River canyons as sources of fish functional diversity
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Introduction

The thirty-five thousand species of fishes make up over half of all vertebrate species diversity (Helfman et al. 2009). Thirty-one thousand of these species are within the Actinopterygii, or the ray-finned fishes. Recent fossil calibrations combined with molecular approaches in the largest available phylogeny of fishes place the origins of the Actinopterygii around 370 million years ago, or around the time of the end-Devonian mass extinction event (Rabosky, Chang, Title al et Alfaro 2018). In the last 370 million years, the Actinopterygii have diversified to fill nearly every imaginable trophic and habitat niche. They dominate the temperate and tropical oceans (Wainwright and Longo 2017), have evolved antifreeze proteins to live under the ice caps of Antarctica (Beers and Jayasundara 2015), and have novel subdermal gelatinous layers to swim more effectively at the high pressures of the deep Kermadec and Mariana trenches (Gerringer et al. 2017). One mechanism that underlies much of the diversification of these species is adaptation to different or complex habitats.

The role of habitat complexity in the diversification of organisms is well-documented, as different components of a habitat promote resource partitioning, and therefore adaptive divergence, to differing resources (MacArthur and MacArthur 1961; Schoener 1974). Complex habitats promote evolution of both species as well as the morphological and functional diversity of those species. In fishes, coral reefs are sources of species diversity and of exceptional morphological diversity due to their complex topography and ecology, even increasing the rate of accumulation of ecological novelty in the large and well-studied family of mostly coral-reef associated wrasses (Alfaro et al. 2007; Price et al. 2011, 2013; though see Rabosky, Chang, Title al et Alfaro 2018).

In freshwater environments, rivers provide an unusually complex habitat with diverse hydrodynamic topology, seasonal heterogeneity, and spatial variation in primary productivity (Wissmar et al. 1981; Winemiller and Jepsen 1998; Willis et al. 2005). Rivers are important to riverine species, but are also sources of environmental connections as they link the freshwater interior with marine habitats. Diadromous fishes migrate through and into rivers, often associated with reproductive shifts in their life cycles (Myers 1949). Over long time periods, rivers can be sources of lineage diversity for lakes, islands, and other rivers, in some cases repeatedly colonizing a lake and then iteratively radiating within the novel habitat (Malinsky et al. 2018). They also provide a range of prey items for hungry fishes. Rivers are home to algae, benthic and pelagic invertebrates, a diversity of zooplankton, and other fishes. Each of these prey types has different requirements for prey capture and processing within a fish's feeding apparatus.

While numerous lineages have made the transition from marine to freshwater habitats or inhabit both in their life cycles (Figure 1), one lineage of fishes has been successful primarily by dominating freshwater fish diversity. The Cypriniformes, with 3,000 species, are fully 10% of all ray-finned fish diversity and easily the most successful radiation of non-spiny-rayed fishes. Just two of these species are truly marine, making this gigantic order essentially exclusively freshwater (Froese and Pauly 2018). In addition to their exceptional

species diversity, Cypriniformes boast 8 or more morphological and functional novelties, many associated with the feeding mechanism (Hernandez and Cohen 2019). A number of these innovations are convergent with those in the other largest radiation of ray-finned fishes (the Acanthomorpha, ~14,000 species), but in several cases the Cypriniformes evolve the functional novelty slightly differently and sometimes to different effect.

The Grand Canyon, a popular river canyon in American culture through which the Colorado River flows, is historically home to eight native species of fishes, all of which are Cypriniformes. While some are now extirpated and many are threatened by invasive species, the historic success of exclusively Cypriniformes implies that Cypriniformes are unusually capable of diversification in freshwater environments. In this paper, I will review three functional novelties of the Cypriniform feeding apparatus that may have contributed to their success in riverine environments and the Grand Canyon.

We will follow the order of these innovations with the path of prey along its travels through the feeding apparatus of a hungry Cypriniform fish. First, prey is captured either by suction feeding or by scraping and biting actions of the oral jaws, made possible by the novel kinethmoid bone. Second, the prey is sorted and filtered within the pharynx by the palatal organ. Third, the pharyngeal jaws, a second set of jaws present in most fish in the back of the pharynx, breaks down the prey. With each innovation, I will describe one or more native species of the Grand Canyon who may be reliant on this innovation for effective feeding.

Prey capture: the kinethmoid

Suction feeding is far and away the dominant mechanism of prey capture in aquatic vertebrates and is the ancestral feeding mode for ray-finned fishes (Wainwright et al. 2015). An effective suction strike leverages the viscous properties of water for rapid prey capture (Ferry-Graham et al. 2003; Wainwright and Day 2007). Rapid expansion of the skull creates a low-pressure region within the mouth that pulls in both water and prey item (Lauder 1980a,b). This process relies on rapid cranial motion, made possible by the over 100 bones of the fish skull with many independently mobile elements (Schaefer and Lauder 1996; Westneat 2006). In most species, kinematics of suction feeding are very consistent, with a sequential anterior-to-posterior wave of expansion that maximizes peak flow into the jaws around the time of maximum gape (Gillis and Lauder 1995; Day et al. 2005; Higham et al. 2006; Bishop et al. 2008; Olsen et al. 2019).

One particularly crucial component of the mobile apparatus is protrusion of the upper jaws, which creates a planar mouth opening and can increase the forces suction feeders exert on their prey by up to 35% (Holzman et al. 2008). This anterior motion of the jaws is exceptional as there are no muscles attached to the primarily protruded bone of the upper jaw, the premaxilla—instead, muscles attached to the nearby maxilla, also an upper jaw bone, and the bones of the lower jaw pull the bones of the upper jaw anteriorly. Jaw protrusion is often mentioned as one of the primary innovations underlying the success of the largest radiation of ray-finned fishes, the Acanthomorpha (spiny-rayed fishes, ~14,000 species) (Wainwright and Longo 2017), but it has evolved independently in the Cypriniformes. However, the mechanism by which Cypriniformes protrude their jaws is unique. Unlike Acanthomorphs, the Cypriniformes have developed an additional median

bone of the upper jaws, the kinethmoid, that allows substantial flexibility of the feeding apparatus (Hernandez et al. 2007).

The kinethmoid decouples the motion of the upper jaws from the lower so that the upper jaws can protrude when the mouth is open or closed—that is, the upper jaws can power their own protrusion (Hernandez et al. 2007). This reduction in kinematic constraint, as the upper jaws are no longer tied to the motion of the lower jaws, allows substantial flexibility in the use of the jaws (Hernandez et al. 2007; Hernandez and Staab 2015). With the kinethmoid, the jaws can modulate the timing of peak flow, with multiple instances of maximum flow within a single strike, creating a much more adaptable feeding mechanism than a standard Acanthomorph suction strike which has just one instance of peak flow through the jaws (Staab et al. 2012a). Increased flexibility in the kinematics of peak suction may be advantageous to picking and detritus feeding from the benthos for which a single burst of rapid flow may not be effective (Hernandez and Staab 2015). However, kinethmoid-mediated jaw protrusion still confers a hydrodynamic advantage during prey capture (Staab et al. 2012b). The evolution of the kinethmoid also shows some signal with trophic evolution across Cypriniformes, with a shortened kinethmoid in species that may rely more strongly on ram feeding rather than suction (Hernandez and Staab 2015).

Nearly any free-floating or evasive prey can be captured using suction feeding. Fishes, plankton, benthic or pelagic invertebrates, and even some molluscs can be captured with a suction strike, and the addition of the kinethmoid may makes suction more effective for benthic invertebrate pickers or detritivores (Hernandez and Staab 2015). These types of prey make up the bulk of the identifiable prey items of several juvenile and adult native fishes in the Grand Canyon: bluehead sucker, flannelmouth sucker, humpback chub, and speckled dace (Kaeding and Zimmerman 1983; Valdez et al. 2001; Taylor et al. 2011). Furthermore, these prey types, particularly evasive prey like insects and fish, make up a major dietary overlap between the endangered humpback chub and rainbow trout (Spurgeon et al. 2015).

The addition of the kinethmoid to the feeding apparatus adds substantial flexibility to the feeding apparatus of Cypriniformes, allowing them to take advantage of multiple prey types, particularly benthic and evasive prey, and to modulate the anatomy of their feeding apparatus to effectively prey on either elusive or benthic prey types. The innovation of jaw protrusion as an innovation is commonly hypothesized to underlie the major radiation of Acanthomorphs (Wainwright and Longo 2017) and may have had a similar effect supporting the 3,000 species of Cypriniformes.

Prey selection: the palatal organ

Particulate feeders are common in many environments. Many plankton feeders use complex topography of the gill rakers to filter prey from the water, or use mucous cells to retain and then transport their prey (Paig-Tran and Summers 2014). However, the mechanisms of prey capture that rely on filtration may be content-agnostic, or may not include any ability to distinguish prey from non-prey items.

A second major innovation of the Cypriniform feeding apparatus, the palatal organ, facilitates prey sorting (Hernandez and Cohen 2019). The palatal organ is a muscular pad located on the dorsal surface of the pharynx, posterior to the oral cavity but anterior to the pharyngeal jaws, and holds numerous papillae of varying shapes and sizes (Matthes 1963).

The muscular pad of the palatal organ depresses onto the edible particulate matter, and the fish then washes prey items that are inedible or prey that are very small through a branchial sieve (Sibbing et al. 1986; Sibbing 1988).

Prey sorting in this case is accomplished using the sensitive papillae of the palatal organ. The many taste buds on the palatal organ are well-innervated by the vagus nerve, which enters the medulla and innervates the vagal lobe (Morita and Finger 1985; Finger 2008). The vagal lobe is receives numerous taste-sensing inputs and, in goldfish (*Carassias auratus*; Cypriniformes: Cyprinidae), makes up nearly 20% of the volume of its entire brain, speaking to the importance of taste sensation some Cypriniformes (Kotrschal and Palzenburger 1992 *in* Finger 2008). This high density of taste-sensitive papillae allows the palatal organ to selectively identify edible prey items to retain, washing away inedible particulate matter with accuracy.

Taylor and coauthors (2011) note that in the Grand Canyon, some juvenile catostomids (bluehead and flannelmouth suckers) disproportionately feed on inorganic matter in comparison to the nearby cyprinids (humpback chub and speckled dace). Humpback chub and speckled dace, in contrast, primarily prey on adult dipterans or other insects as juveniles and as adults in and out of the Grand Canyon, indicating resource partitioning between the two families (Schreiber and Minckley 1981; Kaeding and Zimmerman 1983; Angradi et al. 1991; Valdez et al. 2001; Taylor et al. 2011). Inorganic matter associated with the benthos is likely to require the type of filtration and prey sorting made possible by the palatal organ, making this likely a particularly useful innovation for the catostomids.

Feeding on particulate matter and detritus is not unusual within fishes—many species feed on benthic particulate matter. However, the degree of specialization of the anatomy of the palatal organ of Cypriniformes for prey sorting is 'exceptional' (Matthes 1963). Cypriniformes are likely able to rely less on vision in potentially unclear water and use the many taste buds of the palatal organ to capture their prey, as the barbeled goatfish do (Kiyohara et al. 2002), which may be an advantage in past turbid, heavily sedimented waters of the Grand Canyon.

Prey processing: pharyngeal jaws

After the prey is captured and, in the case of particulate prey, once it has been sorted, it reaches its last obstacle on the way to a hungry Cypriniform's swallow: the pharyngeal jaws. Pharyngeal jaws are modified gill arches in the pharynx of fishes used by most species to crush, crunch, or grind their prey (Wainwright 1989; Wainwright et al. 2012; Gidmark et al. 2014; Pos et al. 2019). The Cypriniform pharyngeal jaw apparatus is a highly diverse crushing and grinding mechanism.

The above sections detail the role the upper jaws play in prey capture, which in a suction strike relies on rapid expansion of the jaws. This emphasis on mobility over stability leaves little opportunity for structurally sound oral jaws that can effectively crush or grind mechanically challenging prey items, and many suction feeders with high mobility eat solely evasive prey that requires less processing (Westneat 2003; McGee et al. 2016; Martinez et al. 2018). However, it has long been hypothesized that evolution of very robust pharyngeal jaws can decouple the mechanisms of prey processing and prey capture (Liem 1973).

The pharyngeal jaws of fishes are a set of modified bones in the back of the throat, or the back of the pharynx, present in numerous fishes. They facilitate processing complex prey by providing a grinding, shearing, or tearing surface, often with 'teeth' on them—essentially, they are how most fishes "chew" their food (Gregory 1933). In fact, the kinematics of the mechanism by which grass carp grind their prey by occluding the jaws and prey against a dorsal bony process and chewing pad converges with the mastication of other vertebrates (Gidmark et al. 2014). These pharyngeal jaws in Cypriniformes are well articulated, with large and beefy muscles supporting their motion (Sagemehl 1884 *in* Gregory 1933).

Notably, few currently present native fishes in the Grand Canyon feed primarily on algae or other hard prey, though the hard shells of insects may require some processing (Taylor et al. 2011). Humpback chub do eat substantial amounts of algae except in recently in flooded environments, indicating that the pharyngeal apparatus may allow them some dietary flexibility in the modern Grand Canyon environment with some water flow variability (Valdez et al. 2001). However, up to 47% of the diets of rainbow trout were made up by algae in one study, indicating that rainbow trout may be the dominant feeders of algae in the modern Grand Canyon (Marsh and Douglas 1997).

Why the Grand Canyon?

The Grand Canyon is home to both immense flows of water and immensely varying flows, which have undergone substantial shifts in the last 50 years. This magnitude of variation creates a diverse habitat that offers many opportunities for fishes of different sizes, shapes, and trophic niches to take advantage of. In the case of Cypriniformes, their many novelties associated with the feeding apparatus likely allowed them to occupy diverse habitats and eat many or all of the available prey items, and they are known to iteratively converge to similar dietary requirements (Pos et al. 2019). However, the diversity of habitats with different flow regimes in different regions of the Grand Canyon likely also allows invasive fishes to easily take hold once introduced to the region, and changing invasive terrestrial flora alters native fish habitats—so much so that removing Tamariz substantially increases the frequency of native fishes (Kennedy et al. 2005).

Some functional innovations of the Cypriniform feeding apparatus may also contribute to their decline when competing against invasive species. With reductions in sediment of the water due to Glen Canyon Dam, the crucial role of the palatal organ as a mechanism for prey sorting in turbid waters may become less important, lending native Cypriniformes less of an advantage in the Grand Canyon against invasive species. Likewise, the highly modified pharyngeal jaws of cichlids in East African Rift Lakes cause limited gapes that constrained their ability to feed on large prey, and when a non-pharyngognathous predator was introduced, it easily outcompeted the cichlids and may now be eating them to extinction (McGee et al. 2015). Though Cypriniformes do not have the most extremely modified pharyngeal jaws, it is possible that a pair of large and beefy pharyngeal jaws of some Grand Canyon Cypriniformes may be causing similar gape limitation and reducing the competitiveness of native species when compared to predators like the rainbow trout or channel catfish that routinely prey on native fishes (Marsh and Douglas 1997).

Overall, the many functional innovations of Cypriniformes make them formidable competitors in any riverine system, and the many functional innovations of the feeding

apparatus have likely contributed to their historic success. In the future, the pace of the changes associated with climate change and human-powered changes to water flows in the Grand Canyon may exceed the ability of fishes to adapt, but standing interpopulation variation and phenotypic plasticity could provide lifelines for rapid evolution of these species (Scoville and Pfrender 2010; Reid et al. 2016). Furthermore, the many functional innovations of Cypriniformes set them up for success in many different feeding scenarios, which may give them an advantage in a changed habitat. Dynamic fish communities in rapidly changing, complex, coral reefs highlight the role of fine-scale niche partitioning to create functional space for many species (Brandl and Bellwood 2014), indicating that there may be a high degree of fine-scale partitioning underlying current fish patterns of diversity in the Grand Canyon that we may not understand. However, due to its high profile, the Grand Canyon may be one of the best opportunities for understanding the effects of anthropogenic change on fish functional diversity in a freshwater system. Well-studied flow experiments and predator removal experiments provide opportunities for comparative studies of the effects of shifting water regimes and predators on the habits of the native species (e.g., Valdez et al. 2001).

References

Alfaro, M. E., F. Santini, and C. D. Brock. 2007. Do Reefs Drive Diversification in Marine Teleosts? Evidence From the Pufferfish and Their Allies (Order Tetraodontiformes). Evolution (N. Y). 61:2104–2126.

Angradi, T. R., J. S. Spaulding, and E. D. Koch. 1991. Diel Food Utilization by the Virgin River Spinedace, Lepidomeda mollispinis mollispinis, and Speckled Dace, Rhinichthys osculus, in Beaver Dam Wash, Utah. Southwest. Nat. 36:158.

Beers, J. M., and N. Jayasundara. 2015. Antarctic notothenioid fish: what are the future consequences of "losses" and "gains" acquired during long-term evolution at cold and stable temperatures? J. Exp. Biol. 218:1834–1845.

Bishop, K. L., P. C. Wainwright, and R. A. Holzman. 2008. Anterior-to-posterior wave of buccal expansion in suction feeding fishes is critical for optimizing fluid flow velocity profile. J. R. Soc. Interface 5:1309–16.

Brandl, S. J., and D. R. Bellwood. 2014. Individual-based analyses reveal limited functional overlap in a coral reef fish community. J. Anim. Ecol. 83:661–670.

Day, S. W., T. E. Higham, A. Y. Cheer, and P. C. Wainwright. 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.

Ferry-Graham, L. A., P. C. Wainwright, and G. V. Lauder. 2003. Quantification of flow during suction feeding in bluegill sunfish. Zoology 106:159–168.

Finger, T. E. 2008. Sorting food from stones: The vagal taste system in Goldfish, Carassius auratus. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 194:135–143.

Froese, R., and D. Pauly. 2018. Fishbase.

Gerringer, M. E., J. C. Drazen, T. D. Linley, A. P. Summers, A. J. Jamieson, and P. H. Yancey. 2017. Distribution, composition and functions of gelatinous tissues in deep-sea fishes. R. Soc. Open Sci. 4.

Gidmark, N. J., J. C. Tarrant, and E. L. Brainerd. 2014. Convergence in morphology and masticatory function between the pharyngeal jaws of grass carp, Ctenopharyngodon idella, and oral jaws of amniote herbivores. J. Exp. Biol. 217:1925–1932.

Gillis, G. B., and G. V. Lauder. 1995. Kinematics of feeding in bluegill sunfish: Is there a general distinction between aquatic capture and transport behaviors? J. Exp. Biol. 198:709–720.

Gregory, W. K. 1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Am. Philos. Soc. 23:75–481.

Helfman, G. S., B. B. Collette, D. E. Facey, and B. W. Bowen. 2009. The Diversity of Fishes: Biology, Evolution, & Ecology. 2nd ed. Wiley-Blackwell, West Sussex, UK.

Hernandez, L. P., N. C. Bird, and K. L. Staab. 2007. Using Zebrafish to Investigate Cypriniform Evolutionary Novelties: Functional Development and Evolutionary Diversification of the Kinethmoid. J. Exp. Zool. B. Mol. Dev. Evol. 308B:625–641.

Hernandez, L. P., and K. E. Cohen. 2019. The Role of Developmental Integration and Historical Contingency in the Origin and Evolution of Cypriniform Trophic Novelties. Integr. Comp. Biol. 59:473–488.

Hernandez, L. P., and K. L. Staab. 2015. Bottom Feeding and Beyond: How the Premaxillary Protrusion of Cypriniforms Allowed for a Novel Kind of Suction Feeding. Integr. Comp. Biol. 55:74–84.

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

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

Kaeding, L. R., and M. A. Zimmerman. 1983. Life History and Ecology of the Humpback Chub in the Little Colorado and Colorado Rivers of the Grand Canyon. Trans. Am. Fish. Soc. 112:577–594.

Kennedy, T. A., J. C. Finlay, and S. E. Hobbie. 2005. Eradication of invasive Tamarix ramosissima along a desert stream increases native fish density. Ecol. Appl. 15:2072–2083.

Kiyohara, S., Y. Sakata, T. Yoshitomi, and J. Tsukahara. 2002. The "goatee" of goatfish: Innervation of taste buds in the barbels and their representation in the brain. Proc. R. Soc. B Biol. Sci. 269:1773–1780.

Kotrschal, K., and M. Palzenburger. 1992. Neuroecology of cyprinids: comparative, quantitative histology reveals diverse brain patterns. Pp. 135–152 in Environmental biology of European cyprinids. Springer, Dordrecht.

Lauder, G. V. 1980a. Hydrodynamics of prey capture by teleost fishes. Pp. 161–181 in D. J. Schneck, ed. Biofluid mechanics. Springer, New York, NY.

Lauder, G. V. 1980b. The suction feeding mechanism in sunfishes (Lepomis spp.): an experimental analysis. J. Exp. Biol. 88:49–72.

Liem, K. F. 1973. Evolutionary Strategies and Morphological Innovations: Cichlid Pharyngeal Jaws. Syst. Zool. 22:425–441.

MacArthur, R. H., and J. W. MacArthur. 1961. On Bird Species Diversity. Ecology 42:594–

598.

Malinsky, M., H. Svardal, A. M. Tyers, E. A. Miska, M. J. Genner, G. F. Turner, and R. Durbin. 2018. Whole-genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow. Nat. Ecol. Evol. 2:1940–1955. Springer US.

Marsh, P. C., and M. E. Douglas. 1997. Predation by Introduced Fishes on Endangered Humpback Chub and other Native Species in the Little Colorado River, Arizona. Trans. Am. Fish. Soc. 126:343–346.

Martinez, C. M., M. D. McGee, S. R. Borstein, and P. C. Wainwright. 2018. Feeding ecology underlies the evolution of cichlid jaw mobility. Evolution (N. Y). 72:1645–1655.

Matthes, H. 1963. A Comparative Study of the Feeding Mechanisms of Some African Cyprinidae (Pisces, Cypriniformes). Bijdr. tot Dierkd. 33:3–35.

McGee, M. D., S. R. Borstein, R. Y. Neches, H. H. Buescher, O. Seehausen, and P. C. Wainwright. 2015. A pharyngeal jaw evolutionary innovation facilitated extinction in Lake Victoria cichlids. Science (80-.). 350:1077–1079.

McGee, M. D., B. C. Faircloth, S. R. Borstein, J. Zheng, C. D. Hulsey, P. C. Wainwright, and M. E. Alfaro. 2016. Replicated divergence in cichlid radiations mirrors a major vertebrate innovation. Proc R Soc B 283:20151413.

Morita, Y., and T. E. Finger. 1985. Topographic and laminar organization of the vagal gustatory system in the goldfish, Carassius auratus. J. Comp. Neurol. 238:187–201.

Myers, G. S. 1949. Usage of Anadromous , Catadromous and Allied Terms for Migratory Fishes Published by : American Society of Ichthyologists and Herpetologists (ASIH) Stable URL : http://www.jstor.org/stable/1438482 REFERENCES Linked references are available on JSTOR for. Copeia 1949:89–97.

Olsen, A. M., L. P. Hernandez, A. L. Camp, and E. L. Brainerd. 2019. Channel catfish use higher coordination to capture prey than to swallow. Proc. R. Soc. B Biol. Sci. 286.

Paig-Tran, E. W. M., and A. P. Summers. 2014. Comparison of the structure and composition of the branchial filters in suspension feeding elasmobranchs. Anat. Rec. 297:701–15.

Pos, K. M., S. C. Farina, M. A. Kolmann, and N. J. Gidmark. 2019. Pharyngeal Jaws Converge by Similar Means, Not to Similar Ends, When Minnows (Cypriniformes: Leuciscidae) Adapt to New Dietary Niches. Integr. Comp. Biol. 59:432–442.

Price, S. A., R. A. Holzman, T. J. Near, and P. C. Wainwright. 2011. Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. Ecol. Lett. 14:462–469.

Price, S. A., J. J. Tavera, T. J. Near, and P. C. Wainwright. 2013. Elevated rates of morphological and functional diversification in reef-dwelling haemulid fishes. Evolution (N. Y). 67:417–428.

Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J. Near, M. Coll, and M. E. Alfaro. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559:392–395.

Reid, N. M., D. A. Proestou, B. W. Clark, W. C. Warren, J. K. Colbourne, J. R. Shaw, S. I. Karchner, M. E. Hahn, D. Nacci, M. F. Oleksiak, D. L. Crawford, and A. Whitehead. 2016. The genomic landscape of rapid repeated evolutionary adaptation to toxic pollution in wild fish. Science (80-.). 354:1305–1308.

Sagemehl, M. 1884. Beitrage zur vergleichenden Anatomic der Fische. I. Das Cranium von Amia calva. Morphol. Jahrb IX:177–228.

Schaefer, S. A., and G. V. Lauder. 1996. Testing Historical Hypotheses of Morphological Change: Biomechanical Decoupling in Loricarioid Catfishes. Evolution (N. Y). 50:1661–1675.

Schoener, T. W. 1974. Resource Partitioning in Ecological Communities. Science (80-.). 185:27–39.

Schreiber, D. C., and W. L. Minckley. 1981. Feeding interrelations of native fishes in a Sonoran Desert stream. Gt. Basin Nat. 41:409–426.

Scoville, A. G., and M. E. Pfrender. 2010. Phenotypic plasticity facilitates recurrent rapid adaptation to introduced predators. Proc. Natl. Acad. Sci. U. S. A. 107:4260–4263.

Sibbing, F. A. 1988. Specializations and limitations in the utilization of food resources by the carp, Cyprinus carpio: a study of oral food processing. Environ. Biol. Fishes 22:161–178.

Sibbing, F. A., J. W. M. Osse, and A. Terlouw. 1986. Food handling in the carp (Cyprinus carpio): its movement patterns, mechanisms and limitations. J. Zool. 210:161–203.

Spurgeon, J. J., C. P. Paukert, B. D. Healy, C. A. Kelley, and D. P. Whiting. 2015. Can translocated native fishes retain their trophic niche when confronted with a resident invasive? Ecol. Freshw. Fish 24:456–466.

Staab, K. L., L. A. Ferry, and L. P. Hernandez. 2012a. Comparative kinematics of cypriniform premaxillary protrusion. Zoology 115:65–77.

Staab, K. L., R. A. Holzman, L. P. Hernandez, and P. C. Wainwright. 2012b. Independently evolved upper jaw protrusion mechanisms show convergent hydrodynamic function in teleost fishes. J. Exp. Biol. 215:1456–1463.

Taylor, P., M. R. Childs, R. W. Clarkson, and A. T. Robinson. 2011. Resource Use by Larval and Early Juvenile Native Fishes in the Little Colorado River , Grand Canyon , Arizona Resource Use by Larval and Early Juvenile Native Fishes in the. Trans. Am. Fish. Soc. 127:620–629.

Valdez, R. A., T. L. Hoffnagle, C. C. McIvor, T. McKinney, and W. C. Leibfried. 2001. Effects of a test flood on fishes of the Colorado River in Grand Canyon, Arizona. Ecol. Appl. 11:686–700.

Wainwright, P. C. 1989. Functional morphology of the pharyngeal jaw apparatus in perciform fishes: An experimental analysis of the haemulidae. J. Morphol. 200:231–245.

Wainwright, P. C., and S. W. Day. 2007. The forces exerted by aquatic suction feeders on their prey. J. R. Soc. Interface 4:553–560.

Wainwright, P. C., and S. J. Longo. 2017. Functional innovations and the conquest of the oceans by acanthomorph fishes. Curr. Biol. 27:R550–R557.

Wainwright, P. C., M. D. McGee, S. J. Longo, and L. P. Hernandez. 2015. Origins, innovations, and diversification of suction feeding in vertebrates. Integr. Comp. Biol. 55:134–145.

Wainwright, P. C., W. L. Smith, S. A. Price, K. L. Tang, J. S. Sparks, L. A. Ferry, K. L. Kuhn, R. I. Eytan, and T. J. Near. 2012. The Evolution of Pharyngognathy: A Phylogenetic and Functional Appraisal of the Pharyngeal Jaw Key Innovation in Labroid Fishes and beyond. Syst. Biol. 61:1001–1027.

Westneat, M. W. 2003. A biomechanical model for analysis of muscle force, power output and lower jaw motion in fishes. J. Theor. Biol. 223:269–281.

Westneat, M. W. 2006. Skull biomechanics and suction feeding in fishes. Pp. 29–75 *in* R. E. Shadwick and G. V. Lauder, eds. Fish Physiology Series: Fish Biomechanics. Academic Press, San Diego, CA.

Willis, S. C., K. O. Winemiller, and H. Lopez-Fernandez. 2005. Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. Oecologia 142:284–295.

Winemiller, K. O., and D. B. Jepsen. 1998. Effects of seasonality and fish movement on tropical river food webs. J. Fish Biol. 53:267–296.

Wissmar, R. C., J. E. Richey, R. F. Stallard, and J. M. Edmond. 1981. Plankton Metabolism and Carbon Processes in the Amazon River, Its Tributaries, and Floodplain Waters, Peru-Brazil, May-June 1977. Ecology 62:1622–1633.