectively. The index ranges from -1 to $+1$, with more negative and more positive values reflecting lower or higher representation, respectively, of a prey species in the gut relative to its availability in the zooplankton assemblage. Last, foraging efficiency on single prey items was calculated as $FE = \text{total number of prey consumed} / \text{total number of strikes recorded}$, and foraging efficiency on biomass was calculated as $FE_{\text{Bio}} = \text{total biomass consumed} / \text{total number of strikes recorded}$.

Morphological Measures

After dissection, all sacrificed fish and our wild-caught fish (an additional 41 stream and 47 lake stickleback) were stained, as outlined in McGee et al. (2013). Next, each stickleback was photographed three times: dorsally, laterally with closed mouth, and laterally with opened mouth (fig. 1B). From these pictures we used 14 landmarks to measure four component traits related to feeding (table 1; see table A1; tables A1–A4 are available online). In addition, the left pectoral fin was removed at the base, spread, and photographed. We used another six landmarks to quantify two component traits and one functional system related to swimming (table 1; see table A1). Finally, we extracted the pharyngeal apparatus, counted all of the gill rakers on the ventral and dorsal limb of the first arch (gill raker number), and measured the length of the second-most-dorsal gill raker on the ventral limb (gill raker length; Berner et al. 2008). Last, the gap between this raker and the next-most-ventral gill raker (gill raker spacing) was measured.

All linear and area component traits or measures were first log or square root transformed, respectively. Subsequently, we either size standardized these traits to account for variation in standard length between ecotypes and ages, as described previously (McGee et al. 2013), or incorporated both standard length and raw trait values in the analysis. All functional systems, except for fineness ratio, were calculated

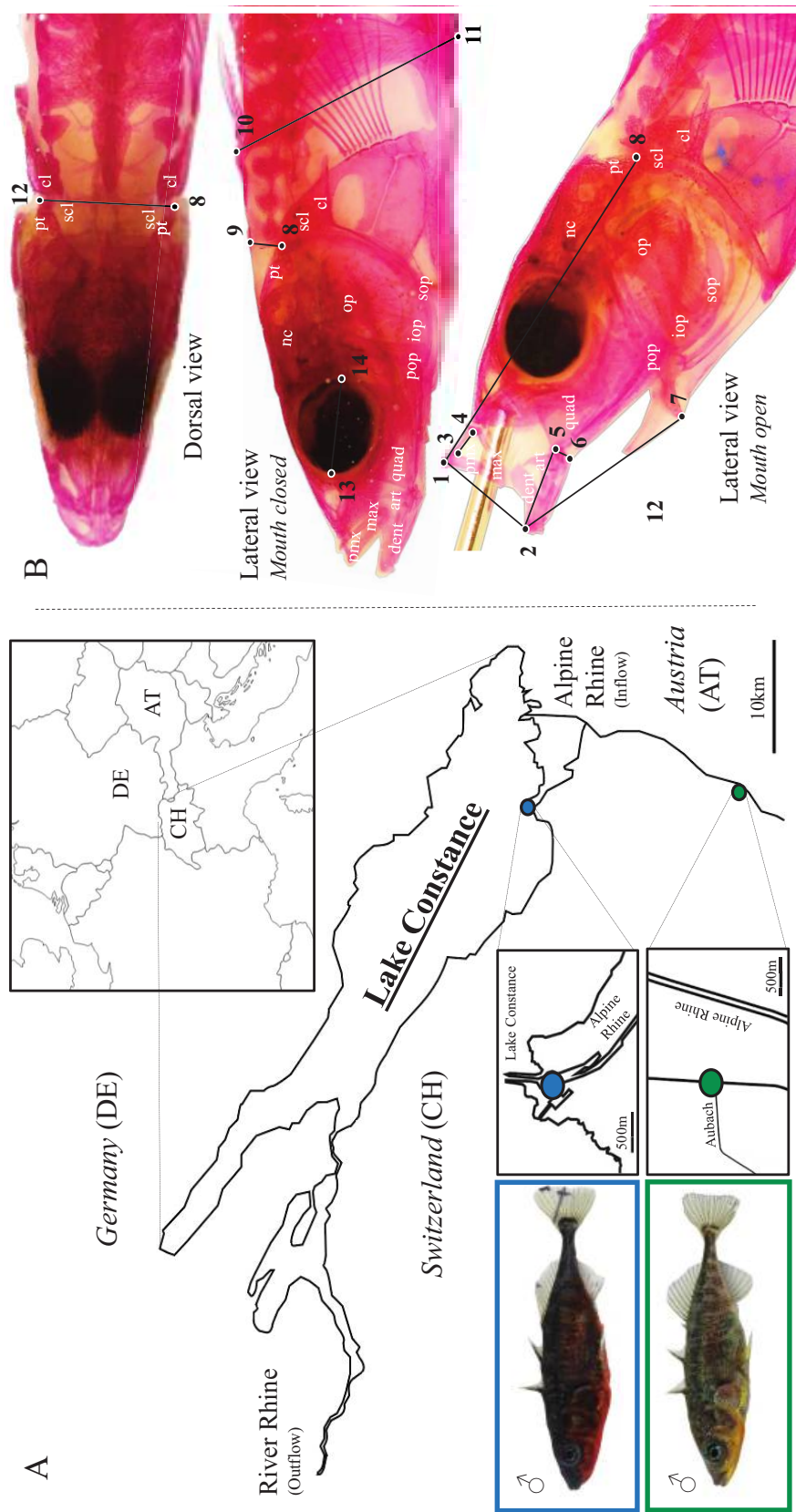


Figure 1: A, Representation of collection sites of Lake Constance river (green) and lake (blue) threespine stickleback. B, Detailed visualization of 14 of 20 landmarks (landmarks on pectoral fins are not shown) used to calculate five functional systems associated with feeding. Landmarks are as follows: 1 = anteriormost extent of premaxilla; 2 = anteriormost extent of dentary; 3 = postero-dorsal extent of premaxilla; 4 = antero-dorsal extent of maxilla; 5 = quadrate-articular jaw joint; 6 = insertion of the interpercular-articular ligament; 7 = posteriormost extent of buccal cavity, measured on the most ventral point of the hyoid; 8 = point of articulation between the supraclathrum and posttemporal; 9 = dorsalmost extent of epaxial, measured dorsal to landmark 8; 10 = anterior base of first spine; 11 = most ventral extent of pelvic girdle; 12 = point of articulation between supraclathrum and posttemporal on opposite side of fish, measured in the frontal plane; 13/14 = edges of eye socket. Bone names are as follows: pmx = premaxilla; max = maxilla; dent = dentary; art = articular; quad = quadrate; pop = preopercule; iop = interopercule; sop = subopercule; op = opercule; pt = posttemporal; scl = supraclathrum; cl = cleithrum; nc = neurocranium.

Table 1: Morphological differences in laboratory-reared threespine stickleback from Lake Constance

Functional system/ component trait	Landmarks	Lake (n = 44)			Stream (n = 44)			Ecotype			Sex			Ecotype × sex			
		♀ (n = 21)	♂ (n = 23)	♀ (n = 17)	♂ (n = 27)	df	F	P	df	F	P	df	F	P	df	F	P
Suction index	1, 2, 7, 8, 9, 12	.028 (.001)	.027 (.001)	.042 (.003)	.036 (.002)	1, 80	31.51	<.001	1, 80	3.93	.051	1, 80	2.27	.136	1, 80	2.27	.136
Gape (mm)	1, 2	3.89 (.16)	4.09 (.13)	4.18 (.17)	4.28 (.20)	1, 84	2.08	.153	1, 84	.73	.394	1, 84	.09	.771	1, 84	.09	.771
Buccal length (mm)	2, 7	7.50 (.27)	7.78 (.29)	7.94 (.36)	7.92 (.31)	1, 84	.85	.359	1, 84	.18	.669	1, 84	.24	.623	1, 84	.24	.623
Neurocranium																	
outlever (mm)	1, 8	13.14 (.51)	13.31 (.45)	14.23 (.59)	13.39 (.51)	1, 84	.89	.346	1, 84	.37	.546	1, 84	.92	.339	1, 84	.92	.339
Epaxial height (mm)	8, 9	1.64 (.07)	1.68 (.07)	2.08 (.14)	2.01 (.08)	1, 83	17.28	<.001	1, 83	.02	.879	1, 83	.38	.541	1, 83	.38	.541
Epaxial width (mm)	8, 12	4.03 (.19)	4.13 (.20)	4.58 (.23)	4.28 (.21)	1, 83	2.22	.14	1, 83	.21	.646	1, 83	.82	.367	1, 83	.82	.367
Jaw protrusion (mm)	3, 4	1.04 (.04)	1.07 (.04)	.93 (.04)	.87 (.03)	1, 84	21.18	<.001	1, 84	.14	.709	1, 84	1.42	.24	1, 84	1.42	.24
Fineness ratio	8, 10, 12, SL	5.90 (.09)	5.81 (.09)	5.59 (.08)	5.57 (.09)	1, 83	9.74	.002	1, 83	.34	.562	1, 83	.13	.722	1, 83	.13	.722
Standard																	
length (mm)	SL (not shown)	39.86 (1.84)	34.90 (1.86)	41.29 (2.12)	35.81 (1.32)	1, 84	.15	.704	1, 84	8.70	.004	1, 84	.02	.884	1, 84	.02	.884
Anterior body depth (mm)	10, 12	10.13 (.48)	9.83 (.42)	11.25 (.50)	9.91 (.40)	1, 84	1.05	.308	1, 84	3.24	.075	1, 84	1.33	.253	1, 84	1.33	.253
Body/epaxial width (mm)	8, 12	4.03 (.19)	4.13 (.20)	4.58 (.23)	4.28 (.21)	1, 83	2.22	.14	1, 83	.21	.646	1, 83	.82	.367	1, 83	.82	.367
Pectoral fin aspect ratio	13, 14, 15, 16, 17, 18 (not shown)	60.75 (4.87)	59.24 (4.76)	69.70 (5.13)	62.76 (4.46)	1, 83	1.28	.261	1, 83	.73	.395	1, 83	.31	.581	1, 83	.31	.581
Pectoral fin area (mm ²)	13, 14, 15, 16, 17, 18 (not shown)	.71 (.02)	.71 (.02)	.75 (.02)	.70 (.02)	1, 83	.02	.882	1, 83	1.56	.215	1, 83	1.31	.255	1, 83	1.31	.255
Pectoral fin height (mm)	14, 18 (not shown)	6.52 (.33)	6.40 (.34)	7.15 (.34)	6.54 (.28)	1, 83	.96	.330	1, 83	1.23	.269	1, 83	.596	.442	1, 83	.596	.442
Displacement advantage	2, 5, 6	6.43 (.24)	6.44 (.16)	5.41 (.19)	5.60 (.15)	1, 82	23.77	<.001	1, 82	.26	.613	1, 82	.27	.608	1, 82	.27	.608
Jaw opening inlever (mm)	5, 6	.49 (.02)	.51 (.02)	.64 (.03)	.60 (.02)	1, 82	22.96	<.001	1, 82	.15	.698	1, 82	1.31	.257	1, 82	1.31	.257
Jaw opening outlever (mm)	2, 5	3.11 (.12)	3.25 (.12)	3.42 (.15)	3.38 (.14)	1, 84	2.59	.111	1, 84	.18	.670	1, 84	.46	.502	1, 84	.46	.502
Eye size (mm ²)	13, 14	.48 (.01)	.50 (.01)	.51 (.02)	.47 (.01)	1, 84	.06	.809	1, 84	.53	.470	1, 84	3.59	.062	1, 84	3.59	.062
Gill raker length (mm)	19, 20 (not shown)	.37 (.03)	.39 (.03)	.40 (.04)	.38 (.03)	1, 83	.06	.811	1, 83	.01	.942	1, 83	.40	.528	1, 83	.40	.528
Gill raker width (mm)	21, 22 (not shown)	.14 (.01)	.14 (.01)	.17 (.01)	.14 (.01)	1, 83	1.54	.218	1, 83	1.21	.274	1, 83	2.75	.101	1, 83	2.75	.101
Gill raker number	Count (not shown)	16.17 (.30)	17.13 (.30)	15.33 (.36)	16.43 (.26)	df = 68	z = -.60	.549	df = 68	z = .68	.494	df = 68	z = .10	.921	df = 68	z = .10	.921

Note: Data are ecotype means (SE) in functional feeding systems and component traits; for landmark specifications, see figure 1B. All numerator degrees of freedom are equal to 1 (two levels of sex and ecotype). SL = standard length.

from standardized data. The suction index model predicts suction potential within the buccal cavity empowered by force generation through the epaxialis and hence is the major determinant of overall suction performance in fish (Carroll et al. 2004; Wainwright et al. 2007). The index is calculated as $SI = (CSA_{\text{Epax}} \times (L_{\text{in}}/L_{\text{out}})) / (\text{Gape} \times \text{Buccal Length})$, a function of the amount of force generated through the epaxial muscle (CSA_{Epax}), the moment arm of the epaxialis (L_{in}) and neurocranial outlever (L_{out}), and the projected area of the buccal cavity as a product of buccal length and gape (fig. 1B; table 1). The cross-sectional area of the epaxial muscle is the product of $CSA_{\text{Epax}} = \pi \times (E_h \times (E_w/2)) / 2$, where E_w and E_h are the epaxial height and width, respectively. Displacement advantage—one of several traits that influences jaw opening velocity (Westneat 1994)—was computed as $DA = \text{Jaw}_{\text{outlever}} / \text{Jaw}_{\text{inlever}}$, and pectoral fin aspect ratio was estimated as $A = h^2 / S_{\text{total}}$, where h and S_{total} are pectoral fin leading edge and area, respectively (table 1; Wainwright et al. 2002). Jaw protrusion, eye and gape size, and gill raker length and width were always used as size-standardized measures (fig. 1B; table 1). Fineness ratio (i.e., a measure of streamlined body shape), $f = SL / (\text{ABD} \times E_w^{0.5})$, was the quotient of non-size-standardized data, with SL as standard length, ABD as anterior body depth, and E_w as epaxial width (fig. 1B; table 1; Walker 2004). Morphological differences between wild and laboratory fish may arise from dissimilarities in development or reproductive status (McGee and Wainwright 2013) or prey environment (e.g., through phenotypic plasticity; Lucek et al. 2014b). However, differences within laboratory fish reared under identical conditions more likely have a genetic origin (Marques et al. 2016).

Ecotype Differences in Traits, Behavior, and Prey Selection

We tested for effects of ecotype and sex on size-standardized traits using linear models (LMs) and a generalized linear model (GLM) for count data (e.g., gill raker number [Poisson distribution]). This was performed for both laboratory-reared and wild-caught fish. To test for differences in latency time, search time, strike frequency, total prey consumed, and foraging efficiency, we used linear mixed effects models with ecotype, sex, and age and their two-way interactions as fixed effects and trial as a random factor. A Friedman test was run to estimate differences in prey electivity (E^*) between ecotypes within trials for each age class separately.

Full-Experiment Bayesian Regression Model

For a more comprehensive approach, we also fit a Bayesian path analysis to explain the total number of prey captured during each trial (i.e., a proxy of efficiency) based on ecotype, sex, and size; our suite of functional traits (jaw protrusion, eye area, gape, gill raker width, gill raker length, dis-

placement advantage, suction index, pectoral fin aspect ratio, and fineness ratio); a behavioral trait (number of strikes); the total number of prey available to the fish; and a random effect of experimental trial. We repeated a similar model analysis where we split the total number of prey into two groups: evasive (copepod species) and nonevasive (cladoceran species) prey. Use of a single Bayesian model including all predictor and response variables (e.g., from ecotype through traits to performance) allowed us to compare the direct effects of ecotype, sex, and size with the effects of our suite of relevant foraging traits. In addition, the model allowed us to directly include both size (standard length) and raw trait values as predictors of feeding success, which is biologically more reasonable because capture success is determined by absolute trait values (e.g., gill raker size relative to prey size) rather than by residual values from size correction. The significance of effects in the model was based on whether 95% credible intervals of effect size (e.g., ecotype, size, or trait) overlapped with zero.

All analyses were performed using R (R Core Team 2016), and the data have been deposited in the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.8rk23t4> (Schmid et al. 2019). All model residuals were checked for normality and homoscedasticity; consequently, where necessary variables were transformed to meet model assumptions. Our regression analyses were performed in a Bayesian framework using STAN (Gelman et al. 2013). STAN is a Markov chain Monte Carlo (MCMC) sampler similar in spirit to BUGS and JAGS (Bürkner 2017 and references therein). However, STAN's MCMC sampler uses Hamiltonian MCMC in conjunction with a no U-turn sampler (NUTS); therefore, it is much more computationally efficient than typical Gibbs or Metropolis-Hastings algorithms and requires many fewer sampling iterations to achieve convergence. This improved computational efficiency makes it possible to run the type of “whole experiment model” described above. To set up the analysis, all continuous variables were transformed to have a mean of 0 and a standard deviation of 0.5, with a normal prior of mean 0 and standard deviation 1 for both slope and intercept terms (Carpenter et al. 2017). All models were run for at least 10,000 MCMC iterations with four chains (equivalent to 1 million generations for a traditional MCMC sampler), and we verified that all four chains converged using the estimated potential scale reduction statistic Rhat (Carpenter et al. 2017).

Results

Functional Traits

Our (G)LM and path analysis approaches report broadly consistent effects of ecotype for several traits (fig. 2A–2E). For example, fineness ratio, displacement advantage, and

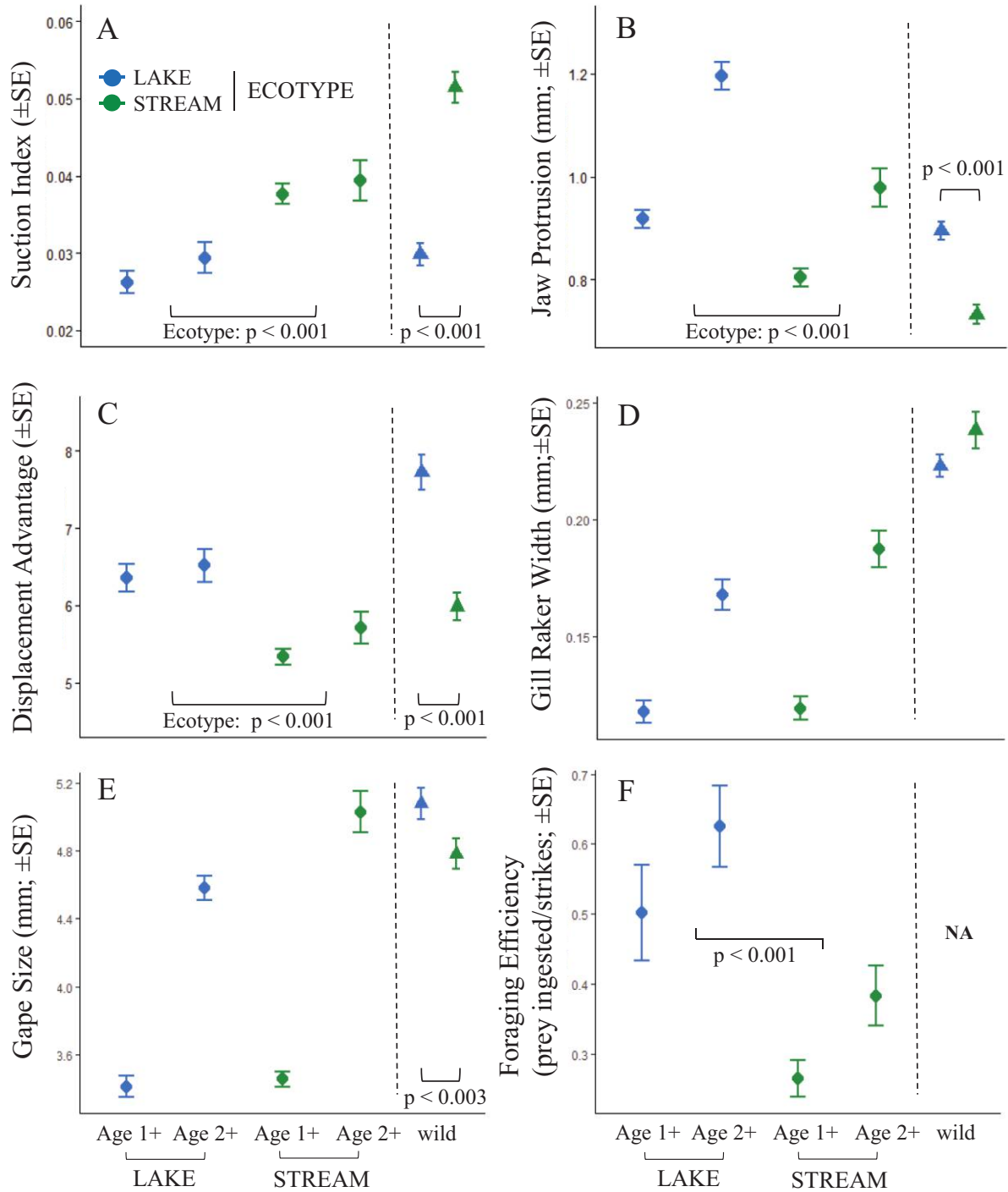


Figure 2: Ecotype differences in morphology and foraging efficiency. Average suction index (A) was higher in stream than in lake fish; lake fish consistently projected their jaw farther (B) and displayed a higher displacement advantage (C) than stream fish; gill raker spacing (D) and gape (E) did not differ significantly between laboratory reared ecotypes; and foraging efficiency on pelagic prey by lake stickleback (F) was twice as high as by stream ecotypes irrespective of age and sex ($F_{1,80} = 20.82$, $P < .001$).

jaw protrusion were larger in lake fish (fig. 3, red lines originating from ecotype), whereas suction index was higher in stream fish ([G]LMs: table 1; Bayesian model: table 2, fig. 3, blue lines originating from ecotype). Neither approach revealed differences in eye size or gill raker traits (number, width, length) between ecotypes (table 2; fig. 3). Unlike the results from the LMs, the path analysis additionally revealed that laboratory-reared stream fish had a larger gape than lake fish (table 2; fig. 2E). As expected, in the path analysis size had strong effects on all traits except our ratio-based functional indices (e.g., displacement advantage; table 2). Trait divergence in wild fish was largely consistent with that in laboratory-reared fish, but the effects of sex in wild fish were more pronounced than those in laboratory-reared fish (table A3).

Foraging Behavior and Efficiency

All foraging-related behaviors differed consistently between ecotypes (table A2). Most notably, pelagic foraging efficiency, in terms of both captured number ($F_{1,82} = 20.82, P < .001$) and biomass of prey per strike ($F_{1,81} = 5.58, P = .021$), was higher for lake fish than for stream fish regardless of age and sex (fig. 2F). On average, stream fish consumed more prey ($F_{1,61} = 4.73, P = .033$) but required more strikes to do so ($F_{1,61} = 53.2, P < .001$). Search time increased with age ($F_{1,61} = 4.07, P = .048$), and females showed a higher frequency of strikes than males ($F_{1,77} = 5.99, P = .017$).

Prey Selectivity and Trait-Mediated Community Change

Prey from the family Bosminidae were the most abundant in the zooplankton mixture, followed by Daphniidae, Diaptomidae, and Cyclopidae (fig. A2). Yet lake stickleback, regardless of their age, preferentially captured more prey of the family Cyclopidae (indicated by a significantly positive selectivity index [E^*]; age 1: $\chi^2 = 4.55, P = .033$; age 2: $\chi^2 = 18.18, P < .001$) and either avoided or were unsuccessful at capturing prey from Bosminidae, Daphniidae, and Diaptomidae (indicated by E^* ranging between -0.5 and 0.5 ; fig. A2; table A3). Stream stickleback showed no clear preference for either of the four prey types (fig. A2; table A3).

Trait Utility

Our path analysis to explain total prey capture success (fig. 3A) revealed positive effects of jaw protrusion and gill raker length and a negative effect of gill raker spacing (table 2). In contrast with our LMs, the path analysis showed that lake fish captured more prey overall than stream fish (fig. 3A, red line from ecotype to total prey) while making fewer strikes (fig. 3A, blue line from ecotype to strikes).

Whereas the latter result is consistent, the difference in overall prey consumption likely stems from differences based on sample means in comparison with estimated marginal means. Our path analysis incorporating prey evasiveness revealed that the capture success of evasive prey (i.e., copepods) increased with greater jaw protrusion and suction index and reduced gill raker spacing (fig. 3B; table A4). In this same analysis we found that capture success of nonevasive prey is positively related to gill raker length and pectoral fin aspect ratio. In addition to the indirect effects via functional and behavioral traits and consistent with the results from the prey electivity index, we found more evasive prey in the guts of lake fish and more nonevasive prey in the guts of stream fish (fig. 3B; table A4).

Discussion

Differentiation in foraging traits is common during adaptive population divergence in general (Schluter 2000; Grant and Grant 2002; Herrel et al. 2008) and during adaptive population divergence of stickleback in particular (Berner et al. 2009; Raeymaekers et al. 2017; Stuart et al. 2017). However, even for well-studied models of adaptive divergence, it remains a challenge to link divergence of specific components of multivariate phenotypes to the community- and ecosystem-wide effects of consumers. Here, we use a pair of lake and stream ecotypes of stickleback from Lake Constance with both phenotypic (Lucek et al. 2010, 2014a) and genomic (Marques et al. 2016) divergence that has evolved within only ~ 100 generations. In this specific population pair, we report new evidence for morphological divergence in several important foraging traits and in feeding efficiency on zooplankton (fig. 2). We also establish a link between individual variation in key foraging traits, such as jaw protrusion and gill raker morphology, and feeding performance on a natural prey assemblage (fig. 3). Our path analyses help elucidate which foraging traits underlie the differential success in the capture of prey species with varying degrees of evasiveness (fig. 3B). Below, we elaborate on how the observed differences in traits and foraging efficiency between ecotypes might help explain the distinct ecological effects of this particular lake and stream population (Matthews et al. 2016; Brunner et al. 2017), illustrating how rapid trait evolution of consumers can have consequences for the biomass structure and species composition of prey communities (fig. 4).

Rapid Morphological Differentiation of Lake and Stream Stickleback

Previous work on functional trait models and kinematics identified several candidate traits that could play an important role in the capture of zooplankton by stickleback (McGee

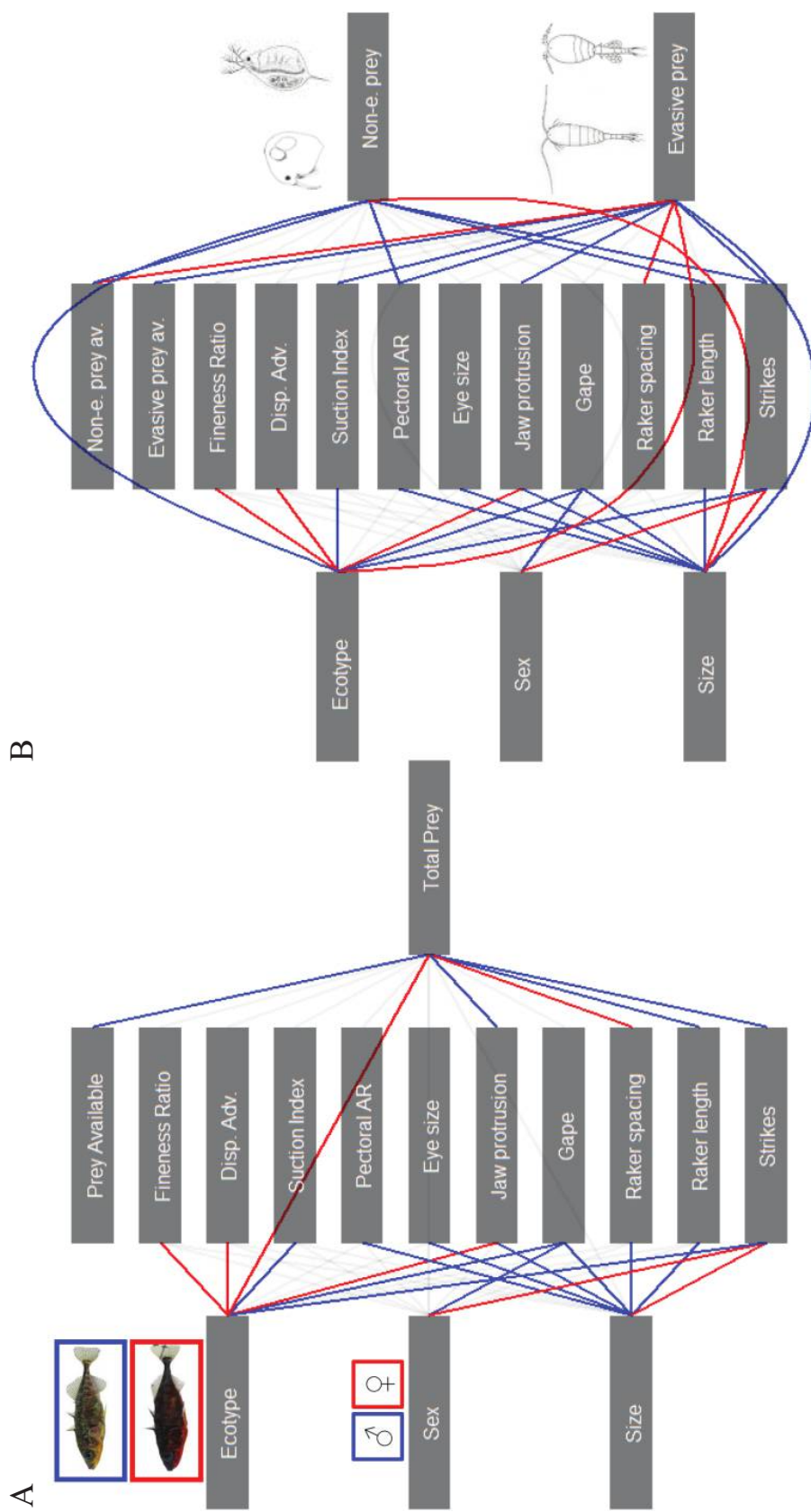


Figure 3. A, The full Bayesian model of the laboratory foraging experiments reveals that jaw protrusion and gill raker length positively affect foraging efficiency (i.e., total prey capture), whereas increased gill raker spacing was negatively associated with foraging efficiency. B, Splitting prey into two categories of evasiveness (copepods [evasive prey] and cladocerans [nonevasive prey]), we found that multiple foraging traits influence the capture of evasive prey (suction index, pectoral fin aspect area, jaw protrusion, gill raker spacing) and nonevasive prey types (raker length, pectoral fin aspect ratio [AR]). Blue and red connections reflect a significantly positive or negative effect, respectively. For example, blue arrows starting from ecotype indicate greater values of the stream ecotype relative to the lake ecotype, and blue arrows originating from sex indicate greater values for males over females.

Table 2: Assessing trait utility in relation to total prey captured via Bayesian path analysis

Response	Explanatory	Estimate	Estimate error	95% CI
Total prey consumed	Strikes	.02	0	.01 to .02
Total prey consumed	Standard length	.43	.24	-.05 to .9
Total prey consumed	Sex (M)	.01	.07	-.13 to .14
Total prey consumed	Ecotype (stream)	-.23	.09	-.4 to -.05
Total prey consumed	Gill raker length	.29	.09	.11 to .47
Total prey consumed	Gill raker width	-.32	.11	-.54 to -.11
Total prey consumed	Gape	-.12	.17	-.45 to .21
Total prey consumed	Jaw protrusion	.29	.1	.09 to .48
Total prey consumed	Eye area	-.34	.18	-.69 to .01
Total prey consumed	Pectoral fin aspect ratio	.1	.1	-.09 to .3
Total prey consumed	Suction index	.08	.08	-.07 to .23
Total prey consumed	Displacement advantage	.16	.09	-.02 to .34
Total prey consumed	Fineness ratio	-.09	.08	-.25 to .07
Total prey consumed	Total prey available	.01	0	0 to .01
Gill raker length	Standard length	.71	.09	.52 to .89
Gill raker length	Sex (M)	.15	.09	-.03 to .33
Gill raker length	Ecotype (stream)	-.01	.09	-.18 to .16
Gill raker width	Standard length	.7	.09	.52 to .87
Gill raker width	Sex (M)	.07	.09	-.1 to .24
Gill raker width	Ecotype (stream)	.12	.08	-.05 to .28
Gape	Standard length	.93	.05	.83 to 1.03
Gape	Sex (M)	.21	.05	.11 to .31
Gape	Ecotype (stream)	.1	.05	.01 to .2
Jaw protrusion	Standard length	.68	.08	.52 to .84
Jaw protrusion	Sex (M)	.06	.08	-.09 to .21
Jaw protrusion	Ecotype (stream)	-.44	.08	-.59 to -.29
Eye area	Standard length	.95	.05	.85 to 1.04
Eye area	Sex (M)	.07	.05	-.02 to .17
Eye area	Ecotype (stream)	-.04	.04	-.13 to .05
Pectoral fin aspect ratio	Standard length	.78	.08	.63 to .94
Pectoral fin aspect ratio	Sex (M)	.02	.08	-.13 to .17
Pectoral fin aspect ratio	Ecotype (stream)	-.13	.08	-.27 to .02
Suction index	Standard length	.17	.11	-.04 to .38
Suction index	Sex (M)	-.11	.1	-.32 to .09
Suction index	Ecotype (stream)	.42	.1	.22 to .61
Displacement advantage	Standard length	.17	.11	-.05 to .38
Displacement advantage	Sex (M)	.08	.11	-.13 to .29
Displacement advantage	Ecotype (stream)	-.5	.1	-.69 to -.3
Fineness ratio	Standard length	.1	.12	-.13 to .33
Fineness ratio	Sex (M)	-.01	.11	-.23 to .21
Fineness ratio	Ecotype (stream)	-.33	.11	-.55 to -.12
Strikes	Standard length	-.12	.03	-.18 to -.06
Strikes	Sex (M)	-.22	.03	-.27 to -.16
Strikes	Ecotype (stream)	.73	.03	.68 to .79

Note: Shown is a full Bayesian path analysis on total prey in relation to all foraging traits, strike frequency, and total prey availability (using trial as a random effect) as well as ecotype, sex, size, and their effects on traits. The directionality of the effect size is given by sign. Effects for which the 95% credible interval (CI) does not overlap zero are significant.

et al. 2013). As predicted from this previous work, we found that lake ecotypes have greater jaw protrusion, greater opening jaw displacement advantage, and a more streamlined body shape, whereas stream stickleback have a higher suction force. For some traits these differences were larger in wild fish: wild stream stickleback exhibited larger suction potential

than stream stickleback raised in the laboratory, and wild lake stickleback exhibited greater displacement advantage than laboratory-reared lake stickleback. It is possible that wild stream fish develop stronger epaxial muscles—the major determinant of suction force (Camp et al. 2015)—than fish reared in the laboratory on frozen chironomid larvae and

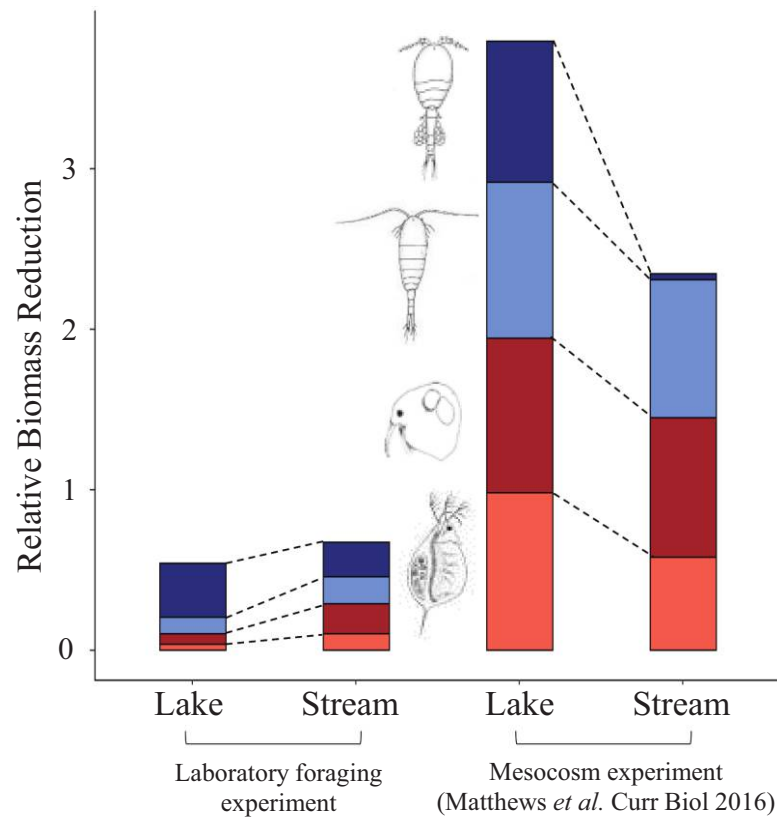


Figure 4: Biomass reduction relative to either the starting biomass in the foraging trials or the biomass in the mesocosms without stickleback (after 1 week). In both experiments, lake stickleback removed a proportionally higher amount of biomass of prey from upper trophic levels (i.e., Cyclopidae). The mesocosm experiment further highlights that in the long term lake stickleback have a higher impact on the zooplankton community than stream stickleback (Matthews et al. 2016). This may be because in the foraging trials they capture zooplankton more efficiently than stream fish, which had to strike much more often to capture a similar amount of prey in the short-term foraging experiment. Colors indicate taxa: orange = Daphniidae; red = Bosminidae; light blue = Diaptomidae; dark blue = Cyclopidae.

live zooplankton. Similarly, wild fish that regularly feed on live prey in open-water environments might develop a greater displacement advantage, in line with previous work on the morphological plasticity of body shape and jaw morphology (Lucek et al. 2014b). The wild fish were also at a more advanced reproductive stage than the laboratory-reared fish, and this could contribute to greater sexual dimorphism (McGee and Wainwright 2013).

Overall, the observed morphological differences between lake and stream ecotypes in our study (fig. 2) are broadly consistent with those from closely related teleost species occupying different habitats where distinct foraging environments drive divergence (Schluter 1996; Seehausen and Wagner 2014) and with those differences in foraging traits observed between other stickleback populations (McGee et al. 2013; Higham et al. 2017; Thompson et al. 2017). The lake-stream pair we studied has a notable lack of divergence in gill raker traits, which is uncommon for other instances of adaptive divergence between lake-stream populations (Kaeuffer et al. 2011; Stuart et al. 2017) and between ben-

thic and limnetic species (Day et al. 1994). However, the pair we chose has a particularly rapid pace of divergence, likely resulting from a combination of divergent selection between lake and stream habitats as well as from the ongoing hybridization among multiple ancient lineages of stickleback that are present in the Lake Constance watershed (Lucek et al. 2010; Marques 2016; Best et al. 2017). This region of Switzerland is a zone of secondary contact between multiple lineages of stickleback that have different evolutionary histories of adaptation to freshwater environments (Lucek et al. 2012). The main population in Lake Constance is from an eastern Baltic lineage, but there is some evidence for adaptive introgression from western lineages that might have accelerated divergence between lake and stream genotypes (Lucek et al. 2012; Marques et al. 2016).

Trait Utility in Stickleback

Jaw protrusion was positively associated with capture success of zooplankton and evasive copepods. This supports

the prediction that evolution of greater jaw protrusion is an adaptation for capturing zooplankton in general (Bellwood et al. 2015) and hints at its utility in capturing evasive zooplankton in particular (Holzman and Wainwright 2009; Yen et al. 2015). The utility of jaw protrusion is consistent with previous morphological work on a limnetic-benthic stickleback species pair (from Paxton lake), which predicted but was unable to show empirically that greater jaw protrusion would increase the capture success of evasive zooplankton species (McGee et al. 2013). This is because jaw protrusion can rapidly place the strongest portion of the flow field next to the prey item before it has a chance to initiate an escape response. This is also consistent with our expectations from our particular lake-stream study system, where we have found that evasive copepods are a common prey item found in guts of wild lake fish (Lucek et al. 2012) and that lake fish cause stronger reductions of copepods in mesocosms over the short term (e.g., over 1–3 weeks) than stream fish (Matthews et al. 2016). More generally, our foraging trials provide the first experimental evidence for trait utility of jaw protrusion in a teleost fish—an essential step toward understanding both the causes and the consequences of adaptive phenotypic evolution of fish in general (Roesch et al. 2013) and of stickleback in particular (Schluter 1993; Holzman et al. 2008; Higham et al. 2017).

Our results also provide some experimental support for the oft-assumed utility of gill raker traits for zooplankton foraging efficiency (Zaret 1980). Specifically, we demonstrate that increased gill raker spacing reduces, while increased gill raker length improves, zooplankton capture success. Indeed, previous studies have outlined how these aspects of gill raker morphology form the mechanistic basis for how gill raker traits can improve the ingestion of small particles from the water column, specifically by redirecting the flow of particles into the esophagus (Sanderson et al. 2001). However, only one previous study of *Coregonus* whitefish (Roesch et al. 2013), which did not quantify gut contents after the feeding trials, addressed gill raker utility in relation to zooplankton capture success. Occupation of a zooplanktivorous niche is a common outcome among instances of postglacial freshwater fish divergence (Berner et al. 2010; Kaeuffer et al. 2011; Stuart et al. 2017). However, our results also illustrate greater complexity of this zooplanktivorous niche and suggest that the species composition and relative abundance of the prey community might influence adaptations to zooplanktivory. For example, our study provides novel evidence for the utility of gill raker length in the capture of nonevasive zooplankton (i.e., cladocerans) and both jaw protrusion and gill raker spacing for the capture of evasive zooplankton (i.e., copepods). Notably, such effects of rakers on prey capture was observed despite a lack of divergence in raker traits between ecotypes.

While our study reveals strong links between functional traits and feeding performance, we nevertheless observed direct effects of ecotype on total prey capture (higher for lake fish) and on both evasive (higher for lake fish) and nonevasive (higher for stream fish) prey capture, suggesting that unmeasured trait differences might explain additional variance (fig. 3). For example, it is likely that quantification of foraging kinematics could help explain variation in prey capture that remains unexplained by the traits we measured. Complex kinematic traits such as ram speed (Higham et al. 2017) and strike accuracy (Kane and Higham 2015), for instance, are highly likely to contribute to prey capture success, depending on the prey community context. In our analysis, the total number of strikes was a strong predictor of successful prey capture, but without high-speed video we could not link individual strikes with specific prey items so as to directly quantify performance on different prey items. Furthermore, it is likely that the basis of prey selection by stream and lake ecotypes is not simply a matter of functional traits and could also reflect unmeasured behavioral traits. In addition to measuring kinematic traits, we suggest that future work could examine, for example, whether behavioral feedbacks (e.g., positive feedback of learning) based on successful and unsuccessful strikes could help further explain individual variation in feeding performance on natural prey assemblages (Svanback and Bolnick 2007; Melián et al. 2014).

Trait-Mediated Community-Wide Effects

Our short-term foraging trials in the laboratory suggest that divergence in foraging traits and prey preference of predators can culminate in differential effects on prey communities, but how do such results scale up to larger and more natural ecosystems? To explore this, we quantified prey-specific biomass reduction from our foraging trials and from a previously published mesocosm study, which used the same fish populations and ecotypes (Matthews et al. 2016), and then compared how selectivity and trait-mediated performance can change zooplankton community composition and trophic structure. The lake ecotype reduced the relative biomass of cyclopoid copepods, the rarest prey (fig. A2), in both the laboratory setting and the mesocosm setting (foraging trial: ~34%; mesocosm experiment: 88%), whereas the stream ecotype had weaker impacts (foraging trial: ~21%; mesocosm experiment: 4%; fig. 4). Overall, lake fish exploited the pelagic prey community more effectively than stream fish in the mesocosm (Daphniidae: 98%; Bosminidae: 97%; Diaptomidae: 97%; fig. 4; Matthews et al. 2016). Yet stream fish also strongly reduced the biomass of multiple species (Daphniidae: 57%; Bosminidae: 88%; Diaptomidae: 85%; fig. 4). The difference in exploitation of cyclopoid copepods, however, is particularly striking. Cyclopoid copepods are voracious predators in the plankton community, have strong top-down

effects on grazers of both the algal- and the microbial-based food chain (Fryer 1957; Matthews and Mazumder 2003), and, despite their evasiveness, may embody a highly profitable prey to target (Chepkwemai et al. 2013). In connection with the link between jaw protrusion/gill raker morphology and capture success of copepod prey, the foraging trials and mesocosms experiments suggest that trait differences underlying performance (and potentially preference) of a top predator can alter the trophic structure of prey communities and may help explain some of the indirect effects of stickleback on ecosystem functioning (Harmon et al. 2009; Best et al. 2017).

Our results also provide new insights about the community context of trait divergence between lake and stream stickleback. In our particular study system, phenotypic differences between lake and stream fish have evolved rapidly over the past 150 years, potentially facilitated by introgression following secondary contact between two distant lineages (Lucek et al. 2010, 2012; Marques et al. 2016). The greater jaw protrusion of the lake stickleback might help explain why their diet in the natural lake environment is dominated by evasive copepods (Lucek et al. 2012). Although we find some evidence for trait utility of gill rakers, we did not find divergence in gill raker spacing and length between our lake and stream populations, even though such divergence is common in other lake-stream pairs (Kaeuffer et al. 2011; Lucek et al. 2013; Stuart et al. 2017). This might reflect differences among systems in (i) the time available for divergence, (ii) the strength and agents of divergent selection, and/or (iii) the genomic substrate for adaptation (i.e., given the presence of hybridizing lineages; Lucek et al. 2010). We also found that the stream fish had a greater suction index, which might explain why their natural diet in streams is dominated by prey associated with substrates (e.g., rocks, sediment, macrophytes), such as chironomid larvae, isopods, and ostracods (Lucek et al. 2012). When lake fish migrate into streams to breed, their diet rapidly converges to be more similar to the stream fish diet. However, more foraging experiments in benthic environments are necessary to identify those traits that are useful when foraging on benthic prey.

The present study links divergence in foraging traits of stickleback mechanistically with both individual performance in a community context (i.e., stickleback feeding on a natural zooplankton community) and the subsequent community-wide effects (i.e., of stickleback feeding on the zooplankton community). Our work highlights how rapid trait evolution of consumers can affect prey biomass and community structure and contributes to the growing body of evidence across multiple systems and taxa indicating that trait evolution can impact community and ecosystem dynamics (e.g., Grant and Grant 2002; Hiltunen and Becks 2014; Hendry 2016). While such research highlights the interplay between evolutionary and ecological dynamics (Schluter 2000; Matthews et al. 2011; Schoener 2011; McPeck

2017), we propose that more experimental tests of trait utility in different environmental contexts are necessary to improve our understanding of the community context of trait evolution (McPeck 2017; terHorst et al. 2018) and the mechanistic basis of feedbacks between trait and community change (Lion 2018; Patel et al. 2018).

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