

Playing out Liem's Paradox: Opportunistic Piscivory across Lake Tanganyikan Cichlids

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ABSTRACT: Trophic specialization is a key feature of the diversity of cichlid fish adaptive radiations. However, K. F. Liem observed that even species with highly specialized trophic morphologies have dietary flexibility, enabling them to exploit episodic food resources opportunistically. Evidence for dietary flexibility comes largely from laboratory studies, and it is unclear whether cichlid fishes undergo diet shifts in the wild. We report observations of diet switching by multiple cichlid species in Lake Tanganyika as a consequence of unusual concentrations of schooling juvenile clupeid fishes. Fish species with varying degrees of trophic specialization converged on a single prey: juvenile sardines that are also endemic to Lake Tanganyika (*Stolothrissa tanganicae* and *Limnothrissa miodon*). We provide evidence for cichlid species acting as jacks-of-all-trades and discuss this evidence in the framework of Liem's classic paradox: that trophic specialization does not preclude dietary flexibility.

Keywords: resource pulses, dietary flexibility, specialization, coexistence, adaptive radiation.

Introduction

In the Great Lakes of East Africa, cichlid fishes have diverged into hundreds of species, in sharp contrast with all noncichlids inhabiting these same lakes (Lowe-McConnell 1969). Numerous hypotheses have been put forth to explain such dramatic intralacustrine diversification. A key feature of many of these hypotheses involves the capacity for cichlids to rapidly evolve highly specialized trophic strategies. Cichlids provide many examples of specialized and—in some cases—bizarre trophic adaptations. These include scale eating (Hori 1993), paedophagy (Greenwood 1956; McKaye and Kocher 1983), piscivory with highly specialized ambush strategies (e.g., death feigning: McKaye 1981; upside-down swimming: Kohda and Hori

1993; Stauffer and Loftus 2010), and biofilm feeding with highly specialized dentition (Greenwood 1974, 1989; Yamaoka 1983, 1991; Konings 2015).

In cichlids with extreme specializations, the functional design of the feeding apparatus is expected to present biomechanical trade-offs associated with differential use of resources (Barel et al. 1977; Yamaoka 1983). Despite this, Liem (1978) argued that feeding structures in cichlid fishes are labile, allowing fish to change their functional repertoire and increase their niche breadth (Liem 1978, 1979, 1980; Greenwood 1991). Under laboratory conditions, dietary flexibility in response to varying resource quality and quantity appeared as strong evidence of widespread niche expansion in cichlid fishes (Liem and Kaufman 1984). Such loose connection between morphology and trophic ecology raised skepticism on the role of resources as the drivers of adaptive diversification in cichlid fish species flocks; this incongruity became known as Liem's paradox (Mayr 1984; Greenwood 1989). However, few studies to date on cichlids have collected evidence for shifts in foraging behavior in the wild (but see McKaye and Marsh 1983; Greenwood 1989; Binning et al. 2009) or in the laboratory (Liem and Kaufman 1984; Liem and Summers 2000). This leaves a gap in our understanding of the relevance of Liem's laboratory experiments in understanding the evolution of trophic diversity in wild cichlid fish communities.

Robinson and Wilson (1998) first provided a potential resolution to Liem's paradox by demonstrating that trophic specialization could still drive adaptive diversification even if phenotypic specialists sometimes acted like ecological generalists (Robinson and Wilson 1998). Specifically, the Robinson-Wilson model (RWM) predicted that a resource that becomes both rapidly abundant and easy to use (e.g., reproductive swarms of aquatic invertebrates, eggs or moribund organisms, pulses of seed or ripe fruit) will also be the preferred food for a variety of organisms, even those with highly specialized trophic morphologies. Once the pulsed resource is absent, these species will resume their usual feeding on dif-

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ferent fallback foods (less preferred resources requiring adaptations for their acquisition and processing; e.g., Marshall and Wrangham 2007). Thus, differences in adaptations to exploit the less-preferred fallback foods would allow similar organisms to coexist in the absence of transient yet preferred food resources.

The RWM described dietary switches in two directions: (1) from a higher-ranked to a lower-ranked resource when the rare higher-ranked resource disappears and (2) from a lower-ranked to a higher-ranked resource when the latter becomes sufficiently abundant. For instance (1), gorillas resume feeding on foliage (a low-ranked fallback food) as fruits (high-ranked resource) become scarce, yet their phenotypic specializations (e.g., morphology, large gut and body size) better reflect adaptations to feed on foliage as opposed to ephemeral fruit (Tutin et al. 1991; Marshall and Wrangham 2007). Conversely (2), Darwin's finches, Arctic char, and North American red crossbills all present distinct ecomorphs that diverge in trophic adaptations and show little overlap in diet throughout the year yet converge in diet during resource pulses, when a preferred higher-quality resource (e.g., insect pupae, fresh or undefended seed) suddenly becomes superabundant (Boag and Grant 1984; Benkman 1987, 1993; Malmquist et al. 1992; C. K. Porter and C. W. Benkman, personal communication). A key problem in evaluating the RWM is the difficulty of observing dietary responses to sudden—therefore rare—pulses of high-quality low-cost prey.

In May 2017, we observed and recorded video footage of a feeding frenzy event involving a massive school of mainly juvenile clupeid fishes and many Lake Tanganyika cichlid species. The transient school attracted a plethora of cichlid fishes, many of them with highly specialized feeding strategies not involving piscivory, and these species preyed on a single prey source: juvenile sardines. We suggest that these unique observations of the feeding behavior of cichlid fishes from Lake Tanganyika provide empirical support for Liem's paradox and the RWM.

Methods

We observed fish foraging behavior over rocky substrate near the village of Kagongo, north of Kigoma, Tanzania, on the eastern shore of Lake Tanganyika (GPS coordinates: 4°48.411'S, 29°36.346'E) using scuba. Two observers conducted fish surveys on a linear transect of an area of approximately 288 m², located perpendicular to the lake littoral and a maximum depth of approximately 15 m. A school of juvenile clupeids recurrently approached the observers throughout the length of the transect, allowing repeated observations of both the resident littoral fish community and the transient school. The observations occurred between 10:00 and 11:00 a.m. on the overcast, rainy morning of May 12, 2017. It is not possible to quantify the number of clupeid larvae

precisely, but we estimate at least 50,000 individuals, since the tightly packed small juveniles were 4–5 cm long and the proportion of the transect occupied by the juvenile fish spanned about 50 m² (almost one-fifth of the total transect area). We identified fish species along the transect and documented their approximate depth and relative abundance. We recorded short video clips in the deep and in the shallow, using a GoPro Hero4 Black Edition 12 MP Action Camera (San Mateo, CA). We analyzed footage frame by frame using video editing software (Premiere Pro CC 2017, Adobe).

In an effort to understand why some cichlid species preyed on the clupeid school whereas others did not, we investigated differences in trophic position among species present at the site. Data on trophic level for each species were obtained from the teleostean trait database FishBase (Froese and Pauly 2019), and data on functional groups were extracted from Fryer and Iles (1972), reviewed by Tada et al. (2017). Using a binomial generalized linear model and a logit link, we modeled the probability of a species to feed on the juvenile fish as a function of trophic level using the package lme4 (Bates et al. 2014) in R version 3.4.2 (R Development Core Team 2019). Data in this study have been deposited in the Dryad Digital Repository (<https://dx.doi.org/10.5061/dryad.72gm17m>; Golcher-Benavides and Wagner 2019).

Results

The clupeid school formed a dense layer 1–10 cm above the substrate in the shallow waters (3–4 m depth) and a less dense school 1–2 m above the rocky substrate at a depth of about 15 m (fig. 1). In the shallowest benthic zone, they attracted large numbers of fish that attacked the school from all angles (video 1, available online). Approximately 870 individuals of 31 species of cichlid fishes within 10 functional groups were observed in the area covered by the school (fig. 2). Trophic level positively influenced the likelihood of feeding on the juvenile clupeids (odds ratio for trophic level = 3.2411 [$P = .036$]; intercept: 0.0283 [$P = .052$]).

Cichlid species feeding on the clupeid school varied in terms of species richness within functional groups and proportion of individuals within functional groups (fig. 2). Out of the 10 observed functional groups, only two were missing among those feeding on the sardines: grazers and scrapers. Piscivores, planktivores, lepidophages, sand scrubbers, invertivores, pickers, suckers, and browsers were all observed attacking clupeid larvae. At ~15 m depth, *Haplotaxodon microlepis* (with an upward-oriented mouth) and *Perissodus microlepis* (with asymmetric mouth morphology) were observed attacking the fish school from below. At this same depth, the largest observed fish—including the apex predators bigeye lates *Lates mariae* and the emperor cichlid *Boulengerochromis microlepis* (trophic levels of 4.5)—came very close to the observers and the school without evidently

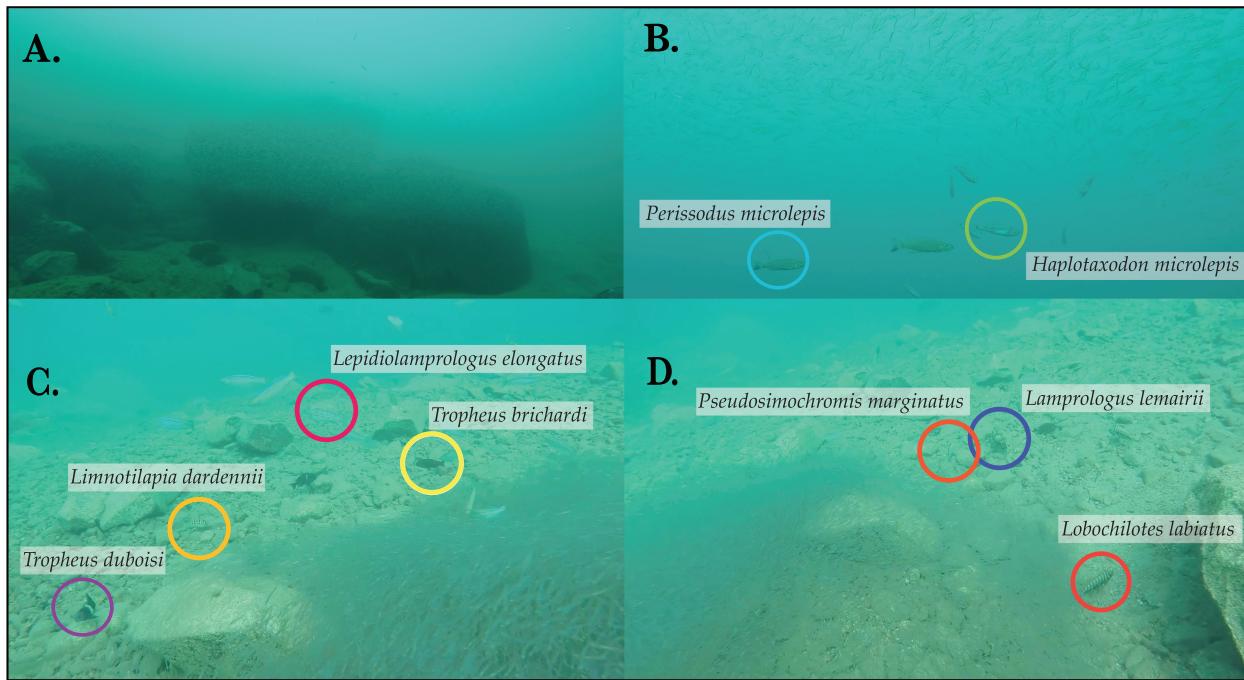


Figure 1: School of juvenile clupeids at a depth of ~15 m (A, B) and ~3 m (C, D). Juvenile clupeids formed a dense school above the substrate in the deep, while fish attempted feeding by surrounding the school (A, B). In the shallow, the school formed a thin dense layer above the substrate, allowing attacks only from above (C, D). One individual of each species of cichlids is circled (shown with unique color codes). When multiple individuals per species are shown, only one is circled.

feeding on it or the cichlids. Browsers in the shallowest benthic zone (biofilm-feeding species) fed on juvenile clupeids (e.g., *Pseudosimochromis marginatus*, *Tropheus duboisi*, and *Tropheus brichardi*, all browsers), but species with extreme subterminal mouths (*Eretmodus cyanostictus*; scraper) and/or tricuspid teeth (*Petrochromis orthognathus*, *Petrochromis polyodon*, *Petrochromis* sp. kazumbe, and *Ophthalmotilapia heterodonta*; grazers) did not attack the juvenile sardines.

Discussion

Our observations provided evidence for opportunistic dietary shifts in some cichlid fish species of the rocky littoral zone of Lake Tanganyika. Trophic position predicted feeding on juvenile clupeids, yet fishes attacking the school of juvenile clupeids represented all trophic levels. All but two functional groups (grazers and scrapers, low trophic level) were observed feeding opportunistically on the juvenile prey. The feeding behavior of the species attracted by the school was consistent with expectations for dietary shifts across a diverse assemblage of cichlid fish species with varying feeding specializations. Observations of dietary flexibility in the wild reported in this study provide empirical evidence in agreement with Liem's paradox and the RWM.

Cichlid fishes do not appear to be solely restricted to optimal feeding strategies. Instead, evidence suggests that they are able to modulate their diet and feeding behavior (Elshoud-Oldenhove and Osse 1976; Liem and Summers 2000). Robinson and Wilson (1998) demonstrated that flexible consumers can still evolve adaptations to exploit resources that account for only a small fraction of their diet and are ignored in favor of other resources when available (solving Liem's paradox). Consistent with the RWM, cichlid fishes in captivity forage only on the resource for which they are adapted to when easier to process resources are unavailable (Liem and Kaufman 1984). Indeed, the vast majority of the cichlid species that we observed were more attracted by the transient school of clupeid juveniles than by any other available food resource (e.g., benthic invertebrates, heavily armored snails, biofilm, adult fish). As seen from the video in slow motion, cichlid fish species across all trophic levels readily engulfed pelagic clupeids from the anterior end, a common feeding method in teleosts feeding on mobile prey (i.e., slow suction feeding: Liem 1984; Liem and Kaufman 1984). For these littoral-specialized cichlid species, juvenile fish schooling in the benthic habitat represented easily available prey relative to fish schooling in the pelagic habitat, where these cichlid species do not occur. Furthermore, juve-



Video 1: Still photograph from a video (video 1, available online) showing a feeding frenzy in the littoral zone of Lake Tanganyika involving multiple species of cichlid fish as predators converging on juvenile clupeids (May 2017).

nile fish are rich in protein and fatty acids relative to other available food resources (Orians and Janzen 1974).

Liem (1980) argued that dietary flexibility was constrained by the strength of biomechanical trade-offs in the function of the teleost trophic apparatus. For instance, biofilm-feeding cichlid fishes have a feeding apparatus characterized by a dominant opercular force efficiency and low head-lifting force efficiency (Liem 1980), while other functional groups (including piscivores) have poor opercular force efficiency and high head-lifting efficiency (Liem 1980; Hori 1991; Liem and Summers 2000). Liem and Summers (2000) established from laboratory experiments that grazers, with the lowest value of head-lifting force efficiency (0.4), rarely fed on novel fish prey that was offered to them (i.e., live juvenile *Poecilia reticulata*), whereas browsers (e.g., *Simochromis diagramma*; with a head-lifting force efficiency of 0.6) and piscivores (e.g., *Lepidiolamprologus elongatus*; with a head-lifting force efficiency of 3.1) readily fed on fish prey. Other differences in trophic apparatus are known to influence foraging rates and likely energy intake rates across biofilm feeders (Yamaoka 1983; Takamura 1984). Grazers comb green algae for diatoms and other microorganisms using loosely packed tricuspid teeth outlining their mouths, whereas browsers (i.e., *Tropheus* spp. and *Simochromis* spp.) nip filamentous algae from the surface of rocks using the tightly packed bicupid teeth outlining their subterminal mouths (Konings 2015). Furthermore, the extremely subterminal mouths of some of these species, such as the scraper *Eretmodus cyanostictus*, may explain their hindered ability to suction feed on juvenile clupeids. It is possible that the extreme degree of morphological specialization found only in scrapers and grazers has reached a point of no return, turning only species within these functional groups into obligate specialists (Takamura 1984).

The RWM added the following nuances onto species interactions models: (1) consumers will ignore less favored resources when more favored resources become sufficiently abundant, and (2) more favored resources are intrinsically easier to use than less favored resources. However, ecological factors other than resource availability and resource acquisition/processing traits may control opportunistic feeding on favored resources (e.g., territoriality, antipredator behavior, past experience). Territory defense and other habitat restrictions may constrain algorivorous males from accessing food resources (Lowe-McConnell 1969, 1996; Yamaoka 1983; Takamura 1984; Takeuchi et al. 2010; Hata et al. 2015; Tada et al. 2017). In the shallow rocky reefs of Lake Tanganyika, grazers aggressively defend feeding territories against conspecifics and congeners (Kohda 1995; Kohda and Takemon 1996). Likewise, defending breeding territories from conspecifics, guarding fry, or hiding from potential predators restricts feeding activities. For instance, mouthbrooding fish cease feeding activities entirely or feed at a lower frequency than nonbrooding fish (Kuwamura 1986). The scraper *E. cyanostictus* (a biparental mouthbrooding species) solely retains a vestigial swim bladder, which further constrains prolonged swimming outside of its habitat in the wave-washed rocks (Brichard 1989; Taylor et al. 2003). Territory defense or anti-predator responses may have inhibited phenotypic specialists (scrapers and grazers) from acting as ecological generalists. Still, these ecological factors do not reject the hypothesis of opportunistic feeding but instead provide an opportunity to explore novel directions building on the RWM.

Transient resource pulses of highly nutritious foods that a wide range of trophic phenotypes can readily consume may be particularly important in facilitating the persistence of small and geographically isolated fish populations. In our study, finding two low-abundance algorivores (*Pseudosimo-*

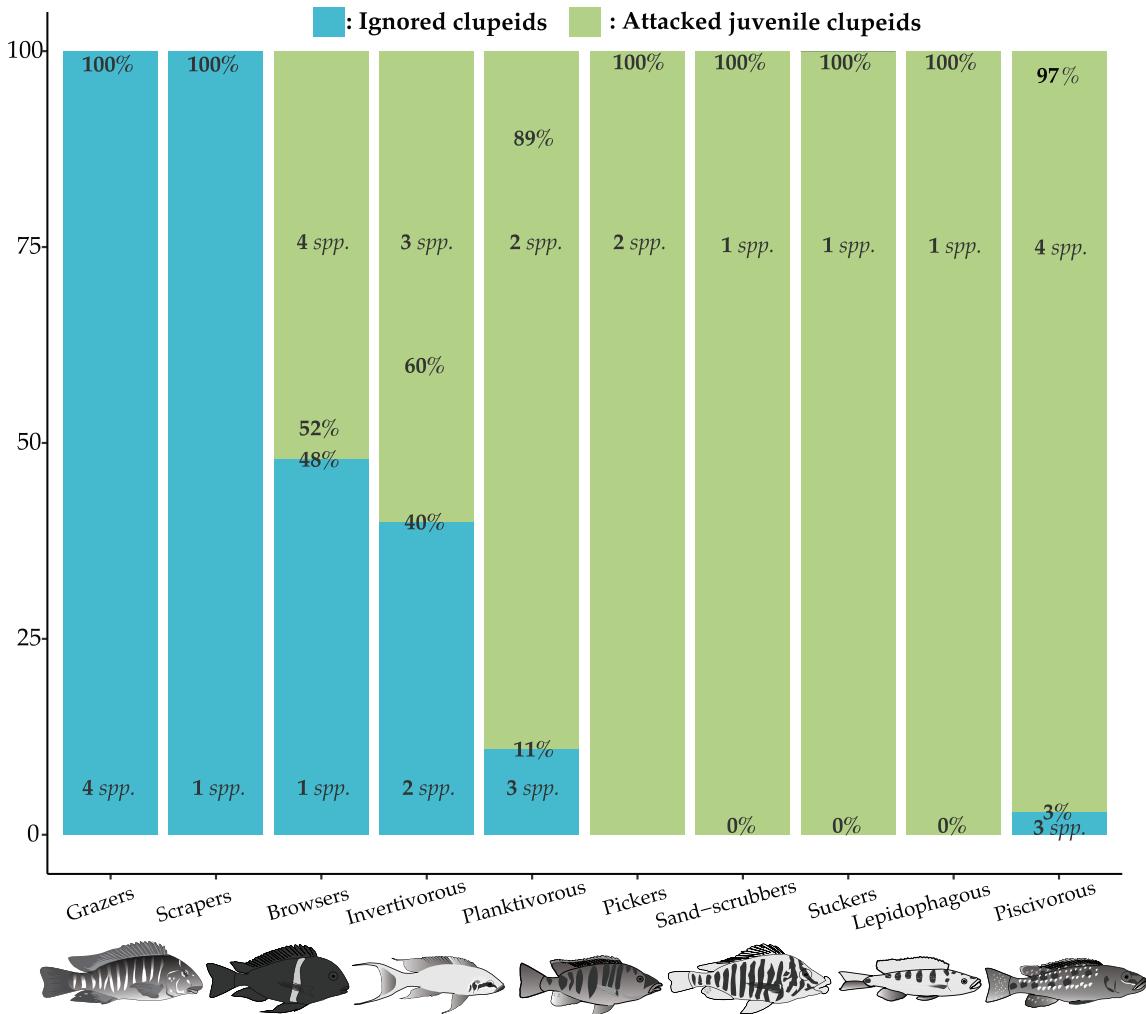


Figure 2: Proportion of individuals within functional groups feeding on juvenile clupeids (green) or not feeding (blue) during a feeding frenzy. Functional groups are ordered by increasing trophic position. Percentages correspond to proportion of individuals within functional groups; number of species per functional group categories are also shown.

chromis marginatus, *Tropheus duboisi*) feeding on the sardine school supports this theory. Pulses of resources may facilitate the increased species richness observed at the micro-habitat scale (Rabenold 1979). Foraging guilds of cichlid fishes are exceptionally species rich in the rocky littoral zone of Lake Tanganyika (Fryer and Iles 1972; Hata et al. 2014; Konings 2015). At the lake-wide scale, the most studied cause of fluctuation in littoral food resources comes from wind-powered, partial nutrient upwelling events occurring in the southern basin of Lake Tanganyika (McIntyre et al. 2006; Cohen et al. 2016), and it is reasonable to expect coupling between the seasonality of such algal blooms and pulses in clupeid densities (Coulter 1991). Transient clupeid schools may thus provide an important transfer of nutrients from pelagic waters to littoral ecosystems, facilitating high littoral biodiversity. Human harvest of pelagic clupeids could

therefore negatively affect the abundance and diversity in the littoral community via density-dependent processes. Additional studies focused on the limnology of the lake are needed to further understand resource dynamics and interactions between pelagic and benthic food webs. The dynamic link between density-dependent processes and phenotypic diversity deserves further research (Reznick 2015).

Because of the history of rapid decline in lake-wide ecosystem productivity due to climate change, further shifts in pelagic and benthic food webs are expected in the near future (Alin and Cohen 2003; O'Reilly et al. 2003; Verburg and Hecky 2003; Verburg et al. 2003; Cohen et al. 2016). Testing predictions of the RWM deserves more attention, and generally it is important to study these spectacularly diverse ecosystems while they are intact and before it is too late (e.g., Lake Lanao; Kornfield and Carpenter 1984;

Mayr 1984). Experimental manipulations of resource availability and monitoring of seasonal shifts in resource abundance will continue to shed light on the potential implications of Liem's paradox and the RWM on ecological divergence in the cichlid adaptive radiations in East Africa and elsewhere (McKaye and Marsh 1983; Sazima 1984; Greenwood 1989; Bouton et al. 1997; Katunzi et al. 2003; Binning et al. 2009; Martin and Genner 2009; Correa and Winemiller 2014). The key uncertainty now is what the frequency of this kind of event is in Lake Tanganyika and other East African lakes. Pelagic clupeids in Lake Tanganyika are known to undergo diel vertical migrations inshore that experience inverse directional shifts in overcast days or in bright moonlight, enhancing avian predator activity (Coulter 1991). Overcast days are more common throughout the wet season, and it is possible that these events have been previously missed by divers because of less frequent fieldwork during these times of the year. Additionally, analogous processes may be important in other African Great Lakes lacking juvenile clupeids. Lowe-McConnell (1987) documented opportunistic feeding on small Ephemeroptera (*Povilla adusta*) by many haplochromine cichlids in Lake Victoria. Adult emergence of chaoborid flies (*Chaoborus edulis*) are known to occur in Lake Malawi as giant dense swarms that may likely overwhelm predators, yet detailed observations are missing from the literature (Lowe-McConnell 1987). Observing this phenomenon, which had previously been missed by divers with decades of experience in Lake Tanganyika, is a reminder of what is left to be unveiled in the Lake Tanganyika ecosystem.

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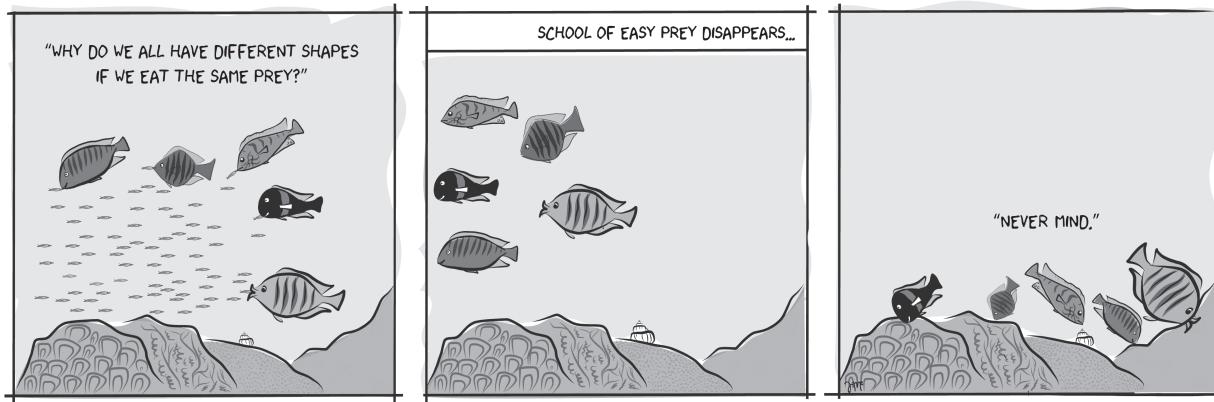
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Liem's paradox (1980) in wild cichlid species from Lake Tanganyika. Credit: Jimena Golcher-Benavides.