A peacock bass (Cichla) functional novelty relaxes a constraint imposed by the classic cichlid pharyngeal jaw innovation

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Innovations may provide access to new resources but often result in significant trade-offs. Pharyngognathy is a classic pharyngeal jaw innovation in which the left and right lower pharyngeal jaw (LPJ) bones are united into a single structure, producing a strong bite but reduced gape. Throughout cichlids, pharyngeal suturing occurs along the entire medial border between LPJ bones, except in peacock bass (Cichla), where these bones are connected by ligaments only in their anterior region. We show that this limited attachment permits the jaw bones to spread apart and we link this feature to an increase in pharyngeal gape that is comparable to non-pharyngognathous species. The capacity of the LPJ bones to spread apart is strongest in juveniles and is mostly lost during development. Juvenile Cichla exhibit size-specific pharyngeal gape similar to non-pharyngognathous percomorphs; however, adults exhibit pharyngeal gape on par with other predatory cichlids. Relaxation of pharyngeal suturing offsets a major deleterious consequence of pharyngognathy by reducing gape limitation and we propose this may accelerate the ontogenetic transition to piscivory. Partial reversal of the classic cichlid pharyngeal jaw innovation highlights the functional trade-offs that often accompany innovations and may be a major cause of variation in their macroevolutionary consequences.


INTRODUCTION

Functional trade-offs impose a constraint on organismal evolution (Futuyma & Moreno, 1988; Koehl, 1996). A trade-off between force transmission and speed is central to many anatomical systems, ranging from feeding mechanics in fishes (Westneat, 1994; 1995) to powered flight in birds (Tobalske et al., 2003), and can have a strong influence on diversification (Collar et al., 2009; Wright et al., 2016; Burress et al., 2020). Functional innovations may permit organisms to achieve substantially enhanced performance that results in access to new resources (Simpson, 1953; Liem, 1973; Kingsolver & Koehl, 1994; Bond & Opell, 1998). However, an interesting feature of innovation is that functional break-throughs usually come with performance trade-offs, rather than universal benefits. While innovations may pave the way to exploitation of novel resources, trade-offs can make use of other resources less viable (McGee et al., 2015). Although there are widespread trade-offs in organismal evolution, these are rarely explicitly discussed in the context of major innovations despite that such trade-offs have the potential to influence the macroevolutionary impacts of the innovation.

All ray-finned fishes have a pharyngeal jaw apparatus formed from modified gill-arch elements that assists with prey processing (Lauder & Wainwright, 1992; Fig. 1). A derived condition of the pharyngeal jaw apparatus, pharyngognathy, is regarded as a major innovation that expanded the functional repertoire of several ecologically diverse lineages of fishes, including marine wrasse and freshwater cichlids (Liem, 1973; Liem & Sanderson, 1986). Pharyngognathy is characterized by three key modifications to the pharyngeal jaw apparatus (Liem, 1973; Stiassny, 1987; Stiassny & Jensen, 1987): (i) the left and right lower pharyngeal jaw bones, the fifth ceratobranchials, are united into a single structure, (ii) the upper pharyngeal jaws articulate directly against the neurocranium, and (iii) a muscular sling suspends the lower pharyngeal
jaw directly from the neurocranium. In combination, these features facilitate exploitation of hard and tough prey by providing a strong bite. In all cichlids, except *Cichla*, the left and right lower pharyngeal jaw bones are united by a suture along their entire medial border (Stiassny, 1981; Casciotta & Arratia, 1993; Fig. 1). In many species, especially those that consume hard and tough prey, this suture is complex and interdigitating, increasing the contact area between the bones (Hulsey, 2006) and presumably increasing the strength of the suture (Jaslow, 1990). In *Cichla*, only the anterior portion of the lower pharyngeal jaw bones are united by a short, straight suture (Stiassny, 1982, 1987; Stiassny & Jensen, 1987; Fig. 1). The functional consequences of this reduced suture is unknown; however, it has been hypothesized to permit the lower pharyngeal jaws to spread apart to accommodate larger prey such as fishes (Stiassny, 1982; Wainwright et al., 2012).

The ontogenetic transition to piscivory is a critical period for many predatory fishes. Transitioning at a small body size can increase growth rate and reduce mortality (Werner & Gilliam, 1984). Body size plays a prominent role in mediating this niche shift because small predators have correspondingly small, more restrictive oral and pharyngeal jaw gapes, and subsequently have prolonged handling time consuming large prey or are prevented from consuming large prey altogether (Mittelbach & Persson, 1998). The horizontal gape of the oral jaws is a strong predictor of maximum prey size (Mihalitsis & Bellwood, 2017); however, pharyngognathous fishes are further limited by a reduced pharyngeal jaw gape due to the union of the lower pharyngeal jaws into a single structure that prevents the two bones from spreading apart to accommodate large prey. Thus, a reduced pharyngeal gape is a consequence of pharyngognathy. Restricted pharyngeal gape and reduced swallowing performance are thought to have facilitated the extinction of piscivorous cichlids in Lake Victoria following the introduction of a non-pharyngognathous competitor (McGee et al., 2015). Thus, the evolution of pharyngognathy imposes a functional trade-off—an expanded capacity to eat hard or tough prey such as molluscs or algae, but reduced capacity to feed on large prey items such as fishes.

In this study, we explore the functional consequences of reduced suturing of the lower pharyngeal jaw in *Cichla*. We test the hypothesis that the short, straight suture that connects the left and right lower pharyngeal jaws permits these bones to spread apart and increase the pharyngeal gape. We further explore whether this novelty offsets the pharyngeal gape trade-off of pharyngognathy associated with consuming large fish prey. We are particularly interested in the possible role of pharyngeal jaw spreading in juvenile individuals, around the ontogenetic shift to piscivory. We also ask whether this feature permits *Cichla* to achieve a pharyngeal gape similar to those of several non-pharyngognathous piscivores to determine whether there is a functional reversal to pharyngeal gape sizes associated with the non-pharyngognathous condition. To address these questions, we first measured mobility of the lower pharyngeal jaw and pharyngeal and oral gape across an ontogenetic series of *Cichla ocellaris* and two other cichlids that represent independent evolutionary origins of piscivory but have complete pharyngeal sutures (*Crenicichla lugubris* and *Parachromis dovii*), as well as a non-cichlid, non-pharyngognathous piscivore (*Micropterus salmoides*) that has been described as a North American
We measured oral and pharyngeal jaw gape across *Cichla* (Norton & Brainerd, 1993). Finally, we compared pharyngeal gapes of juvenile *Cichla* to a broad spectrum of pharyngognathous and non-pharyngognathous piscivores sampled from across percomorph fishes.

**MATERIALS AND METHODS**

**GAPE AND PHARYNGEAL JAW MEASUREMENTS**

We measured oral and pharyngeal jaw gape across an ontogenetic series of *Cichla ocellaris* (*N* = 28; 2.7–27.0 cm standard length (SL)), two distantly-related Neotropical cichlid piscivores: South American *Crenicichla lugubris* (*N* = 29; 5.4–25.1 cm SL) and middle American *Parachromis dovii* (*N* = 17; 2.5–14.1 cm SL), and a non-pharyngognathous piscivore: North American *Micropterus salmoides* (*N* = 37; 6.2–32.5 cm SL). These are large-bodied species that principally eat fish as adults (Table 1). The horizontal gape of the oral jaws is a strong predictor of maximum prey size that fish are able to feed on (Mihalitsis & Bellwood, 2017); therefore, we used this measure to characterize oral gape. Measurements were taken on anesthetized individuals immediately after a lethal dose of MS-222 using digital calipers to the nearest 0.1 mm and defined as the maximum horizontal distance that could pass through the oral jaws and into the buccal cavity. Pharyngeal jaw gape was measured with a series of circular cross-section rods and defined as the maximum diameter that could easily pass through the upper and lower pharyngeal jaws and into the oesophagus (Burress et al., 2015; McGee et al., 2015). For *Cichla* specimens, the lower pharyngeal jaw was then removed by dissection. The distance between the posterior tips of the left and right lateral processes was measured at rest and then again after being gently spread to the maximum extent permitted by the suture. In small specimens, the lateral processes were somewhat flexible, a feature that may contribute to the mobility of the lower pharyngeal jaw; however, this was not considered in our measurements. We then calculated a response ratio by dividing the spread distance by the at-rest distance, which characterized the added separation permitted by the reduced suturing between the fifth ceratobranchial bones. All references to body size are standard length, measured from the anterior tip of the upper jaw to the posterior edge of the hypural plate.

Following the same protocol, we also measured oral and pharyngeal gape across a wider spectrum of piscivorous species, including other pharyngognathous cichlids as well as non-pharyngognathous percomorph fishes. We focused on juvenile size classes (6–15 cm) for comparison because the species reach very different adult sizes and we were particularly interested in this body size range when many ontogenetic transitions to piscivory occur. We sampled six *Cichla* species (*Cichla ocellaris* (*N* = 3), *Cichla monoculus* (*N* = 3), *Cichla temensis* (*N* = 2), *Cichla piquiti* (*N* = 3), *Cichla kelberi* (*N* = 3) and *Cichla melaniae* (*N* = 2). We also sampled other piscivorous cichlids that exhibit fully sutured lower pharyngeal jaws, including: five Neotropical species (*Crenicichla lugubris* (*N* = 3), *Parachromis dovii* (*N* = 3), *Petenia splendida* (*N* = 3), *Caquetaia myersi* (*N* = 3) and *Nandopsis haitiensis* (*N* = 3); six species from Lake Malawi (*Rhamphochromis esox* (*N* = 2), *Nimbochromis livingstonii* (*N* = 3), *Dimidiochromis compressiceps* (*N* = 3), *Aristochromis christyi* (*N* = 3), *Champsosochromis spilorhynchos* (*N* = 3) and *Champsosochromis caeruleus* (*N* = 3); three species from Lake Tanganyika (*Boulengerochromis microlepis* (*N* = 1), *Lepidiolamprologus kendalli* (*N* = 3) and *Cyphotilapia frontosa* (*N* = 3), and one species from Madagascar (*Paratilapia polleni* (*N* = 3)). We also sampled non-pharyngognathous species that are distributed across the percomorph phylogeny (Alfaro et al., 2018), including the Centrarchidae (black basses and sunfishes: *Micropterus salmoides* (*N* = 6), *Pomoxis nigromaculatus* (*N* = 3), *Lepomis gulosus* (*N* = 1) and *Lepomis cyanellus* (*N* = 3)), Serranidae (groupers and sea basses; *Serranus tigrinus* (*N* = 3) and *Serranus baldwini* (*N* = 3)); the Sebastidae (rockfishes: *Sebastes ruberminus* (*N* = 1)); the Scorpaenidae (scorpionfishes and lionfishes: *Pterois volitans* (*N* = 1)); the Antennariidae (frogfishes: *Antennarius commerson* (*N* = 3)); the Batrachoididae (freshwater tripeltails: *Batrachoides microlepis* (*N* = 3)); the Anabantidae (Asian pikehead gourami: *Nandus nandus* (*N* = 3)); the Ophichthidae (Asian pikehead gourami: *Luciocephalus aura* (*N* = 3)), and the Polycentridae (South American leaffish: *Monocirrhus polyacanthus* (*N* = 3)). These species shift to varied degrees of piscivory as adults (Table 1). In order to correct for differences in body size, pharyngeal gape was expressed as a proportion of oral gape and SL, and oral gape as a proportion of SL. A key aspect of our measurements of pharyngeal gape is that we made measurements on anesthetized specimens, ensuring that soft tissues were supple and the degree of stretching could be realistically determined. The use of formalin fixed material, as in many previous studies, limits these inferences because fixation results in considerable stiffening of soft tissues. All of the data presented here are new and previously unpublished.

**PHYLOGENETIC COMPARATIVE ANALYSES**

We compared pharyngeal and oral jaw gape among pharyngognathous species, non-pharyngognathous species, and Neotropical cichlids.
Table 1. Dietary and trait data for the species used in the study

<table>
<thead>
<tr>
<th>Species</th>
<th>Region</th>
<th>Degree of piscivory (%)</th>
<th>Piscivory state</th>
<th>Trait state</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antennarius commerson</td>
<td>Pacific Ocean</td>
<td>100</td>
<td>High</td>
<td>NP§</td>
<td>Pietsch and Grobecker (1990)</td>
</tr>
<tr>
<td>Aristochromis christyi</td>
<td>Lake Malawi</td>
<td>–</td>
<td>High</td>
<td>P†</td>
<td>Konings (2016)</td>
</tr>
<tr>
<td>Boulengerochromis microlepis</td>
<td>Lake Tanganyika</td>
<td>–</td>
<td>High</td>
<td>P</td>
<td>Wagner et al. (2009); Konings (2015)</td>
</tr>
<tr>
<td>Caquetaia myersi</td>
<td>South America</td>
<td>68</td>
<td>High</td>
<td>P</td>
<td>Winemiller (1989)</td>
</tr>
<tr>
<td>Champsochromis spliorhynchus</td>
<td>Lake Malawi</td>
<td>–</td>
<td>High</td>
<td>P</td>
<td>Konings (2016)</td>
</tr>
<tr>
<td>Champsochromis caeruleus</td>
<td>Lake Malawi</td>
<td>–</td>
<td>High</td>
<td>P</td>
<td>Konings (2016)</td>
</tr>
<tr>
<td>Cichla kelberi</td>
<td>South America</td>
<td>100</td>
<td>High</td>
<td>INT¥</td>
<td>Gomiero et al. (2010)</td>
</tr>
<tr>
<td>Cichla monoculus</td>
<td>South America</td>
<td>100</td>
<td>High</td>
<td>INT</td>
<td>Novaes et al. (2004)</td>
</tr>
<tr>
<td>Cichla ocellaris</td>
<td>South America</td>
<td>100*</td>
<td>High</td>
<td>INT</td>
<td>Layman et al. (2005); Jepsen et al. (1997); López-Fernández et al. (2012); Montaña &amp; Winemiller (2013)</td>
</tr>
<tr>
<td>Cichla piquiti</td>
<td>South America</td>
<td>100*</td>
<td>High</td>
<td>INT</td>
<td>Luiz et al. (2011)</td>
</tr>
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<td>Cichla temensis</td>
<td>South America</td>
<td>100</td>
<td>High</td>
<td>INT</td>
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<td>Cichla melaniae</td>
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<td>100*</td>
<td>High</td>
<td>INT</td>
<td>Layman et al. (2005); Jepsen et al. (1997)</td>
</tr>
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<td>Ctenicichla lugubris</td>
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<td>70–91</td>
<td>High</td>
<td>P</td>
<td>Layman et al. (2005); Montaña &amp; Winemiller (2009, 2013); López-Fernández et al. (2012)</td>
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<tr>
<td>Clenopoma aquirostre</td>
<td>Africa</td>
<td>–</td>
<td>Moderate</td>
<td>NP</td>
<td>Dutta (1979)</td>
</tr>
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<td>Cyphotilapia frontosa</td>
<td>Lake Tanganyika</td>
<td>–</td>
<td>Moderate</td>
<td>P</td>
<td>Konings (2015); Ou et al. (2017)</td>
</tr>
<tr>
<td>Datnioides microlepis</td>
<td>South-east Asia</td>
<td>–</td>
<td>Moderate</td>
<td>NP</td>
<td>Konings (2016)</td>
</tr>
<tr>
<td>Dimidiochromis compressiceps</td>
<td>Lake Malawi</td>
<td>–</td>
<td>High</td>
<td>P</td>
<td>Wagner et al. (2009); Konings (2015)</td>
</tr>
<tr>
<td>Lepidiolamprologus kendalli</td>
<td>Lake Tanganyika</td>
<td>–</td>
<td>Moderate</td>
<td>P</td>
<td>Collar et al. (2009); Montaña &amp; Winemiller (2013)</td>
</tr>
<tr>
<td>Lepomis gulosus</td>
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<td>26</td>
<td>Moderate</td>
<td>NP</td>
<td>Collar et al. (2009)</td>
</tr>
<tr>
<td>Lepomis cyanellus</td>
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<td>16</td>
<td>Moderate</td>
<td>NP</td>
<td>Collar et al. (2009)</td>
</tr>
<tr>
<td>Luciocephalus aura</td>
<td>Asia</td>
<td>–</td>
<td>High</td>
<td>NP</td>
<td>Lauder &amp; Liem (1981)</td>
</tr>
<tr>
<td>Micropterus salmoides</td>
<td>North America</td>
<td>61–95</td>
<td>High</td>
<td>NP</td>
<td>Collar et al. (2009); Montaña &amp; Winemiller (2013)</td>
</tr>
<tr>
<td>Monocirrhus polyacanthurus</td>
<td>South America</td>
<td>90</td>
<td>High</td>
<td>NP</td>
<td>Catarino &amp; Zuanon (2010)</td>
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<tr>
<td>Nandopsis haitiensis</td>
<td>Middle America</td>
<td>–</td>
<td>Moderate</td>
<td>P</td>
<td>Říčan et al. (2016)</td>
</tr>
<tr>
<td>Nandus nandus</td>
<td>Asia</td>
<td>80</td>
<td>High</td>
<td>NP</td>
<td>Parameswaran et al. (1971)</td>
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<tr>
<td>Nimbochromis livingstonii</td>
<td>Lake Malawi</td>
<td>–</td>
<td>Moderate</td>
<td>P</td>
<td>Konings (2016)</td>
</tr>
<tr>
<td>Parachromis dovii</td>
<td>Middle America</td>
<td>55</td>
<td>High</td>
<td>P</td>
<td>Winemiller et al. (1997)</td>
</tr>
<tr>
<td>Paratilapia polleni</td>
<td>Madagascar</td>
<td>–</td>
<td>Moderate</td>
<td>P</td>
<td>Stiassny &amp; Gerstner (1992)</td>
</tr>
<tr>
<td>Petenia splendida</td>
<td>Middle America</td>
<td>87–100</td>
<td>High</td>
<td>P</td>
<td>Hinojosa-Garro et al. (2013); Cochran-Biederman &amp; Winemiller (2010); Pease et al. (2018)</td>
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<td>Pomoxis nigromaculatus</td>
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<td>NP</td>
<td>Collar et al. (2009); Montaña &amp; Winemiller (2013)</td>
</tr>
<tr>
<td>Pterois volitans</td>
<td>Indo-Pacific</td>
<td>78</td>
<td>High</td>
<td>NP</td>
<td>Morris &amp; Akins (2009)</td>
</tr>
</tbody>
</table>
species, and *Cichla* using phylogenetic ANOVA with a residual randomization permutation procedure (Collyer and Adams, 2018) implemented in the geomorph R package (Adams and Otárola-Castillo, 2013). Statistical significance of the model was determined using 1000 permutations. Statistical significance of pairwise comparisons was assessed using the pairwise function implemented in the RRPP package (Collyer and Adams, 2018). For these analyses, we used an existing phylogeny of fishes (Rabosky et al., 2018), pruned to include only the species we sampled. In two cases, the species associated with the tip in the phylogenetic tree and morphological measurements were not exact matches. We associated morphological data for *Luciocephalus aura* with its congener *Luciocephalus pulcher* in the phylogenetic tree. We also associated morphological data from *Datnioides microlepis* with closely-related *Lobotes pacificus* in the phylogenetic tree (Near et al., 2013).

### RESULTS

**Pharyngeal Gape through Ontogeny**

In *Cichla*, pharyngeal gape increased with body size; however, the degree of mobility between the left and right LPJs was significantly negatively correlated with body size (Fig. 2). Juvenile specimens (2–3 cm SL) could separate their lateral processes to 1.7-times their resting distance, whereas this fell to 1.05-times in subadults and adults (>14 cm SL; Fig. 1). The suture between left and right lower pharyngeal jaw bones in *Cichla* was limited to 15% of the length of the ceratobranchial in small

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**Table 1.** Continued

<table>
<thead>
<tr>
<th>Species</th>
<th>Region</th>
<th>Piscivory state</th>
<th>Degree of piscivory (%)</th>
<th>Trait state</th>
<th>References</th>
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<td><em>Rhabdosynodontis esox</em></td>
<td>Lake Malawi</td>
<td>High</td>
<td>63−78</td>
<td>High</td>
<td>Hulsey et al. (2007); Konings (2017).</td>
</tr>
<tr>
<td><em>Scatophagus debilis</em></td>
<td>North Pacific</td>
<td>Moderate</td>
<td>11−77*</td>
<td>Moderate</td>
<td>York (2005); Labropoulou &amp; Markakis (2008); Morato et al. (2007); Bilecenoglu (2009).</td>
</tr>
<tr>
<td><em>Serranus tigrinus</em></td>
<td>Western Atlantic</td>
<td>Moderate</td>
<td>11−77*</td>
<td>Moderate</td>
<td>Labropoulou &amp; Markakis (2008); Morato et al. (2007); Bilecenoglu (2009).</td>
</tr>
<tr>
<td><em>Serranus baldwini</em></td>
<td>Western Atlantic</td>
<td>Moderate</td>
<td>11−77*</td>
<td>Moderate</td>
<td>Labropoulou &amp; Markakis (2008); Morato et al. (2007); Bilecenoglu (2009).</td>
</tr>
</tbody>
</table>

*Data from representative congeners. †P = Pharyngognathous; NP = Non-pharyngognathous; INT = Intermediate.*

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**Figure 2.** Ontogenetic series depicting the inverse relationship between pharyngeal gape and the expandability (response ratio (RR)) of the lower pharyngeal jaws of peacock bass (*Cichla ocellaris*). The shaded region depicts the general period in which *Cichla* switch to piscivory. Each point is an individual.
specimens (2–3 cm SL) but increased to 45% in 15 cm specimens. Except in the largest specimens, *Cichla* pharyngeal and oral gape were consistently higher than other cichlids, but less than *Micropterus* (Fig. 3A). In all four species, pharyngeal gape was smaller than oral gape throughout ontogeny (Fig. 3A); however, *Crenicichla* and *Parachromis* had shallower slopes indicating that they became more pharyngeal gape limited during ontogeny than *Micropterus* (Fig. 3A). In comparison, pharyngeal gape of juvenile *Cichla* was similar to *Micropterus*, but at larger body sizes was less than *Micropterus* and similar to other cichlids (Fig. 3A). This ontogenetic transition from a pharyngeal gape on par with a non-pharyngognathous piscivore to one that is similar to pharyngognathous species coincides with the period in ontogeny when *Cichla* exhibit a loss of mobility between the left and right lower pharyngeal jaws (Figs 2 and 3A).

**Pharyngeal Gape among Juvenile Percormorphs**

All 35 species of cichlids and non-pharyngognathous percomorphs had pharyngeal gapes that were smaller than their oral gape, indicating that they were pharyngeal gape limited (Fig. 3B). Cichlids, with the exception of *Cichla*, had smaller pharyngeal gapes than non-pharyngognathous species (Fig. 3B). After accounting for body size with a phylogenetic ANCOVA, pharyngeal gape differed between pharyngeal jaw states ($f = 3.63; P = 0.032$). Pharyngognathous cichlids had significantly smaller pharyngeal gapes relative to their standard length than non-pharyngognathous percomorphs ($P = 0.0001$; Fig. 4). The pharyngeal gapes of *Cichla* species were significantly larger than pharyngognathous cichlids ($P = 0.003$) but were similar to the non-pharyngognathous percomorph fishes ($P = 0.799$; Fig. 4). Similarly, size of the pharyngeal gape relative to oral gape differed among pharyngeal jaw states ($f = 4.86; P = 0.012$). Pharyngognathous cichlids had significantly smaller pharyngeal gapes relative to oral gape than non-pharyngognathous percomorphs ($P = 0.0001$; Fig. 4). *Cichla* had significantly larger pharyngeal gapes relative to their oral gape than other cichlids ($P = 0.001$) and similar pharyngeal gapes as non-pharyngognathous percomorph fishes ($P = 0.784$; Fig. 4). Pharyngeal jaw states did not differ in their oral gapes ($f = 0.28; P = 0.744$).

**DISCUSSION**

Pharyngognathy has evolved independently at least five times, including in cichlids (Cichlidae), wrasses and parrotfishes (Labridae), damselfishes (Pomacentridae), surfperches (Embiotocidae), and within the Beloniformes—in halfbeaks (Hemiramphidae) and flying fishes (Exocoetidae) (Stiassny & Jensen, 1987; Stiassny & Chen, 1998).

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**Figure 3.** The relationship between oral and pharyngeal gapes among percomorph fishes. Ontogenetic series depicting the relationship between untransformed oral and pharyngeal gape (A). The relationship between log-transformed oral and pharyngeal gape among juveniles (B). The 1:1 line indicates where oral gape limitation (to the left) gives way to pharyngeal gape limitation (to the right). The inset graph depicts the residuals calculated for *Cichla* if considered an in-group of pharyngognathous and non-pharyngognathous datasets. The dashed box in panel A depicts the gape sizes depicted in panel B. Each point in panel A depicts an individual. Each point in panel B depicts species means (± 95% confidence interval (CI)).
Evolved independently at least a dozen times, including 2013). The only pharyngognathous group in which fishes feed principally upon plankton (Van Noord et al., 2013). Small invertebrates (Schmitt & Coyer, 1983; Holbrook and surfperches feed on algae, crustaceans and other drifting algae, seagrasses and plankton (Tibbets & Carseldine, 2005; Tibbets et al., 2008), whereas flying fishes feed principally upon plankton (Van Noord et al., 2013). The only pharyngognathous group in which piscivory is widespread is the cichlids, where it has evolved independently at least a dozen times, including in Lakes Tanganyika, Malawi and Victoria, as well as the Americas (Muschick et al., 2012; Seehausen, 2015; Burress, 2016).

It is unclear how cichlids have frequently transitioned to piscivory despite pharyngognathy. These lineages are usually either single species (e.g. Boulengerichromis microlepis and Petenia splendida) or are relatively species-poor (e.g. Bathymbates and Cichla), perhaps indicating that piscivory is functionally demanding or that piscivory represents a high adaptive peak that limits subsequent diversification (Collar et al., 2009). Piscivorous cichlids tend to have a dorsal-ventrally shallow lower pharyngeal jaw with long, slender lateral processes and, in some cases, numerous, simple, low-profile teeth (Burress et al., 2015; Burress, 2016). This gracile morphology may ease gape limitation by increasing pharyngeal gape; however, our results show that these species exhibit significantly smaller pharyngeal gapes than our sample of non-pharyngognathous

Figure 4. Gape among juvenile (5–10 cm) predatory percomorph fishes. Pharyngeal jaw gape relative to body size (A) and oral gape (B) as well as oral gape (C) relative to body size among pharyngognathous cichlids, Cichla and non-pharyngognathous percomorph fishes. Values are mean (± 95% CI). Illustrations depict the pharyngeal jaw morphology of each group. Images depict an adjacent species (top-to-bottom): A. christyi, C. caeruleus, N. livingstonii, B. microlepis, C. myersi, C. melanias, M. polyacanthus, S. tigrinus, S. baldwini, C. acutirostre, L. aura, and A. commerson.
fishes (Fig. 4; see also McGee et al. (2015)). Large body size is associated with piscivory in some cichlids, such as *Boulengerochromis*, *Parachromis* and some *Crenicichla*, a pattern that at least in part reflects that gape scales with body size (Mittelbach & Persson, 1998). In combination with a transition to piscivory, large body size would ease the effect of gape limitation. Although fish are the dominant prey item in adult diets of most piscivorous cichlid species, there is a large amount of variation in how fully and quickly cichlids shift to piscivory during ontogeny (Burress et al., 2013a). Species often progress through a gradual transition in which they also eat crustaceans and insects rather than shift exclusively to fish prey. Juveniles (up to 5–7 cm) feed on zooplankton and midges and then shift towards piscivory, consuming principally fish by 10–15 cm (Arcifa, 1993; Jepsen et al., 1997; Meschiatti & Arcifa, 2002; Novaes et al., 2004). In comparison, 5–7 cm *Crenicichla* generally consume less than 25% fish prey, even species that go on to consume > 75% as adults (Burress et al., 2013a; Montaña & Winemiller, 2009), 6–7 cm *Parachromis* consume about 34% fish prey (Figueiredo et al., 2015), and 5–7 cm *Cauqueta* consume about 10% fish prey, but shift to about 60% at around 8–10 cm (Winemiller, 1989).

The transition to piscivory that occurs during ontogeny is a crucial event for piscivorous fishes (Buijse & Houthuijzen, 1992; Olson et al., 1995; Mittelbach & Persson, 1998; Post, 2003). The switch is typically associated with an acceleration in growth rate fuelled by the higher quality diet and can translate into larger body size and higher long-term survival (Olson, 1996; Post et al., 1998). We suggest the possibility that the small-bodied shift to piscivory in *Cichla* may be supported by their reduced pharyngeal suturing, which permits dynamic expansion of the pharyngeal gape of juveniles (Fig. 2). It is interesting that the shift to piscivory occurs at a similar body size in *Cichla* and the largemouth bass (*Micropterus salmoides*), a species that has been held up as an ecomorphological counterpart (Norton and Brainerd, 1993). *Micropterus salmoides* shift to piscivory between 5–10 cm to 5–7 cm feed on zooplankton and midges and then shift to piscivory at a relatively small body size. Juveniles (up to 5–7 cm) feed on zooplankton and midges and then shift towards piscivory, consuming principally fish by 10–15 cm (Arcifa, 1993; Jepsen et al., 1997; Meschiatti & Arcifa, 2002; Novaes et al., 2004). In comparison, 5–7 cm *Crenicichla* generally consume less than 25% fish prey, even species that go on to consume > 75% as adults (Burress et al., 2013a; Montaña & Winemiller, 2009), 6–7 cm *Parachromis* consume about 34% fish prey (Figueiredo et al., 2015), and 5–7 cm *Cauqueta* consume about 10% fish prey, but shift to about 60% at around 8–10 cm (Winemiller, 1989).

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A noteworthy strategy that may have allowed some cichlids to feed on fishes is specialization on small fishes. Diets in several highly piscivorous Neotropical cichlids are dominated by small-bodied characids (Winemiller, 1989; Montaña & Winemiller, 2009; Burress et al., 2013b) that are well below any limitations set by maximum gape. Small-bodied characids are often dominant components of fish assemblages throughout the Americas and Africa (Arrington & Winemiller, 2006; Montaña et al., 2015), and their high availability may have been a factor in the widespread evolution of piscivory in cichlids. *Cichla* have been found to rely on small characids during the dry season, but otherwise are known to consume comparatively large prey (Winemiller et al., 1997), including anecdotal evidence that juveniles are capable of consuming prey one-third their body size (Stiassny, 1991).

**CICHLA PHARYNGEAL JAW INNOVATION**

In all cichlids other than *Cichla*, the left and right lower pharyngeal jaw bones are sutured together along their entire medial border (Stiassny, 1981; Casciotta & Arratia, 1993). The suturing of these bones produces a single lower jaw structure, a robust jaw element that can resist occlusal forces (Hulsey, 2006). Further reinforcement of the lower pharyngeal jaw element, suture and musculature are associated with consumption of hard-shelled prey and the diversity of these features occurs largely along the soft-body to hard-shell prey axis (Hulsey, 2006; Burress, 2016). On one extreme of this axis, prey processing by the pharyngeal jaws does not require forceful biting or shearing of prey items. Piscivores use their pharyngeal jaws to grasp and transport prey to the oesophagus. Pharyngognathy makes this process less efficient due to reduced pharyngeal gape (McGee et al., 2015; Fig. 4).

In *Cichla*, the left and right lower pharyngeal jaw bones are united by a short, straight suture at their anterior tip (Stiassny, 1981; Casciotta & Arratia, 1993; Fig. 1). This configuration allows the lateral processes of the lower pharyngeal jaw bones to spread apart, producing an increased pharyngeal gape (Fig. 2). The capacity for spreading in the lower pharyngeal jaws declines sharply during ontogeny and is negligible by 14 cm. In juveniles, mobility in the midline joint is made possible by a relatively loose ligamentous connection between the bones. During ontogeny, the suture expands and becomes tighter, spanning about 15% of the length of the lateral process in juveniles (~1.5 cm SL) and up to about 45% in adults, reducing the capacity of the pharyngeal jaw bones to spread. The initial suturing of the lower pharyngeal jaw occurs sometime between 1 and 3 months of age in Nile tilapia, *Oreochromis niloticus* (Pabic et al., 2009). It is unknown if this process proceeds from the anterior end and expands posteriorly; however, a heterochronic mechanism through retardation of suture growth rate or delay in the onset of its development may be involved in the evolution of the reduced suturing found in *Cichla*.

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The potential for evolution to lead to a reduction of the connection between the pharyngeal jaw bones in *Cichla* may depend on an important feature of cichlid pharyngognathy. The left and right lower pharyngeal jaw bones are sutured together in cichlids (as they are in the false scorpion fish *Centrogenys*); however, they are fused together in the other pharyngognathous groups, including labrids, pomacentrids, embiotocids and beloniforms (Wainwright et al., 2012). This sutured condition may have presented less of a barrier to its reduction in *Cichla*, as there are no other known instances of such a feature in taxa with fused lower pharyngeal jaws.

The reduced connection between lower pharyngeal jaw bones in *Cichla* allows them to overcome one functional trade-off incurred with pharyngognathy when they are young. An expandable pharyngeal gape facilitates consumption of large prey and may be an important factor in permitting the switch to piscivory to occur at a small body size. A relatively early ontogenetic shift to piscivory may have positive consequences for growth, fitness, and survivorship in *Cichla*, as it does in some other piscivores (Post, 2003). Therefore, gape limitation is especially influential for juveniles because gape scales strongly with body size (Mittelbach & Persson, 1998). The *Cichla* pharyngeal jaw novelty permits juveniles to have a pharyngeal gape size that is similar to non-pharyngognathous percomorphs (Figs 3 and 4). As adults, *Cichla* pharyngeal jaw mobility wanes and their pharyngeal gape becomes similar to other pharyngognathous cichlids; however, at this point in ontogeny, large body size may ease gape limitation (Mittelbach & Persson, 1998).

The reduced suturing in the lower pharyngeal jaw of *Cichla* is one of several anatomical features that have previously been proposed to relate to piscivory (Stiassny, 1982, 1991; Norton and Brainerd, 1993). Other noteworthy pharyngeal features include an extreme lower pharyngeal jaw shape (Burress, 2016), simplified dentition of the lower jaw and enlarged third pharyngobranchial bones of the upper jaw (Casciotta & Arratia, 1993), several specific positional and shape changes in bones of the upper pharyngeal jaws and the presence of a dorsal articulating facet on pharyngobranchial 3 (Stiassny, 1982), reduced cross sectional diameter of the muscular sling (Burress et al., 2020), and the loss of the semi-circular ligament system (Stiassny, 1991). This latter trait is plesiomorphic or widespread among percomorphs, was lost in other cichlids, and appears again in *Cichla* (Stiassny, 1982, 1991). Reduction of pharyngeal suturing could also be thought of as a return to a more ancestral condition, although reduced suturing is not known in outgroup taxa. Other traits, such as the dorsal articulating facet on pharyngobranchial 3, show no parallel in outgroup taxa. Reappearance of the semi-circular ligaments in *Cichla* has been termed atavistic (Stiassny, 1991) and the appearance of a more ancestral condition in this trait and the suturing of the lower pharyngeal jaws of *Cichla* raises the possibility that they may be united by a common developmental genetic process that has been slowed or started later in development in *Cichla*, resulting in derived traits that represent more plesiomorphic conditions found outside cichlids (Stiassny, 1991). Although we have identified important functional consequences of one of these novelties, the reduced suturing of the lower pharyngeal jaw bones, we consider it likely that some of the other derived traits contribute to functional aspects of piscivory in *Cichla* and we look forward to future research that explores the functional morphology of this taxon more fully.

Our observations on the functional consequences of reduced pharyngeal suturing in *Cichla* highlight the importance of trade-offs that often accompany functional innovations. Trade-offs may be expected to affect the evolutionary consequences of innovations by biasing subsequent diversification away from niches that are blocked by the trade-off (Mc Gee et al., 2015). We suggest that significant trade-offs are a general feature of functional innovations and should be considered when exploring their impacts on ecological diversification. Indeed, it may be that the more substantial the innovation, the more substantial the trade-off. As an example, the evolution of powered flight clearly affected bird diversification in positive ways (Padian & Chiappe, 1998), but it also introduced a constraint on body mass due to metabolic and performance demands (Mc Nab, 1994; Tobalske & Dial, 2000; Elliot et al., 2013). There is a tendency to focus on the enabling consequences of functional innovations; however, the potency of trade-offs may be a major factor in shaping the diversity of macroevolutionary outcomes from life’s innovations.

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SHARED DATA

Data deposited in the Dryad digital repository (Burress & Wainwright, 2020).