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Research Article

More non-native fish species than natives, and an invasion of Malawi cichlids, in ancient Lake Poso, Sulawesi, Indonesia

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Abstract

Ancient Lake Poso in Central Sulawesi, Indonesia, is among the deepest lakes in Asia, and hosts a largely endemic fauna of fishes, crustaceans, and molluscs. Introduction of non-native fish species started at least a century ago to foster local fish production. Recent fieldwork suggests that introduction of non-native fishes is ongoing, including species that originate from the ornamental pet trade. These include the hybridogenic ornamental "flowerhorn" cichlid, a fish that spread rapidly in Sulawesi's Malili Lakes, and the "golden cichlid," *Melanochromis auratus* from African Lake Malawi. This popular aquarium species colonized Lake Poso even more rapidly than the flowerhorn, and is omnipresent at benthic habitats across most of the lake. Here, we list records of 17 non-native fish species from Lake Poso, present the first assessment of golden cichlid stomach contents outside of their native habitat, report the occurrences of non-native crustaceans, molluscs and plants, and discuss potential impacts on the native fauna and ecosystem. Most of the non-native species have established substantial populations, and it appears very plausible that the non-native fauna affects endemics. This is supported by the finding that golden cichlid stomachs contained a broad spectrum of items, including fish, their scales, fins, eggs and larvae, and various invertebrates. We conclude that non-native species introduction poses a substantial and increasing threat to the Lake Poso fauna, a major hotspot of aquatic biodiversity in the Wallacea region.

Key words: species flock, conservation, ancient lakes, non-native fishes, freshwater

Introduction

The introduction of non-native fish species is a serious threat to freshwater biodiversity (Reid et al. 2019). This applies especially to species restricted to isolated lakes (Sala et al. 2000). Ancient lakes, i.e., lakes that have existed for at least 100,000 years, promote high levels of endemic biodiversity, but are heavily affected by changes associated with human activities (Hampton et al. 2018). Ancient lakes in Sulawesi, namely the Malili Lakes system and

Lake Poso, harbour endemic radiations of different systematic groups of fishes as well as spectacular invertebrate species flocks (Kottelat 1990, 1991; Kottelat et al. 1993; von Rintelen K and Cai 2009; von Rintelen K et al. 2007, 2010; Haase and Bouchet 2006; Herder et al. 2006a, b; summarized in von Rintelen T et al. 2012; Vaillant et al. 2011, Klotz et al. 2021). Several non-native fish species have been introduced to the Malili Lakes, including the Asian striped snakehead *Channa striata* (Bloch, 1793) and the Amazon sailfin suckermouth catfish *Pterygoplichthys pardalis* (Castelnau, 1855) (Herder et al. 2012). None of those species has been reported colonizing Sulawesian lakes as successfully as "flowerhorn" cichlids. Flowerhorns are artificial hybrids of different Neotropical cichlids, created for the ornamental fish trade and pose a serious threat for Lake Matano's endemic fauna (Herder et al. 2012; Hilgers et al. 2018).

Lake Poso is an oligo-mesotrophic lake of tectonic origin, located in the central highlands of Sulawesi at about 500 m above sea level (Vaillant et al. 2011). With a maximum depth of 450 m and about 320 km^2 surface area, it is the second largest and also the second deepest lake of the island (Whitten et al. 1987 a); von Rintelen T et al. 2012). Lake Poso was formed during the collision of two major tectonic plates, and is estimated more than 1 million years old, though this estimation remains to be critically tested (Vaillant et al. 2011; Klotz et al. 2021). Typical features are the lake's extensive sandy beaches and rocky habitats or coarse gravel where the shore is steeper (von Rintelen T et al. 2012). The lake drains at its north-eastern corner through the Poso River into the Bay of Tomini. An operating hydroelectric dam at the Poso River is equipped with a fishway to support the commercially important eel fisheries in the lake; the system, however, lacks a downstream migration facility (Baumgartner and Wibowo 2018). A second dam of 515 megawatts is under construction, and terraforming for re-shaping the outlet region of the lake has started just recently (Mongabay 2020).

Lake Poso's native fauna exhibits an exceptionally high degree of endemism. The native endemic invertebrate fauna forms both, small and comparatively large species flocks of atyid shrimps (von Rintelen and Cai 2009; Klotz and von Rintelen 2013; Klotz et al. 2021), decapod crabs (Chia and Ng 2006; Schubart and Ng 2008), cyrenid bivalves (von Rintelen T and Glaubrecht 2006), as well as pachychilid (von Rintelen T et al. 2010), planorbid (Albrecht and Glaubrecht 2006; Albrecht et al. 2020) and hydrobiid gastropods (Haase and Bouchet 2006; Zielske et al. 2011). Ten out of the 13 native freshwater fish species are endemic to the lake and its tributaries: two gobies (Gobiidae: *Mugilogobius* spp.), the halfbeak *Nomorhamphus celebensis* Weber & De Beaufort, 1922 (Zenarchopteridae), and seven species of ricefishes (Adrianichthyidae: *Adrianichthys*, *Oryzias*) (Kottelat et al. 1993; Meisner 2001; Parenti and Soeroto 2004; Kraemer et al. 2019). The ricefishes comprise two phylogenetic lineages (Herder et al. 2012; Mokodongan and Yamahira 2015), small species flocks with highly derived morphology and modes of reproduction (Kottelat 1990; Parenti 2008). Three eel species, the Celebes longfin eel *Anguilla celebesensis* Kaup, 1856, the Giant mottled eel *A. marmorata* Quoy & Gaimard, 1824 and the Indian shortfin eel *A. bicolor pacifica* Schmidt, 1928 are native in Lake Poso and important for local fisheries (Arai 2014; Hagihara et al. 2018a, b). *Anguilla marmorata* is the predominant eel species, whereas *A. celebesensis* occurs frequently in tributary rivers but is apparently rare within the lake itself (Hagihara et al. 2018a). *Anguilla bicolor pacifica* appears to be generally rare. Another species, *A. interioris* Whitley, 1938, has been recorded in the lower Poso River (Sugeha et al. 2008; Hagihara et al. 2018a, b), but not in the lake.

The first records of non-native fish species in Lake Poso date to over a century ago by Weber (1913), who reported the snakehead *Channa striata* and the climbing perch *Anabas testudineus* (Bloch, 1792) from the lake. Whitten et al. (1987a, b) and Kottelat (1990) added the common carp *Cyprinus carpio* Linnaeus, 1758, the silver barb *Barbonymus gonionotus* (Bleeker, 1849), Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852) and a walking catfish *Clarias* sp. to the list of non-native species. Whitten et al. (1987 a, b), Kottelat (1990), Larson (2001), Parenti (2011) and Parenti and Soeroto (2004) already considered fish introductions, especially parasites accompanying non-native fishes, a major threat that likely explained the decline of native fish stocks in Lake Poso, including potential extinctions.

Indeed, one of the two endemic gobies, *Mugilogobius* (*Weberogobius*) *amadi* (Weber, 1913), as well as the two ricefish species, *Adrianichthys kruyti* and *A. roseni*, have not been recorded since the mid-1980s (Kottelat 1990; Larson 2001; Parenti 2011). Whitten et al. (1987b) supposed that they might be extinct. However, Kottelat (1990) argued that data are deficient and assumed declaring them extinct might be premature. This point remains valid as systematic field investigations of the native fish fauna, including pelagic and deepwater-dwelling species, remain fragmentary.

Here, we report recent records of non-native fish species from Lake Poso. We visited several locations around the lake between 2012 and 2019, including the lake's pelagic and outlet areas. We recorded 17 non-native fish species, including the flowerhorn cichlid, and traced a massive expansion of a new invader, the golden cichlid *Melanochromis auratus* (Boulenger, 1897). To estimate possible impacts on the native fauna, we conducted stomach content analyses of juvenile and adult golden cichlids.

Materials and methods

Fish species occurrence was recorded in September 2012, November 2013, and May to July 2019 at 38 sites around Lake Poso in Central Sulawesi, Indonesia (Figure 1). Sampling and visual surveys were conducted using snorkelling and scuba diving to 15 m of depth, snorkelling-aided gillnetting (6-, 8- and 10-mm mesh size), cast netting, dip netting, beach seining, and

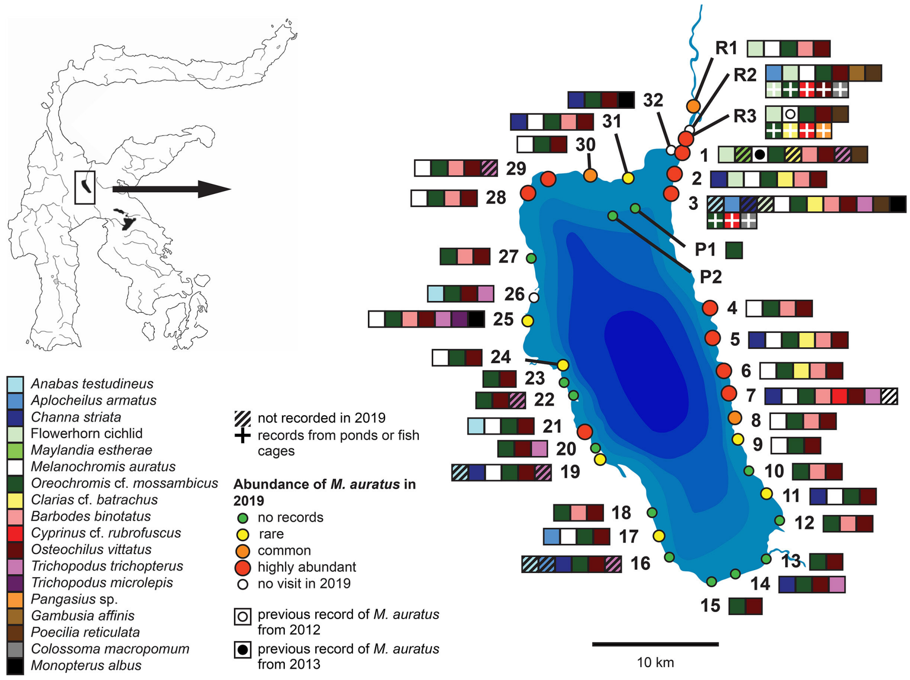

Figure 1. Map of Lake Poso, Central Sulawesi (Indonesia), showing location records of non-native fish species from 2012, 2013 and 2019. P indicates pelagic sites, R habitats in the river draining the lake to the sea. *Pangasius* sp. was only recorded captive in a net cage in the outlet mouth, with no indication that feral fish occur in the region. Map by Thomas von Rintelen, modified (with permission).

angling. Visibility ranged from < 1 to about 10 m, depending on site and conditions. Shallow and sandy habitats usually had lower visibility, whereas rocky areas with steeper slopes had clearer water in most cases. Non-native invertebrates and plants were recorded where obvious. Two pelagic sites were sampled to a max. depth of 80 m using two vertical 2 × 20 m multimesh gillnets with panels of 2 × 2 m alternating in mesh size (6, 8, 10 mm), five times each, for 30 to 60 minutes.

Abundances of *M. auratus* were evaluated using a randomized point abundance survey approach. The surveyor (JM) slowly snorkelled a zig-zag course in transverse direction (45°) along the shoreline. Every estimated 10 m, he stopped and counted fishes within a radius of 2 m. Individuals between observation points were ignored. After reaching the lower (5 m) or upper (0.5 m) depth limit of this survey, he changed snorkelling direction by 90°, thereby moving again in a 45° course relative to the shoreline, to shallower or deeper areas, respectively. This strategy implements habitat heterogeneity and avoids revisits of observation points. 32 sites were investigated, with 40 to 100 observation points per site. Frequencies were calculated by dividing the total count of cichlid specimens per site by the number of observation points; categories were defined as < 0.2 rare, 0.2–0.5 common, > 0.5 highly abundant (Figure 1).

Local aquaculture units located within the lake and its drain were inspected where possible. Catches of local fishermen were incorporated when observed, and if related to a specific locality. Local fishermen and residents who had clear affinities to the lake were interviewed when possible. Records of non-native fishes from an artificial pond directly at the lake's shoreline were considered (and marked) because the owner stated that all fishes in the pond had originated from the lake.

The stomach contents of 58 golden cichlids which were fixed in formalin or 80% ethanol, were examined under a stereo microscope and volumetric proportions of food items identified as described in Hilgers et al. (2018). Specimens originated from four different sites (3, 5, 7, 29, see Figure 1). Data from juveniles were combined because of limited specimens. Cichlids above 50 mm standard length (SL; N = 45) were considered mature, given the first occurrence of nuptial colouration at that size; individuals under 50 mm SL (N = 13) were considered immature.

Results

Records of non-native fish species in Lake Poso

We recorded 17 fish species clearly or most likely not native to Lake Poso (Figure 1, Supplementary material Table S1). Six of the non-native species had previously been reported (Weber 1913; Whitten et al. 1987a; Kottelat 1990). Three of those are confirmed here (*Anabas testudineus*, *Channa striata*, *Trichogaster trichopterus*), whereas the species identities of the tilapia (*Oreochromis*), walking catfish (*Clarias*), and carp (*Cyprinus*) are unconfirmed.

Three of the non-native fish species recorded for the first time in Lake Poso are cichlids that originated from the ornamental fish trade: "Flowerhorn cichlids" (also called "Luohan" or "Louhan") are artificial hybrids composed of Central American lineages (see Nico et al. 2007; Ng and Tan 2010; McMahan et al. 2010). This species caused severe problems in other Sulawesi lakes (Herder et al. 2012; Hilgers et al. 2018). Flowerhorns are well established in north-eastern Lake Poso close to the outlet but were not recorded elsewhere in the lake (Figure 1). *Maylandia estherae* (Konings, 1995), the East African "red zebra cichlid", was observed only at a single location in the outlet area of the lake, and it is unclear if the species has established a reproducing population. In contrast, the "golden cichlid" *Melanochromis auratus* (Figure 2) introduced from Lake Malawi became established in Lake Poso. While *M. auratus* was observed only at the outlet in 2012—this was the first record of the species in the lake—it was already highly abundant at a nearby location within the lake in 2013 was abundant in 2019 across the lake except for its southernmost habitats (Figure 1).

The carp recorded here from ponds and fish cages were coloured "Koi." There are no indications that the carp reproduce in the lake, and we assume that those fish present are stocked. As the current study does not include further examination of carp characters, we refer to these fish as *Cyprinus* cf. *rubrofuscus* Lacepède, 1803. Thus, the identity of carp reported

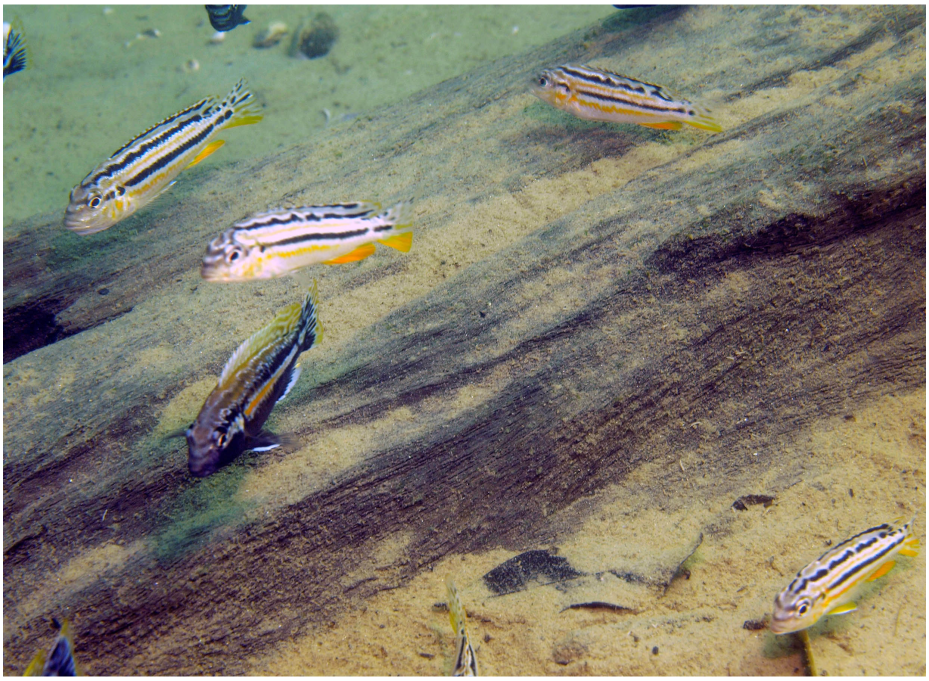

Figure 2. The "golden cichlid" *Melanochromis auratus,* a species originally endemic to Lake Malawi in East Africa, at its habitat in Lake Poso. Males and females differ in their colouration. Females (four adults in the picture) and juveniles have yellowish-golden bodies with two distinct black lateral stripes, whereas adult males (one individual in the left foreground) have blackish bodies with a single turquoise lateral stripe and a blueish to yellowish brown back.

by earlier authors cannot be validated. The same applies to tilapia and walking catfish. The specimens recorded here are apparently aquaculture stocks; pending focal investigations, we refer to these as *Oreochromis* cf. *mossambicus* and *Clarias* cf. *batrachus*.

Oreochromis cf. *mossambicus* and *Osteochilus vittatus* are omnipresent throughout the lake's inshore habitats. *Channa striata* occurs in most of the shallow habitats suited for snakeheads, but in low abundances. Juvenile *O. vittatus* and *O.* cf. *mossambicus* are most common in the shallows, commonly associated with *Barbodes binotatus*, whereas adults inhabit the full observation depth. Adult *O.* cf. *mossambicus* are most frequent above sandy or muddy habitats, where they also breed, down to several meters deep. *Anabas* and *Clarias* were recorded only occasionally, the latter possibly due to their nocturnal behaviour. *Anabas testudineus*, *T. trichopterus*, *A. panchax*, and *P. reticulata* were seen mostly in the shallows, predominantly in habitats associated with human activity. This applies also to the single record of *Gambusia* sp. *Monopterus albus* was observed twice in tributary mouths, and one dead specimen found in a disturbed swampy beach area. The second gourami species, *T. microlepis*, was only observed once, together with *T. trichopterus*, near a river mouth close to agricultural land.

Stomach contents of Melanochromis auratus

The stomachs of *M. auratus* (Figure 3) contained a broad spectrum of food items, with substantial variation among individuals taken from different sites.

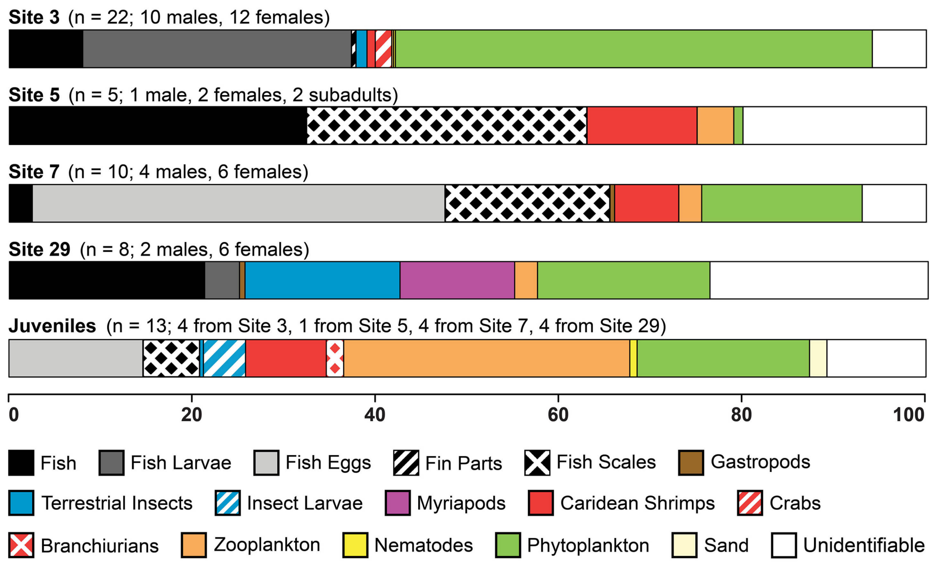

Figure 3. Stomach contents (in percent) of golden cichlids taken from four sites in Lake Poso. The upper four bars represent adult fish, the lowermost bar juveniles (see Figure 1 for sampling site localities). Stomach content composition of adults covers a wide array of prey, from fish and fish eggs to shrimps and phytoplankton, and varies strongly among sites. The juveniles inspected contained prominent amounts of zooplankton.

Variation ranged from contents dominated by phytoplankton (floating green algae) and fish larvae (site 3: a sandy site; mostly ricefish, which are abundant in this habitat; Figure 1) to substantial amounts of eggs and scales of fish (site 7: a rocky spawning habitat of *O. orthognathus* and *O. nebulosus*; eggs and scales match those of endemic *Oryzias*). In most samples, records of scales were not accompanied by other remains of similar-sized fish, pointing towards lepidophagy. In contrast to larvae and juveniles, little evidence of predation on subadult or adult fish occurred. The cases recorded include two immature individuals of the endemic goby *Mugilogobius sarasinorum* (sites 5, 29), and an adult male *O. nebulosus* (site 7). Samples from site 29 (rocky) contained mostly juvenile *Caridina* and other types of zooplankton, complemented by terrestrial arthropods like insects and myriapods.

Hydrobiid gastropods were rarely present in the stomachs (one operculum of a hydrobiid snail at site 29, an empty shell at site 7). Despite their abundance in Lake Poso, remains of adult *Caridina* shrimps were surprisingly rare in the records. Attacks on *Caridina* shrimps were observed several times, i.e., at site 29 (J.M., 2019 *pers. obs.*). Juvenile *M. auratus* appear to consume more zooplankton than do adults, which in turn consumed higher proportions of fish. Taken together, our preliminary data show that *M. auratus* is highly opportunistic in food consumption and feeding habitat. Items are obviously obtained from the substrate, throughout the water column and at the surface. The data also show that a wide range of the endemic fauna of Lake Poso is eaten by the golden cichlid.

Records of other aquatic non-native species

Fishes and their parasites are not the only aquatic organisms introduced to Lake Poso. Two floating plant species with pantropic introductions were recorded: the water hyacinth *Eichhornia crassipes* (Mart.) and the water lettuce *Pistia stratiotes* L. Both occurred in limited numbers, and mostly at sites substantially affected by anthropogenic influence such as the outlet area. However, in 2019, single *Eichhornia* patches were observed drifting in open-water habitats of the lake.

Non-native molluscs include at least two species, the golden apple snail *Pomacea canaliculata* (Lamarck, 1822), a species popular among aquarium hobbyists, and the Chinese pond mussel *Sinanodonta* cf. *woodiana* (Lea, 1834). *Pomacea* is locally abundant at the outlet area and in other shallow habitats affected by anthropogenic activities. *Sinanodonta* is highly abundant in sandy areas at the southern tip of the lake around the village of Pendolo. One non-native crustacean species was recorded: the rice prawn *Macrobrachium lanchesteri* (de Man, 1911), widespread in southeast Asia (De Grave et al. 2013), which we recorded at night at site 3 (Figure 1).

Observation of parasite infestations

Many native fishes, especially *Oryzias* spp. and *Mugilogobius sarasinorum*, but also *Adrianichthys* spp., were infested by parasites. Copepods of the genus *Lernaea* are most common. However, parasitic branchiurans, the identity of which could not be identified more precisely, were also observed. Individuals of these were also found in the stomach of an immature *Melanochromis auratus*, suggesting they were picked from a host fish. In addition to parasites, many *Oryzias* individuals showed necroses, fungal infections and fin rot. More rarely, fish with bent spines were seen.

Discussion

The golden cichlid invasion

Melanochromis auratus was first observed in 2012, spread rapidly across most of Lake Poso and now is present at high numbers in most habitats. As most of the records were collected by snorkelling, we assume that distribution gaps, which are mostly shallow sites, might be closed when deeper habitats are incorporated. Focal scuba diving revealed presence of golden cichlids down to 25 m, and they likely occur even deeper, as in Lake Malawi (Ribbink et al. 1983).

The golden cichlid belongs to the predominantly algae-scraping group of “mbuna” cichlids of Lake Malawi where it inhabits a wide array of rocky habitats, including transition zones (Konings 1995). Habitat use in Lake Poso partially exceeds that reported from its native range. Especially at the northern and eastern shore, i.e., in the area close to the probable initial introduction, the species also inhabits open and shallow sandy areas lacking rocks, a habitat type not used by the species in Lake Malawi (Markert et al. 1999). We hypothesize that high population densities may drive individual cichlids to colonize less preferred habitats, while potentially lower competition compared to Lake Malawi may allow them to thrive in habitats not normally occupied in their native lake.

Among Lake Malawi's mbuna cichlids, *M. auratus* consumes a conspicuously high proportion of animal components, including fish and copepods (Reinthal 1990; Konings 1995). It also consumes a broad feeding spectrum in Lake Poso, including substantial amounts of native fishes, their eggs and fry, aquatic invertebrates, and phytoplankton (Figure 3). Site-dependent differences in stomach contents in combination with a broad diet spectrum indicate opportunistic feeding habits of *M. auratus*. Fish scales recorded in the cichlid stomachs might even indicate a further expansion of its diet spectrum. Lepidophagy has so far been reported from the closely related *Melanochromis lepidiadaptes* Bowers and Stauffer, 1997 (see also Konings 1995 p. 170) and is not known for *M. auratus*. Our analyses provide only a first snapshot of the trophic profile of *M. auratus* as the examined fish were taken from just four sites, and overall sample size from each site was small. However, the diversity of prey species was high, so that when a larger number of individuals is analyzed, the trophic niche width may expand. Given that data describing the trophic ecology and habitat use of the Lake Poso ichthyofauna are virtually absent, conclusions regarding competitive interactions with non-native species remain largely speculative. In the case of *M. auratus*, niche overlap with ricefishes and gobies (e.g., zoo- and phytoplankton) may occur, and competition with molluscs and shrimps for algae is also possible. Levels of resource limitation in this system have not been studied.

The golden cichlid is a popular ornamental aquarium fish, and it is likely that it was either intentionally or accidently introduced to the lake by aquarists. Factors that probably add to its colonization success are its broad trophic niche (Vazques 2006; Hill et al. 2015), the great similarity of habitats in Lake Poso to its natural habitat in Lake Malawi, maternal care by mouthbrooding, lacking stationarity, and pronounced aggressive behaviour (see Konings 1995; Nico and Fuller 1999; Strayer 2010). We observed interactions with native species that included golden cichlid individuals of various sizes (males and females) chasing endemic gobies (*Mugilogobius sarasinorum*), ricefishes (*Oryzias nigrimas*, *O. orthognathus*, *O. nebulosus*, juvenile *Adrianichthys* spp.), and shrimps (*Caridina* spp.) (J.M., J.M.F., I.V.U., L.H., F.H. *pers. obs.*).

In sum, *M. auratus* is a rapidly spreading opportunistic feeder that uses a wide array of available dietary items, including the endemic taxa. However, there are no indications of extreme decreases in population size of endemic species so far. Nonetheless, it should be noted that research on the lake's diversity and particular species abundances is limited. We also assume that population expansion may not have reached the invasion peak approximately one decade after introduction. Consequently, monitoring of the ecological effects of the golden cichlid in Lake Poso is urgently needed.

A species-rich non-native fish assemblage that likely affects the native fauna

The number of fish species introduced into Lake Poso (17 species) now exceeds the native-fish species diversity (13 species). Ten of the non-native fish species recorded in Lake Poso have also been reported from Sulawesi's Malili Lakes (Herder et al. 2012), including *Aplocheilus*, *Clarias* and *Cyprinus* (discussed below). The list of non-native fishes (Figure 1, Table S1) demonstrates that introductions have taken place in the past (Weber 1913; Kottelat 1990) and continue today. Direct effects of fish introductions may include competition, predation, and the introduction of parasites and pathogens (McHugh et al. 2006; Meeuwig et al. 2011; Strecker 2006; Witte et al. 1992). While tests for competitive interactions require the analysis of niche overlap in detail (e.g., Hilgers et al. 2018), first indications for predation may be derived from field observations, known feeding habits of the invader from other habitats, and focal stomach content analyses. Tracing the causalities of infestation with parasites and pathogens requires increased efforts, but field observations can also provide valuable first indications. The impacts by most of the non-native fish species introduced to Lake Poso have not been assessed. Most of the species are, however, well-known from aquaculture and introduction to other locales, permitting estimates.

The striped snakehead *Channa striata* and the walking catfish *Clarias* cf. *batrachus* are valuable, robust and air-breathing food fishes, transplanted for aquaculture and stocking purposes throughout the tropics, including Indonesia (Berra 2007; Kottelat et al. 1993). Both are target species of spearfishing in Lake Poso. The striped snakehead was already present more than a century ago in Lake Poso (Weber 1913) and was mainly observed in vegetation or between branches of fallen trees of the shallows. *Clarias* were reportedly introduced into the lake by Javanese transmigrants at the village of Pendolo prior to the disappearance of native *Adrianichthys* and *Mugilogobius* species in the 1980s (Kottelat 1990). As *Clarias* is mostly nocturnal, observational records are limited. However, they were repeatedly observed during the day in the outlet region, juveniles were caught in the lower reaches of tributaries, and individuals of various sizes were observed at night at site 3. This suggests a wide distribution in the lake. *Channa* and *Clarias* are predators with broad diet breadths (e.g., Talwar and Jhingran 1992; Bhattacharjee and Chandra 2016; Chakraborty et al. 2017), and substantial direct impacts on the native aquatic fauna appear plausible.

The African tilapia *Oreochromis* cf. *mossambicus* is a food fish of global importance and a prime target for fishing at Lake Poso. Tilapia was introduced to Sulawesi as early as the 1940s (Kottelat and Whitten 1996) and has reportedly been fished in the lake for generations. Tilapia is caught by spearfishing, angling or trapping and is also raised in the lake in wire cages. These cages typically have large mesh sizes that allow transition of food particles and small fish. Observations include repeated cases, where such cages contained mature fish of both sexes, highlighting the potential of unintentional release of fry from local aquaculture. Tilapia species are among the most successful aquatic invaders on a global scale (Lowe et al. 2000), outcompeting many native species (e.g., Weyl 2008). Their introduction had profound impacts on the fish communities of other tropical lakes (e.g., Lake Nicaragua: McKaye et al. 1995; Canonico et al. 2005; Lake Victoria: Barel et al. 1985), and eradication programs are suggested, for example, for Lake Malawi (Genner et al. 2013). In contrast to Lake Poso, *Oreochromis* population growth remained limited in Lake Matano, possibly due to nutrient limitation (Herder et al. 2012). However, they perform better under the less oligotrophic conditions of Lake Poso, but population dynamics as well as their relevance in the lake remain unstudied.

Flowerhorn cichlids are a major threat for the local fauna in Lake Matano (Herder et al. 2012; Hilgers et al. 2018) and were first recorded at Lake Poso in September 2012. These records were near the lake's outlet, including in fish cages mostly used for growing small fish trapped in the outlet of the lake to market size (sites R2, R3; Figure 1). We observed that these cages contained a collection of non-native fish species, from tilapia and carp (various colour morphs of *C.* cf. *rubrofuscus*), to *O. vittatus* and the East African golden cichlid. The owner of the cages stated that flowerhorns are frequently present in his traps; in one of the cages, flowerhorns were breeding. The small size of free-swimming flowerhorn fry allowed them to escape the fish cages, so we assume that many juveniles escaped to add to the population proliferating in the outlet area. In 2019, flowerhorn cichlids still appeared to be restricted to the outlet area, with the most distant record originating from only around 1 km south of the outlet mouth. The cichlid *Maylandia estherae* was restricted to a single observation in Lake Poso in 2013 close to the outlet.

The blue panchax *Aplocheilus armatus* and the climbing perch *Anabas testudineus* are fishes with wide distributions in Southeast Asia. We follow Katwate et al. (2018) in recognizing *Aplocheilus armatus* (van Hasselt, 1823) as the valid name of the Indonesian blue panchax, previously listed as *A. panchax*. Whether the species is native or introduced to Sulawesi is debatable. Phylogenetic analyses place panchax from Sulawesi close to populations from Java, although forming a separate haplogroup (Beck et al. 2017). While arguing that blue panchax colonized the island independently ~ 27,000 years, it could also suggest that they were introduced from a location on Java not sampled by Beck et al. (2017), possibly for mosquito control (e.g. Welcomme 1988). In the Malili Lakes and also in Lake Poso, blue panchax tend to be frequent in shallow habitats strongly affected by human activities (see Herder et al. 2012), frequently in the mouth and lower reaches of tributaries, or close to flooded (rice) fields. For that reason, Herder et al. (2012) assumed that the occurrence of *A. panchax* in the Malili Lakes is likely due to human-mediated dispersal, and the same might be true for Lake Poso. We hence tentatively assume that *A. panchax* is not native to Lake Poso. Air-breathing *Anabas* are frequently seen in markets and used by subsistence fisheries and aquaculture throughout most of Indonesia, including Sulawesi. It is known from Lakes Poso, Matano and Towuti since Weber (1913). Jamsari et al. (2010) reported conspicuously low levels of variation in the mtDNA control region among populations from Sumatra and Peninsular Malaysia, a finding that would be congruent with human translocation. It remains unclear if *Anabas* is introduced or native to Sulawesi. As in the blue panchax, it has been observed predominantly at sites strongly affected by human activity, and we hence follow Herder et al. (2012) in assuming its introduction to the lake. *Anabas* is considered omnivorous, including small gastropods (Bhattacharjee and Chandra 2016), and might accordingly affect endemic invertebrates.

Live-bearing guppies *Poecilia reticulata* Peters, 1859 and mosquitofish *Gambusia* spp. (Baird & Girard, 1853) have been widely introduced in Asia for mosquito control, with guppies also popular as ornamental aquarium fish (Berra 2007). Both inhabit shallow waters and were observed in Lake Poso exclusively at heavily disturbed habitats such as shallow lagoons or muddy entrances of rice field ditches, near fields, villages or cottages. In contrast, three-spot gourami *Trichopodus trichopterus*, bonylip barb *Osteochilus vittatus* (Valenciennes, 1842), spotted barb *Barbodes binotatus* and tilapia *Oreochromis* cf. *mossambicus* (Peters, 1852) were abundant to highly abundant throughout nearly all of Lake Poso's inshore habitats. *Trichopodus trichopterus* are confined mostly to rather shallow areas, where they form shoals especially in or close to submerged vegetation. Observed abundance of this species was substantially lower in 2019 compared to 2012 and 2013, suggesting severe fluctuations in population size. Conspicuously, a single three-spot gourami was caught in pelagic waters (about 1 km offshore at site 3) in 40 m depth at night with a gillnet. A second species of the genus, the moonlight gourami *Trichopodus microlepis* (Günther, 1861) was observed once in a shallow inshore habitat located on the lakes west coast.

The pacu *Colossoma macropomum* was listed from the lake already by Parenti and Soeroto (2004). The present record is restricted to individuals present in an ornamental pond directly at the lake's shore (site 3, Figure 1). The owner of the pond stated that all fish he kept in this pond originated from angling in the lake (*C.* cf. *rubrofuscus*, *O.* cf. *mossambicus*), or from fish cages used to raise juveniles trapped in the lake's outlet at Tentena (*C.* cf. *rubrofuscus*, *Oreochromis* cf. *mossambicus*, *C. macropomum*). He also reported that *C. macropomum* and *C.* cf. *rubrofuscus* are commonly caught in the lake by local fishermen and complained that stocks of *C.* cf. *rubrofuscus* as well as those of *T. trichopterus* have decreased over the last few years. Though some caution might be appropriate regarding taxonomic skills of local people (Kottelat 1990), we consider it unlikely that the species recorded in the pond have been taken from elsewhere than the lake. Adult *C.* cf. *rubrofuscus* were also sold in the local fish market at Tentena. During the 2019 survey, no *C. macropomum* were observed within the lake, and only a single large *Cyprinus* cf. *rubrofuscus* was observed at site 7. In contrast to the introduced barbs, no juvenile *Cyprinus* were observed, indicating a lack of reproduction (likely due to constantly high water temperatures) and unsuccessful establishment in the lake. The silver barb *Barbonymus gonionotus*, reported by Whitten et al. (1987a) from Lake Poso, was not observed by us, pointing towards unsuccessful establishment, an extreme population decline, or potentially a previous misidentification.

Heavy infestation of endemic lake fishes with ectoparasites, fungal infections and necroses was already reported by Kottelat (1990) and confirmed during the present fieldwork. *Oryzias* spp. and *Mugilogobius sarasinorum* with fungal infections were observed regularly, as well as *Oryzias* spp. and, to a lesser extent, also *Adrianichthys* spp. carrying parasitic copepods (mostly *Lernaea* sp). As stated by Kottelat (1990), it appears plausible that the parasites were introduced into the largely isolated watershed of Lake Poso by stocking. Focal research is required to the hypothesis of introduced fish parasites.

Non-native invertebrates and plants

The water hyacinth and the water lettuce both have an enormous growth potential and may cause massive impacts on whole ecosystems by overgrowing waterbodies (e.g., Villamagna and Murphy 2010). Nutrient limitation (Ripley et al. 2006) might provide an explanation to their so far restricted expansion in Lake Poso. The two invasive mollusc species, the Chinese pond mussel and particularly the golden apple snail, are distributed almost globally (e.g., Cowie et al. 2017; Ng et al. 2016). Whereas the golden apple snail has been introduced for food and mainly via the aquarium trade (Cowie et al. 2017), the Chinese pond mussel was at least accidently introduced in Europe via larvae attached to the gills of commercially traded cyprinids (Beran 2008). Both species are supposed to displace or outcompete native species for food resources and habitats or even fish hosts (see Ng et al. 2016 and references therein), but potential impacts on the native southeast Asian freshwater fauna have, to our knowledge, not been assessed. The rice prawn (de Man, 1911) is used as live food for cultivated fish and for human consumption (Phone et al. 2005; Khanarnpai et al. 2019). It is invasive in Singapore freshwaters (Tan and Tan 2003) and is reported for the first time from Lake Poso here.

Vectors of species introduction into Lake Poso

Three major vectors appear plausible for the introduction of non-native organisms into Lake Poso, namely intentional stocking, aquaculture escapes, and aquarium releases. Several non-native fishes were likely stocked intentionally to enhance local fisheries. The relevant species are valuable food fishes popular throughout Indonesia. Some, such as the striped snakehead and the walking catfish, have established stable populations, whereas carp likely depend on continuous restocking. The set of species stocked substantially overlaps with fishes cultured in fish cages, and it is common that small fish caught in the lake are raised in nearby ponds, or small cage facilities within the lake. Finally, especially the smaller fish species were likely introduced from aquarium sources. The global aquarium trade is a major source of aquatic invasions (e.g., in Singapore; Tan et al. 2020), and poses a significant threat to global biodiversity (Magalhães and Vitule 2013). Presence of non-native fishes popular in the aquarium hobby within and around small aquaculture facilities especially at Lake Poso's densely populated outlet area suggests that introduction of aquarium species might involve aquaculture escapees. As awareness of the potential damage caused by non-native species is largely absent in the region, introduction of additional fish species via ornamental trade, stocking, and local aquaculture will likely continue.

Ecosystem changes and the endemic radiations

Our observations and reports by local people confirm Kottelat's (1990) view that local fisheries on native gobies and ricefishes has largely disappeared. Eels remain the only native freshwater fishes that continue to play a significant role in Lake Poso fisheries (see Sugeha et al. 2006 for catch estimations; Watanabe et al. 2016 and Hagihara et al. 2018a, b provide recent studies on Poso eel), supplemented mainly by the non-native target fishes *Oreochromis*, *Channa*, *Cyprinus,* and *Clarias*.

During our visits, we saw small fishing canoes only sporadically, and local people reported that catching the small pelagic ricefishes that are attracted traditionally at night by lights attached to the boat is not done regularly anymore. Eel fishing in the lake takes place especially at the lake's shallow outlet area, using a narrow labyrinth of traditional eel traps ("waya masapi"). The erection of the second major hydropower dam is complemented by substantial ongoing terraforming activities, aimed at optimizing water flow. This poses a serious threat to the lake ecosystem in general, the unique habitats at the outlet that will be destroyed, Poso River that will be affected even more heavily, and finally the local eel fisheries. Lake Towuti in South Sulawesi might serve as an example, where the formerly abundant eel stocks have disappeared after the massive dam constructions at the Larona River.

Stocking eel from other sites in Indonesia, or even Sulawesi, appears a risky management option in Lake Poso, for two reasons. First, downstream migration that would enable contribution to natural reproduction is prevented by the existing dam construction (Baumgartner and Wibowo 2018). Second, only three (Hagihara et al. 2018b) of the nine eel (sub)species native to Indonesia (Sugeha et al. 2008) make up the stocks of Lake Poso and its headwaters, bearing the risk of stocking non-native species (see also Parenti and Soeroto 2004 for comments regarding governmental stocking programs, and freshwater fishes introduced to Sulawesi).

Among the apparent, yet unquantified, observations of recent changes in species abundances are the locally reduced number of endemic dwarf gobies *Mugilogobius* (*Tamanka*) *sarasinorum* in rocky habitats. *Mugilogobius sarasinorum* was highly abundant at all lake sites visited in 2012 and 2013, in depths from few centimetres down to several meters, and across all types of benthic habitats. In 2019, densities appeared substantially reduced at some of the coastal stretches characterized by hard substrate, coinciding with the abundant occurrence of *M. auratus*. It remains to be tested whether and to what degree golden cichlid predation and/or competition contribute to the decline in the goby populations.

In sum, Lake Poso's non-native fish fauna is now more species-rich than its native fish community. Some of the non-native species have established substantial populations, which likely interfere with the local fauna. It appears plausible that the infestations observed in different native fish species are related to non-native vectors. Surprisingly, the hybridogenic flowerhorn cichlids have not colonized much of the lake so far, unlike in Lake Matano (cf. Herder et al. 2012). The golden cichlid did show rapid expansion and population growth, and there are clear indications that endemic species are affected. That species is of no use to local people, being disregarded for consumption due to its small size and lack of flesh. In line with the overwhelming evidence from multiple ecosystems, we stress that the introduction of fishes into isolated freshwater systems such as ancient Lake Poso comes at substantial risks for species diversity, the ecosystem, and ultimately local communities. Regular monitoring campaigns accompanied by education would in our view be advisable to prevent further damage to both, local communities and their environment: "Lake Poso".

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Author's contribution

F.H., J.M. and J.P. designed the study. F.H., B.S., L.H., J.S. and J.P. collected occurrence data. J.M. performed extensive occurrence surveys in 2019, sampled most of the specimens, and collected and analyzed stomach content data. I.V.U. conducted behavioral observations, J.M. and J.M.F. made diving observations. D.W., F.B.B., I.V.U. and L.W. enabled research in Indonesia. F.H. and J.M. wrote the paper. All authors contributed to species determination, critically discussed the results and the manuscript, and gave final approval for publication.

Ethics and permits

The study was carried out under research permits from the Kementerian Negara Riset dan Teknology (RISTEK), Indonesia (permits no. 131/E5/E5.4/SIP/2019) and in cooperation with the Indonesian Institute of Sciences (LIPI) (presently Badan Riset dan Inovasi Nasional (BRIN)). No protected species were involved. All procedures followed the Guidelines for the Use of Fishes in Research from the American Fisheries Society and the legal requirements of Indonesia and Germany.

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Supplementary material

The following supplementary material is available for this article:

Table S1. List of non-native fish species reported from Lake Poso, including their English and Indonesian common names, their native distribution and their most recent record.