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Research Article

Alien invasion in Wallace's Dreamponds: records of the hybridogenic "flowerhorn" cichlid in Lake Matano, with an annotated checklist of fish species introduced to the Malili Lakes system in Sulawesi

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Abstract

Invasive fish species can have major impacts on freshwater faunas, particularly in isolated systems harbouring adaptive animal radiations. Here, we report on the occurrence and recent rapid expansion of the hybridogenic "flowerhorn" cichlid in ancient Lake Matano, the hydrological head of the Malili Lakes system in Central Sulawesi, Indonesia. We show that flowerhorns rapidly dispersed along the lake's shoreline, inhabited most of the southern inshore habitats in 2010, and were present all around the lake in mid-2012. In addition, we present stomach content and observational data supporting the hypothesis that this cichlid threatens the local fauna through both predation and competition. We discuss 13 additional alien fish species recorded in the Malili Lakes drainage since 2000, including the recent, first record of the invasive sailfin catfish *Pterygoplichthys pardalis* for Sulawesi, highlighting the multitude of artificial introductions of foreign fish species into these unique and highly isolated freshwater systems. We conclude that alien fish species pose both serious and diverse threats to the fauna of the Malili Lakes system – an ecosystem of high socio-economic importance and an exceptional natural laboratory for study of evolution, referred to as "Wallace's Dreamponds". Finally, we provide recommendations for minimizing future alien species introductions.

Key words: invasive species; ancient lakes; adaptive radiation; biodiversity hotspot; conservation; flowerhorn cichlid; *Pterygoplichthys*

Introduction

The introduction of alien fish species into freshwater ecosystems can have profound consequences, including loss of species diversity, extinction of endemic species, distortion of food web function, and changes to ecosystem productivity (Barel et al. 1985; Rahel 2000, 2002; Vitule et al. 2009; Gozlan et al. 2010; Hoffmann et al. 2010; Zambrano et al. 2010). However, not all species introductions lead to the establishment of permanent populations or even invasions (Gurevitch and Padilla 2004; Gozlan 2009), as populations of invaders may collapse under certain conditions (Cooling et al. 2011). Isolated ecosystems harbouring adaptive radiations are particularly vulnerable to the establishment of invasive species, and in some cases have been seriously affected by the resulting impacts (Vitousek 1988; Cox and Elmqvist 2000; Sax et al. 2002; Strecker 2006; Sax and Gaines 2008).

There are several potential impacts of foreign fishes to native freshwater ecosystems, especially in evolving radiations (Strecker 2006). Piscivorous or omnivorous species can be a direct threat to smaller fish species, juveniles, fry, or eggs. Invertebrate species of evolving species flocks, such as shrimps and gastropods (K von Rintelen et al. 2010; T von Rintelen et al.

2010) are likely affected by fish predation. Introduced fish might also out-compete native species by exploiting limited resources (e.g., food or spawning sites). Finally, introduced fishes can act as vectors for diseases and parasites (Kottelat 1990; Strecker 2006; Nico et al. 2007; Vitule et al. 2009). Examples, such as the Nile perch (*Lates niloticus*) introduction in Lake Victoria about half a century ago (Barel et al. 1985), have highlighted the potentially devastating impact invasive species can inflict on evolving species flocks. In that case, Nile perch introduction contributed to the decline of the native fish stocks, including the loss of hundreds of haplochromine cichlid species, with massive impacts to the whole ecosystem (Ogutu-Ohwayo 1990; Witte et al. 1992), and serves to date as the textbook example for negative ecological and economical impacts of alien fish species invasion (Lowe et al. 2000).

The ancient Malili Lakes system in Central Sulawesi (Indonesia) harbours endemic radiations of various freshwater organisms, including fishes, molluscs, shrimps and crabs (reviewed in von Rintelen et al. 2012 and Vaillant et al. 2011). In the last decade, these species flocks of "Wallace's Dreamponds" (Herder et al. 2006a) have been used as valuable model systems for testing hypotheses on the adaptive character of intralacustrine radiations (von Rintelen et al. 2004, 2010; Herder et al. 2006a, 2008; Pfaender et al. 2010, 2011), on gene flow among evolving species (Herder et al. 2008; Schwarzer et al. 2008; Walter et al. 2009a, 2011), on behavioural specialization and filial cannibalism (Gray et al. 2007, 2008a; Cerwenka et al. 2012), on the evolution of male colour polymorphisms (Gray et al. 2008b; Walter et al. 2009b), and on geographic modes of speciation, including mechanisms of ecological speciation in sympatry (Herder et al. 2008; Pfaender et al. 2011; Walter et al. 2011).

Most of the lacustrine organisms of the Malili Lakes system are endemic to one or a few of the lakes (von Rintelen et al. 2012). The endemism is a result of the zoogeographic isolation of Sulawesi from the nearby Sunda shelf with its rich Southeast Asian fauna (Whitten et al. 2002), the isolation of the Malili Lakes from other freshwaters of the island (Brooks 1950), and due to natural barriers between the lakes (Schwarzer et al. 2008; Walter et al. 2011). With respect to the freshwater fishes of the Malili Lakes drainage, research has largely focused on the adaptive radiation of sailfin silversides (Atheriniformes: Telmatherinidae): small, colourful relatives of Australian and New Guinean rainbow fishes (Melanotaeniidae) (see Herder et al. 2006b for a taxonomic checklist, and Herder and Schliewen 2010 for a review on evolutionary studies). However, the native ichthyofauna also comprises small endemic species flocks of ricefish (Adrianichthyidae), gobies (Gobiidae), endemic species of halfbeaks (Zenarchopteridae), and at least one eel species (Anguillidae) (Kottelat et al. 1993). Descriptions of fish species new to science continue to emerge, including taxa from a variety of different fish families (e.g. Kottelat 1990, 1991; Larson 2001; Herder and Chapuis 2010; Huylebrouck et al. 2012), showing that the aquatic faunal diversity of the area is still not completely explored.

Sulawesi's freshwater biodiversity is facing manifold threats. In the Malili Lakes area, major threats come from surface nickel mining operations, including one of the largest mines in the world, currently extending principally between Lakes Matano and Mahalona. Impacts from mining include various direct (land use and transformation destroying stream and river habitats; mine effluents; erection of dams for power supply) and indirect (increased logging and urbanization, with related pollution; loss of swamp and forest habitats; land use at the lake's shoreline) consequences for aquatic habitats and their endemic species assemblages. In addition, commercial fisheries, especially nocturnal light fishing in Lake Towuti, put pressure on native lake fish stocks (Parenti and Soeroto 2004). Introduction of alien fish species adds another component to the disruption of the natural ecosystem.

The main sources of non-native and potentially invasive fish species in the Malili Lakes include: stockings intended for developing local fisheries; fishes that escape from aquaculture ponds or enclosures; and release of ornamental fishes from ponds or pet aquaria (Wittenberg and Cock 2001; Parenti and Soeroto 2004; Keller and Lodge 2007). Even by the early 1990s, Kottelat reported as many as 10 confirmed or likely introduced fish species from Lake Matano alone (Kottelat 1989, 1991), and successive workers have confirmed and added additional records of alien fish species in the area (Hadiaty and Wirjoatmodjo 2002; Hadiaty et al. 2004). In lakes Poso and Lindu in Central Sulawesi, exotic fish species likely contributed to the threat imposed on those endemic fish communities, including species extinctions (Kottelat 1990, 1992; Kottelat et al. 1993; Whitten et al. 2002). Unfortunately, much of the public is unaware that the Malili Lakes habitat is a unique freshwater biodiversity "hotspot" and that its existence is threatened. Moreover, studies estimating the impact of species introductions on the ecosystem are lacking.

Here, we provide records of alien fish species in the Malili Lakes area, including the recent, rapid spread of a cichlid (family Cichlidae) in Lake Matano, known in the ornamental fish trade by various names, mainly flowerhorn, Luohan or Kirin cichlid (Nico et al. 2007; Ng and Tan 2010). Flowerhorns constitute a man-made hybrid complex, reportedly composed of parental species of the neotropical cichlid genera *"Cichlasoma", Amphilophus* and *Paraneetroplus (Vieja)* (Nico et al. 2007; Ng and Tan 2010; McMahan et al. 2010). Flowerhorns are named for their distinctive head shape and vivid colours, and have become popular aquarium fish over the last decade. Recently, cichlid hybrids originating from aquarium flowerhorn stocks have been reported as invasive aliens in several Asian countries (Nico et al. 2007; Knight 2010; Ng and Tan 2010). We confirmed that flower-horns have established proliferating populations in Lake Matano, and also document that this invasive hybrid has rapidly spread along the lake's coast defending new territories and feeding on the local endemic fauna, including fishes. Our data clearly demonstrate that this is a successful invasion and a serious threat to the lake's biodiversity. In addition, we present updates and records of 13 other alien fish species recorded since 2000 during field work in the Malili Lakes watershed; however, none of the other alien fish species so far approaches the rapid increase of population density and speed of flowerhorn dispersal observed in Lake Matano.

Material and methods

Study area

The tropical Malili Lakes consist of three main lakes, interconnected by small rivers, and two small satellite lakes connected by peripheral streams (Figure 1a). Lake Matano (Figure 1b) is the hydrological head of the system (Brooks 1950). It is the eighth deepest lake in the world (590 m deep), and unique among the tropical ancient lakes due to its very low productivity and correspondingly crystal clear waters (Crowe et al. 2008a, 2008b). Lake Matano's effluent is the high-gradient River Petea that flows to Lake Mahalona. From there, the flow continues more gently to the largest water body of the system, Lake Towuti, which drains to the sea.

Field work

Alien fish species were recorded between 2000 and 2012 in various field campaigns (November 2000, October to December 2002, January and February 2003, January to May 2004, October to December 2004, November 2006, January 2007, June to August 2010, September 2012). Field work focused mostly on Lake Matano, covering sites around the lake's shoreline, but also included sampling in lakes Towuti, Mahalona, Lontoa and Masapi, as well as most of the permanent streams and rivers of the system. Sampling and visual surveys were conducted using SCUBA- and snorkelling-aided gillnetting (6 and 8-mm mesh size), a DEKA 3000 portable electrofishing device, cast netting, dip netting, beach seining, angling, observations by snorkelling and SCUBA diving, and underwater video recording. Catches of local fishermen were incorporated if clearly related to a specific locality.

Abundances and distribution of flowerhorns within Lake Matano were recorded during focal investigations from June to August 2010 at 134 sampling locations distributed equally around the lake's shoreline (see Figure 1b for sampling locations). This approach covered different habitat types with varying substrates, up to 13 m depth. Abundances were estimated by a single observer (J.P.) based on 5 minutes of standardized snorkelling observation in the following categories: absence (no single individual observed); low abundance (<10 individuals observed), medium abundance (<20 individuals observed); and high abundance (records exceeding 20 individuals). In 2012, this approach was repeated in a brief follow-up survey, at a few selected sites mainly near the northern shore.

Material and species determination

Collected voucher specimens were sedated and euthanized in chlorobutanol (1,1,1-trichloro-2-methyl-2-propanol), then preserved either in 70% ethanol or in 4% formalin, and later transferred to 70% ethanol for storage. To determine diet we examined the stomach contents of

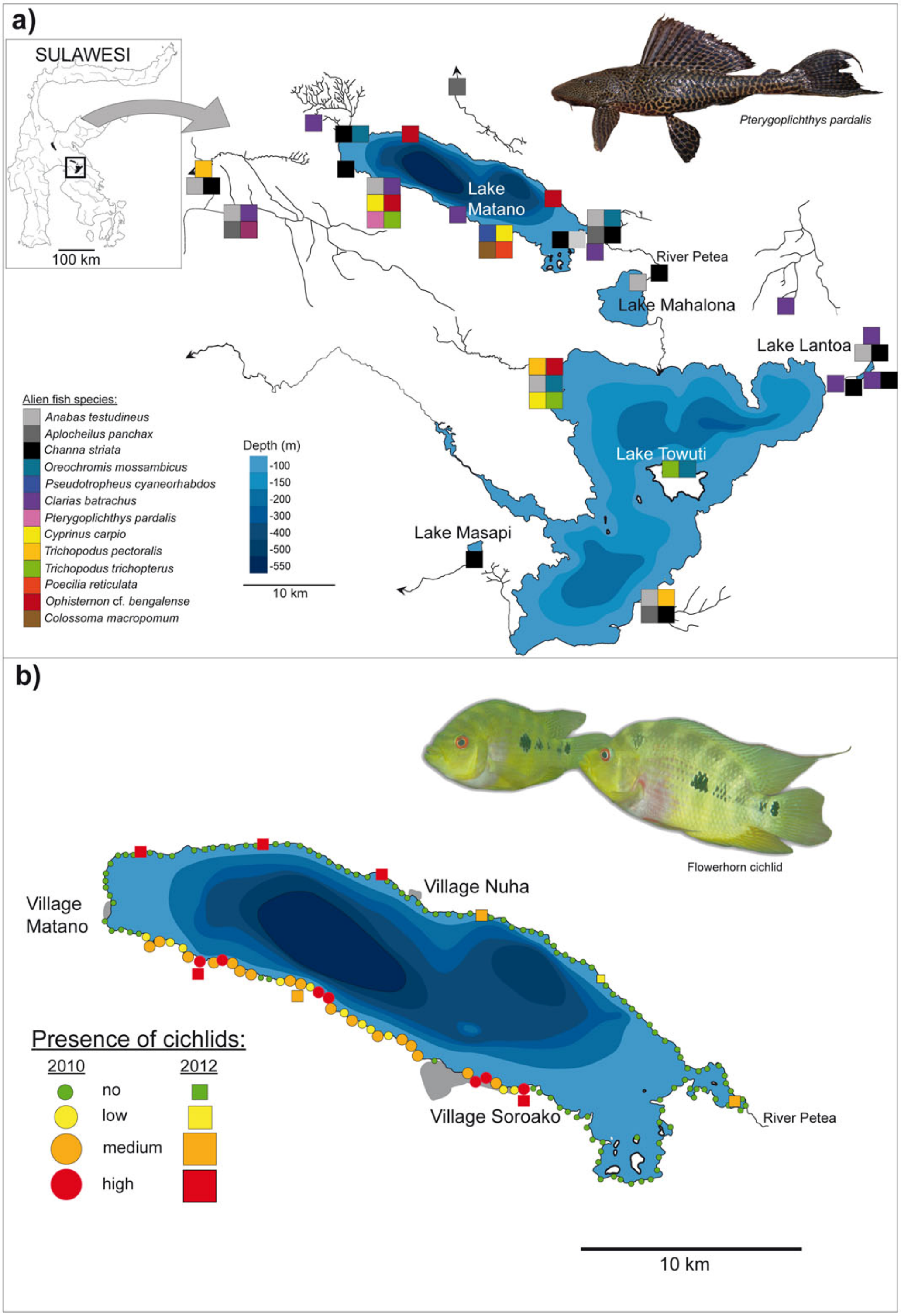

Figure 1. (**a**) Map of the Malili Lakes system (including associated streams), Central Sulawesi (Indonesia), showing location records for 13 non-native fish species from 2000 to 2012. (**b**) Map of Lake Matano showing sites where flowerhorn cichlid were captured or observed in 2010 and 2012, based on 134 sampling locations covering the shoreline at 500 m intervals in 2010 and nine locations re-visited in 2012. Maps by T. von Rintelen, modified (with permission).

15 flowerhorn cichlid specimens from five sampling locations. Food items between the oesophagus and pylorus were embedded in Gelvatol (Polyvenylalcohol) or stored in 70% ethanol. Food items were identified to the lowest feasible taxonomic level, and their relative volumetric proportion was estimated for each specimen (see Herder and Freyhof 2006 for details).

Voucher specimens of the flowerhorn cichlid and most of the other alien fish species recorded are stored in the collections of Research Centre for Biology, the Indonesian Institute of Sciences (LIPI, formerly the Museum Zoologicum Bogoriense – MZB 21239-21246), Cibinong, Indonesia, and Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK 48849-48852; ZFMK 48854-48859; ZFMK 48865-48871; ZFMK 48874-48875). Alien fish species, with the exception of the flowerhorn, *Colossoma* sp., and *Pseudotropheus* (*Melanochromis*) *cyaneorhabdos* were determined following Kottelat et al. (1993). Assignment of walking catfish specimens to *Clarias batrachus* remains tentative (thus: *C.* cf. *batrachus*), and positive identification will not be possible until clariid systematics and taxonomy are resolved (see Ng and Kottelat 2008). The determination of the suckermouth armored catfish as *Pterygoplichthys pardalis* follows Page and Robins (2006); the key character is the colouration, including a pattern of unconnected dark spots on a light background on the underside.

Identification of the swamp eel, *Ophisternon* cf. *bengalense*, was based on obvious external characters: fin reduction, absence of pectoral and pelvic fins, characteristic habitus of the head with small, fused ventral gill opening; and was later confirmed by voucher specimen examination (ZFMK 48851). Abbreviations used: TL - total length, from snout to distal tip of caudal fin; SL - standard length, from snout to end of hypural plate.

Results

Records, observations and stomach content analyses of the flowerhorn cichlid in Lake Matano

Specimens of the invasive cichlid were determined to be flowerhorns, following Nico et al. (2007) and Ng and Tan (2010). Breeding pairs and numerous juveniles were first recorded in June 2010 at the southern shore of Lake Matano (western Soroako: Salonsa Beach). Flowerhorns were subsequently recorded at 38 of the 134 sampled sites visited in 2010, all along the lake's southern shore (Figure 1b). The species occured in mostly medium to high abundances along the shoreline area from -2,46701667; +121,23238333 to -2,53843333; +121,41291667 (Figure 1b). Within this distribution, flowerhorns were rarely observed in soft-bottom bays, likely indicative of a less-preferred macrohabitat. However, soft-bottom habitats do not represent barriers to flowerhorns, as its 2010 range included several predominantly muddy or sandy shoreline habitats (compare the detailed habitat map in T. von Rintelen et al. 2010). In September 2012, flowerhorns were also recorded at all five locations visited at the northern shoreline, and were also present at the lake's outlet to River Petea (D. Haffner, pers. comm.).

Flowerhorns were not recorded during earlier field campaigns (see Material and Methods); however, they were observed in two local aquarium pet shops of Soroako, the main city at Lake Matano in 2004 and 2006 (F.H., pers. obs.). Both shops held various alien fish species, with one of the shops located directly above a small channel (a former stream) draining directly to Lake Matano, just a few dozen meters from the present-day harbour. In 2010, we found this part of the town restructured, with the shop gone, including all fishes. We also recorded adult flowerhorns in a small park pond in Salonsa, the western part of Soroako (J.P. and F. H., pers. obs.).

In Lake Matano, flowerhorns were found from the shoreline out to >13 m depth. Territories of adults were associated mostly with hard substrate such as rock or coarse gravel, which they aggressively defend. All stages of reproduction were observed, including clutches of eggs deposited on the surface of stones within territories, clouds of juveniles of various sizes guarded by parental fish, and schools of immature individuals found mostly in the shallow lake habitats.

One immature specimen (about 7 cm total length) was observed feeding on eggs of the endemic goby *Glossogobius matanensis*, a species that deposit their eggs on rocks (F.H., pers. obs.; see Figure 3). The cichlid seemed to ignore the guarding male goby (which was approximately three times the cichlid's body length), and fed for at least 10 minutes on the

Figure 2. Lateral view of an adult flowerhorn cichlid (approx. 15 cm SL) taken from Lake Matano on June 16, 2010. The fish was photographed in the field immediately after capture.

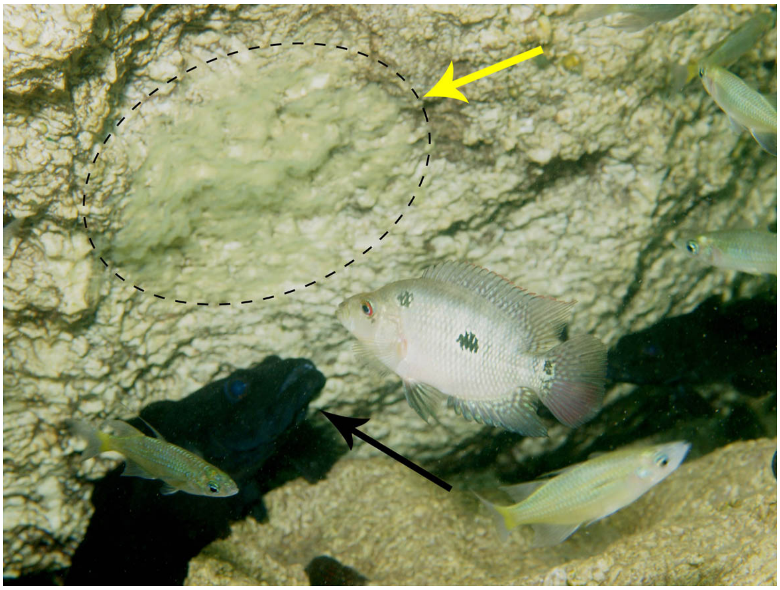

Figure 3. A flowerhorn cichlid feeding on eggs of the endemic goby *Glossogobius matanensis* in Lake Matano. The clutch consisted of numerous small, yellowish eggs (yellow arrow) deposited on a rock in approx. 0.8 m depth, guarded by the male goby (black arrow).

eggs, without significant interruption. The feeding disturbance also attracted another egg-eating fish (sailfin silversides, *Telmatherina sarasinorum*; see Figure 3); and ultimately the entire clutch was destroyed. We also captured an adult flowerhorn and adult sailfin silverside (*Telmatherina antoniae* "small"; see Herder et al. 2006b for a species overview). When placed together in a bucket, the flowerhorn immediately attacked and consumed the smaller silverside.

Stomach content analyses of 15 individuals show that flowerhorns in Lake Matano prey on endemic fauna, including atyid shrimps, a gecarcinucid crab, and hydrobioid gastropods (Figure 4). One stomach contained fish remains, most likely a fish of the genus *Telmatherina*. The record of a gecarcinucid crab is based on a single leg, of approx. 20 mm length, found in the stomach of one flowerhorn, which suggested the fish ingested only part of a larger crab specimen.

Records of other alien fish species in the Malili Lakes drainage

Besides the invasive flowerhorn, 13 additional alien fish species have been recorded by the

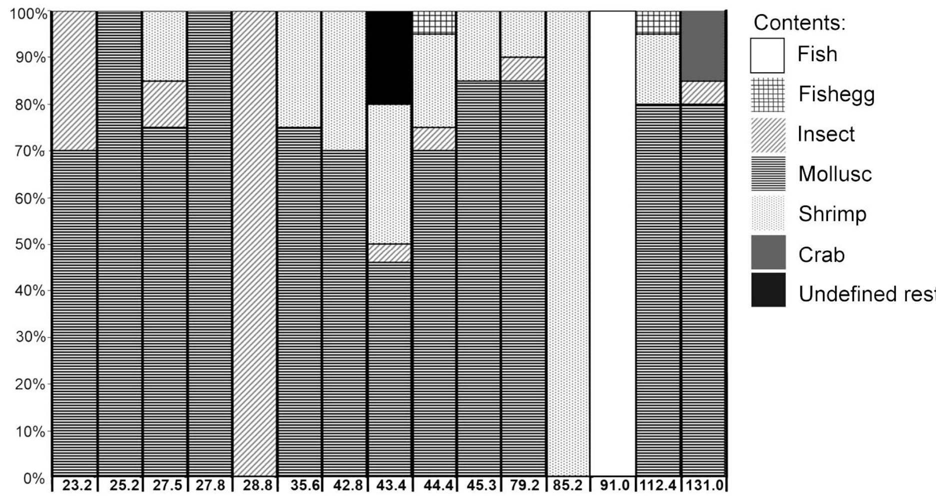

Figure 4. Stomach contents (in percent) of 15 flowerhorn cichlid taken from different sites in Lake Matano. Values on the x-axis are standard length (cm) of each individual fish. Molluscs (hydrobioid gastropods) are the most prominent content in flowerhorn stomachs, but shrimps, fish and their eggs, crabs, and insects are also represented in the diet spectrum

Table 1. Frequency distribution of fin spines, lateral bars and the midline blotch of 15 flowerhorn cichlids (same individuals as used for stomach content analyses).

	Number of anal-fin spines				Number of dorsal-fin spines				
	7	8	Mean	SD	16	17	18	Mean	SD
n=13	11	2	7.15	0.1	3	8	2	16.92	0.18
	Number of lateral bars				Midline blotch on 4th bar				
	7	8	Mean	SD		Present		Absent	
	12	1	7.08	0.08		13		0	

authors in the Malili Lakes drainage since 2000 (Appendix 1). These included members of the families Anabantidae (1 sp.): *Anabas testudineus* (Bloch, 1792); Aplocheilidae (1 sp.): *Aplocheilus panchax* (Hamilton, 1822); Channidae (1 sp.): *Channa striata* (Bloch, 1797); Cichlidae (2 sp.): *Oreochromis mossambicus; Pseudotropheus cyaneorhabdos* (Bowers & Stauffer, 1997) (Maingano population) - see Konings & Stauffer (2012) for generic classification); Clariidae (1 sp.): *Clarias* cf. *batrachus* (Linnaeus, 1758); Cyprinidae (1 sp.): *Cyprinus carpio* (Linnaeus, 1758); Loricariidae (1 sp.): *Pterygoplichthys pardalis* (Castelnau, 1855); Osphronemidae (2 sp.): *Trichopodus* (*Trichogaster*) *pectoralis* (Regan, 1910); *Trichopodus* (*Trichogaster*) *trichopterus* (Pallas, 1770); Poecilidae (1 sp.): *Poecilia reticulata* (Peters, 1859); Serrasalmidae (1 sp.): *Colossoma macropomum* (Cuvier, 1816); and, Synbranchidae (1 sp.): *Ophisternon* cf. *bengalense* McClelland, 1844.

Many of the alien species records were found to be associated with sites strongly affected by human activity, especially around the towns of Soroako (Lake Matano) and Timampu (Lake Towuti). All alien species recorded were present in Lake Matano, followed by eight species in Lake Towuti and two in Lake Mahalona. The snakehead *Channa striata* was the only introduced species found in Lake Masapi, where it is extremely abundant. Six non-native species were present in streams and rivers. Two species (*Channa striata*, *Clarias* cf. *batrachus*) are comparatively large predators and pose a potential threat, even for adult native fish and crustaceans.

Throughout the period of study, we frequently observed juvenile *Channa striata* packed live per dozen in plastic bags at local markets for stocking purposes, reflecting the potential for introduction into the wild. Ponds and ditches stocked with *C. striata* were found in the flooding area of River Petea (outlet Lake Matano) and close to several streams draining into the lakes (Figure 1; F. Herder, pers. obs.). Specimens of all size classes were observed in all lakes, most of them in areas close to human settlements. Extremely high population density was observed in Lake Masapi: according to local people this is the result of direct stocking. Even a small and very remote lake in the hills north of Lake Matano, far from the closest human settlement, was found to contain many *C. striata*, most likely introduced by local loggers. Like *C. striata*, juveniles of the walking catfish *Clarias* cf. *batrachus* are widely available for stocking purposes in Sulawesi, and live adults marketed as popular food fish. The same applies to the climbing perch *Anabas testudineus,* likely introduced to Lakes Matano, Mahalona and Towuti, and present also in surrounding streams. The swamp eel *Ophisternon* cf. *bengalense* was not abundant at any of the field locations visited, but present down to 20 m depth in Lakes Matano and Towuti, a notable finding for an air-breathing species.

A single specimen of the sailfin catfish *Pterygoplichthys pardalis* (Figure 1a) was captured in 2 Sept. 2012 at south-western Lake Matano, in a habitat characterized by mud and rocks at 14 m deep (A. Indermaur, pers. comm.). This site is located few hundred meters from some forsaken aquaculture cage facilities; the fish was about 40 cm long and in very good condition.

Tilapia of the genus *Oreochromis* were commonly observed in small aquaculture ponds of the region, often connected to natural streams. Shoals of *Oreochromis* and their sand bowers ("breeding craters"), are common in Lake Matano and present at different depths. Likewise, catches of tilapia marketed at Timampu originated, according to local fishermen, from Lake Towuti. Tilapia are also frequently available at the local fish market of Soroako (Lake Matano). However, many of the *Oreochromis* observed within Lake Matano appeared to be in poor condition, judging from their disproportionally large head size and emaciated bodies.

There are indications for infections of indigenous fishes with fungi: *Oryzias matanensis* and *Telmatherina* and *Glossogobius* species in Lake Matano, as well as *Tominanga* in Lake Towuti. These infections are uncommon in the Malili Lakes, and are largely associated with the occurrence of introduced fish species near the large towns of Timampu and Soroako, but also in remote areas where (forsaken) fish cages or aquaculture ponds are present (e.g. at Lake Matano, S2 28.458, E121 15.570). In Lake Mahalona, introduced *Anabas* carried fish louse (*Argulus* sp.), a non-indigenous fish ectoparasite.

Discussion

Introduction, dispersal and potential impact of flowerhorns in Lake Matano

The introduction of flowerhorns into Lake Matano is likely of very recent origin. This hybrid was not observed during intensive field sampling campaigns conducted prior to 2010. Therefore, it appears that the initial introduction does not date further back than approximately 2005. The most likely sources are possible releases during the closing of local aquarium pet shops, or by local aquarists. Based on the assumption that only a single or a few releases took place, most likely in the Soroako area, and the 2010, approx. 21 km distribution area along the lake's southern coastline, we estimated that the rate of expansion of this cichlid along the coast has been about 6 km of shoreline per year. Given roughly constant rates of dispersal, we expected the two invasion fronts to meet at the lake's northern shore around 2013. Flowerhorns were, however, even faster. In September 2012, they were present at each single location visited, including several sites at the lake's northern shore. All of these sites harboured mixed populations of immature and mature flowerhorns, including several brooding pairs, indicating that population expansion is still in progress.

Natural habitat heterogeneity in the lake appeared at first glance to possibly decelerate the cichlid's dispersal, as most specimens were observed associated with rocky habitats. The 2010 distribution roughly corresponded to the borders of predominantly soft-bottom areas in the west and east of the lake; however, the soft-bottom bay at the town area of Soroako did not prevent dispersal, and the 2012 distribution demonstrated that soft-bottom habitats do not form a barrier for these fishes in Lake Matano. In addition, the wide array of habitats successfully used by flowerhorns in Lake Matano and elsewhere (Knight 2010; Ng and Tan 2010) raises the question if the River Petea constitutes an effective downstream barrier preventing cichlid dispersal to the lower lakes, and rivers and streams in the Malili lakes system.

Stomach content data and observational records are consistent with an expected omnivorous diet, similar to that of related cichlids (Nico et al. 2007). Although the diet of only a few specimens (n = 15) were examined, representatives of all major animal radiations native to Lake Matano were found to be preyed upon by flowerhorns, including gastropods, shrimps, crabs, and fishes. Admittedly, cichlid predation is likely affecting different members of the native species flocks unequally. In the case of the hydrobioid gastropods, only some of the shells were crushed, a pattern also observed in stomach content samples of the endemic sailfin silversides (Pfaender et al. 2010) and likely a result of the gastropod's minute size. In summary, stomach content data and field observations support the notion that the flowerhorn cichlid is a highly opportunistic predator, which is consistent with published records from other cases in Asia where flowerhorns or the closely related "*Cichlasoma*" *urophthalmus* are invasive (Nico et al. 2007; Knight 2010). In addition, competitive interactions with nearly all of the highly specialized endemic lake fish species (Pfaender et al. 2010, 2011) appear likely.

Given the apparent preference of flowerhorns for hard substrate, such as rock or coarse gravel, native species inhabiting such habitats are likely most susceptible to predation by this invasive fish. Fish species most likely to be affected are those brooding on open rocks, such as *Glossogobius* gobies, and those specialized on foraging in rocky or gravel habitats, such as *Telmatherina* sp. "elongated" or *T.* sp. "thicklip" (Herder et al. 2006b). In contrast, native species that inhabit habitats less preferred by flowerhorns, predominantly soft substrate habitats or even open waters, are likely less affected such as sailfin silversides of the "roundfin" clade, especially the highly abundant *Telmatherina antoniae* "small". The implications for the lake's ecosystem, including its invertebrate radiations, remain to be studied in detail.

Records of other alien fish species in the Malili Lakes drainage

Most of the alien fish species recorded in the Malili Lakes system are commercially valuable and popular food fishes. Their introduction appears related to intentional stocking, or to escapees from aquaculture ponds or enclosures. *Anabas testudineus*, *Channa striata*, *Clarias* cf. *batrachus*, and the gouramis *Trichopodus pectoralis* and *Trichopodus trichopterus* are air-breathing species with exceptional tolerance of transport conditions, and consequently are transported, marketed and introduced throughout Southeast Asia (Kottelat et al. 1993; Berra 2007 and references therein). Their native distributions are considered to be restricted to Asia west of Wallace's line, and therefore those populations found in Sulawesi are considered introduced (Kottelat et al. 1993; Berra 2007). *Anabas*, *Channa* and *Clarias* are moreover known for their resistance against droughts and their ability to disperse even across short stretches of land (Dutta and Munshi 1985; Kottelat et al. 1993). *Anabas testudineus* (as *A. scandens*) and *Channa striata* (as *Ophiocephalus striatus*) had been reported for Lakes Matano, Towuti and Poso nearly one hundred years ago by Weber (1913), supporting the hypothesis of introduction by early settlers (Larson and Kottelat 1992).

In contrast to the rather small and omnivorous *Anabas* and *Trichopodus*, *Channa striata* and *Clarias* cf. *batrachus* are comparatively large predators, and potentially pose a serious direct threat to indigenous fish, crustaceans, and even amphibians. Kottelat (1990) discussed the strong population decline in Lake Poso's (Central Sulawesi) species flock of ricefishes in association with (among other factors) the introduction of alien fish, including *Channa* and *Clarias*. However, in the Malili Lakes, we found *Channa* mostly in shallow habitats characterized by dense vegetation or wood, or among large boulders, suggesting that their impact might be restricted to species inhabiting these habitats. We also did not find indications of a noteworthy increase in *Channa* population densities within Lake Matano over the last decade, indicating that *Channa* might - at least currently - not pose a major threat in this lake. Likewise, records of the walking catfish, *Clarias* cf. *batrachus*, in Lake Matano are comparatively rare so far, but specimens were also observed in depths exceeding 5 m, suggesting that a broad range of lake species might be affected by this nocturnal predator.

Like *Channa* and *Anabas*, the snakeskin gourami *Trichopodus pectoralis* as well as the three spot gourami *Trichopodus trichopterus* typically inhabit shallow habitats with dense vegetation, such as rice field ditches, where these fish feed on small invertebrates. This habitat type occurs in the Malili Lakes region predominantly near towns or villages, reflecting increased nutrient levels. *Trichopodus pectoralis* was observed exclusively in such habitats, possibly due to repeated introductions from ponds or rice fields. The closely related *T.*

trichopterus was reported earlier by Kottelat (1989) from Lake Matano, but actual records are restricted to one site in Lake Matano and two sites in Lake Towuti (Figure 1a). The record in Lake Matano is a shallow, polluted beach site with unusual macrophyte growth, where it co-occurs with abundant *T. pectoralis*, *Anabas testudineus* and *Oreochromis mossambicus*. The two sites in Lake Towuti appeared however not visibly disturbed.

Swamp eels like *Monopterus* and *Ophisternon* are also able to breathe atmospheric air, are commonly marketed live, and occur widespread in local aquaculture (Kottelat et al. 1993; Berra 2007). Information on swamp eels in Sulawesi is scarce (T. Roberts, pers. comm.), and their taxonomy needs to be updated (Allen et al. 2002). Here, we follow T. Roberts (pers. comm), Berra (2007) and Allen et al. (2002) in tentatively assigning the *Ophisternon* found in the Malili Lakes to *O. bengalense*, a taxon distributed from the Indo-Malaysian region to New Guinea (Berra 2007). We follow Kottelat (1991) and Whitten et al. (2002) by assuming that swamp eels are likely not native to the Malili Lakes drainage, but introduced for aquaculture purposes; however, further investigations are required to test this assumption.

The common carp, *Cyprinus carpio*, and the Mozambique tilapia, *Oreochromis mossambicus*, are not air-breathers, but nevertheless extraordinarily resistant to hypoxic conditions. As valuable food fish, both species have been used extensively for aquaculture purposes throughout Asia, including programs for increasing fisheries productivity by stocking in natural waters; neither is native to Southeast Asia (Berra 2007). According to the local district governor, tens of thousands of *C. carpio* have been stocked regularly in Lake Towuti. These stockings explain sightings in Lake Towuti, some kilo-metres away from Timampu, as well as the pre-sence of fresh adult individuals in fish markets in Timampu and Soroako. *Cyprinus carpio* has also been recorded in Lake Matano, is known to change the habitat by digging up the sediment, and may pose a direct threat to eggs and fry of indigenous fish species. Moreover, common carp can be assumed to feed on native invertebrates, aufwuchs and plants. However, and contrary to its invasive potential demonstrated elsewhere (e.g., Koehn 2004), there are as yet no indications for successful reproduction of *C. carpio* in the lakes, and there are also no signs of dispersal to the other lakes or streams.

Tilapias (e.g., *Oreochromis niloticus*, and various hybrids) were widely introduced throughout tropical freshwaters as a potential human food source. As such, they have become a major pest in freshwaters throughout the tropics (Lowe et al. 2000), with significant impacts on evolving species flocks (Canonico et al. 2005; Strecker 2006). *Oreochromis mossambicus* feed mainly on plant matter (Allen et al. 2002), and, in contrast to *C. carpio*, have been observed breeding within the Malili Lakes (F. H. and S.M.G., pers. obs. 2002, 2003, 2004). Coupled with substantial resistance against hypoxia and high temperatures, the species' parental care and low habitat stenotopy explain the globally invasive character of this valuable food fish (Allen et al. 2002; Berra 2007). Interestingly, many of the *O. mossambicus* observed in Lake Matano, at different sites and over several years, were in poor condition, possibly indicating resource limitation for these species in this ultraoligotrophic lake (Haffner et al. 2001; Crowe et al. 2008a; Vaillant et al. 2011). However, this does not apply to all specimens recorded, and was also not observed in Lake Towuti. Moreover, the situation might change with increasing nutrition in the lake's ecosystem, in addition to contemporary evolution triggering local adaptation of introduced fishes (Lee 2002).

The blackfin pacu *Colossoma macropomum* from South America is another non-indigenous food fish species introduced to Asian waters, including parts of China, Taiwan, Singapore, Bangladesh, the Philippines and Indonesia (FAO Fisheries and Aquaculture Department Database; 10-2011). Weighing up to 30 kg, it is mainly herbivorous, generally feeding on fruits, seeds, and leaves. The Pacu is known as very resistant to diseases, but not much information is available regarding its impact on native faunas. The present record of a single specimen caught in Lake Matano dates back to 2000 (see also Parenti and Soeroto 2004).

The sailfin or suckermouth armored catfish *Pterygoplichthys pardalis* from the Amazon basin is the most recent exotic fish species discovered in Lake Matano. At least three species of the genus are invasive in Southeast Asia, including Taiwan, Thailand, Vietnam, the Philippines, Singapore, Malaysia, Java and Sumatra (Page and Robins 2006; Levin et al. 2008). Local people reported that sailfin catfish have also been caught elsewhere in Lake Matano in the recent past, suggesting that the species is spreading in the lake. This record adds Sulawesi to this list of countries or islands affected by invasive *Pterygoplichthys*; we expect that the species might also disperse downstream to Lakes Mahalona and Towuti. Ecological and economic effects reported from invasive sailfin catfish elsewhere comprise environmental degradation and ecological disruption, including degradation of banks and siltation problems in reservoirs and streams caused by burrowing and tunnelling behaviour, competing with native species for food resources, and additional unexpected interactions such as attaching and grazing on the bodies of other aquatic animals (Nico and Martin 2001; Page and Robins 2006; Levin et al. 2008; Nico et al. 2009). Competition for limited resources might be critical for some of the endemic animals in the ultraoligotrophic and potentially resource-limited (Vaillant et al. 2011) Malili Lakes ecosystem; siltation may pose additional threats especially to the highly adapted invertebrate fauna (von Rintelen et al. 2012).

The guppy *Poecilia reticulata* and the blue panchax *A. panchax* have both been widely introduced for mosquito control, and are also used as aquarium pets (Berra 2007). *Aplocheilus panchax* is native to parts of Sulawesi, but we tentatively assume that it is not native to the study area. This species is tolerant of increased salinity (Lim and Ng 1990), and may have crossed Wallace's line naturally (Parenti and Louie 1998; Whitten et al. 2002; Berra 2007). Nevertheless, *A. panchax* has mostly been observed at sites in the Malili Lakes modified by human activity, mainly polluted swamps or inshore habitats close to major settlements. Guppies are widely available in the local aquarium trade in Sulawesi and the Malili Lakes region, and present in urban ditches and streams draining to Lake Matano. The species is not especially effective in controlling mosquito numbers, at least on a broad scale, but it has had marked negative impacts on native fishes and certain invertebrates (see Kottelat et al. 1993 for comments).

Introductions of both *Pseudotropheus cyaneorhabdos*, a species endemic to East African Lake Malawi (Maingano population), and flowerhorns, likely resulted from release of pet specimens. The record of *P. cyaneorhabdos* is based on a single observation (by S.G. and J.S.M in Feb. 2004). The fish was caught and removed from the lake.

Prospects and recommendations

The number of alien fish species recorded for the Malili Lakes system is almost certainly incomplete. There are likely many unreported cases of other species that have either failed to become established or others that are present but remain undetected. Nevertheless, the diversity of alien fish species recorded shows that there is a huge likelihood for harmful introductions into this unique and naturally isolated lake system. However, most of these introductions have, in line with expectations derived from theory and other fish invasions (Britton et al. 2011), so far not resulted in massive invasions, and one of the species recorded by earlier investigators has apparently not established stable populations (Appendix 1). Nevertheless, presence of obviously stable populations of alien predators in the lakes, such as snakehead or walking catfish, warrants careful monitoring.

The present case of the flowerhorn cichlid invasion demonstrates the speed at which a successfully invading species can establish across a lake, and our data highlight its threat to the native fauna. Attempts at population control through targeted harvesting unfortunately appear neither realistic nor promising given the flowerhorn's high fecundity in this very sensitive aquatic environment (Zipkin et al. 2009). The challenge remaining is to monitor its impact carefully, with an emphasis on preventing the colonization of the other Malili Lakes. Well-studied species invasions, such as the Nile perch disaster in Lake Victoria, or the direct and indirect impacts of alien fish on the *Cyprinodon* species flock in Yucatan (Mexico) (Strecker 2006), have shown the destructive potential arising from such introductions.

Endemic fishes of the Malili Lakes also likely suffer from diseases and parasites introduced with alien fishes. So far, observed infections related to alien fish vectors are restricted to a few cases, but fish diseases and parasites can spread rapidly and have seriously affected other species flocks (e.g. Strecker 2006), including lake radiations in Central Sulawesi (Kottelat 1990; Whitten et al. 2002).

To date, we cannot fully assess the impacts of the flowerhorn invasion, neither for the environment with its endemic species flocks, nor for the people exploiting it. The fishes of the Malili Lakes are traditionally used for subsistence fisheries (Haryani 2006), which are, however, of limited capacity due to the ultraoligotrophic character of the lakes (Haffner et al. 2001). Nevertheless, the stocks of the large, predatory *Glossogobius* gobies, the most valuable indigenous food fishes of Lake Matano, are likely among those species most affected by the flowerhorns due to the gobies' spawning sites on open, hard substrate (Figure 3). In line with this expectation, non-quantitative observations by the first author in September 2012 revealed extremely low abundances of *Glossogobius* at all sites visited, an observation standing in stark contrast to their abundances observed in 2002, 2004, 2006 and 2008). Of similar economic importance, stocks of the colourful endemic *Caridina* shrimps exported as aquarium pets will also likely suffer from cichlid predation.

The majority of native species in the Malili Lakes drainage face many threats, primarily due to habitat loss and pollution. Because many are endemic to very restricted geographic ranges and few in number, these species are especially vulnerable (von Rintelen et al. 2012). The introduction of more and more invasive fishes to the Malili Lakes exacerbates the existing threats to native organisms. Actions to prevent further species introductions are urgently needed, a seemingly simple step towards developing sustainable use of these unique lakes. Authorities and agencies should be aware that production of exotic freshwater fish species poses a very high risk for species loss by introducing invaders in this hotspot of freshwater biodiversity. For the long-term maintenance of the Malili Lakes ecosystem and its endemic species radiations, we strongly recommend prohibition of stocking, culture of exotic fish species in fish cages, and other releases of freshwater organisms into natural waters of the lakes' drainage. We also recommend accompanying programs raising local awareness of the endemic fauna, and the creation of a regular monitoring program, tasked with providing the baseline data for future control and management.

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Appendix 1. List of alien fish species reported from the Malili Lakes drainage, including their English and Indonesian common names, their native distribution and their most recent record.

Family	Species	English name	Indonesian name	Native distribution	Latest record
Anabantidae	*Anabas testudineus* (Bloch, 1792)	climbing perch	Betok, Puyu, Oseng	from India to Taiwan, SE Asia	this study
Aplocheilidae	*Aplocheilus panchax* (Hamilton, 1822)	tinhead, blue panchax	Kepala Timah	India, SE Asia	this study
Channidae	*Channa striata* (Bloch, 1797)	chevron snakehead	Gabus, Ikan Salo	India, China, SE Asia	this study
Channidae	*Channa lucius* (Cuvier, 1831)	forest snakehead	Runtuk	Sundaland, Indochina	Kottelat (1989, 1991)
Cichlidae	artificial hybrid	flowerhorn cichlid	Lou Han	Neotropics	this study
Cichlidae	*Oreochromis mossambicus* (Peters, 1852)	Mozambique tilapia	Mujair, Tilapia	Africa	this study
Cichlidae	*Pseudotropheus cyaneorhabdos* (Bowers & Stauffer, 1997)	Maingano cichlid	not available	East Africa: L. Malawi	this study
Clariidae	*Clarias batrachus* (Linnaeus, 1758)	walking catfish	Lele	India, Indochina, Sundaland, Philippines	this study
Cyprinidae	*Cyprinus carpio* (Linnaeus, 1758)	common carp	Mas, Karpers	Central Asia, Japan, widely distributed	this study
Loricariidae	*Pterygoplichthys* cf. *pardalis*	sailfin catfish	Bertulan Sejati	South America (Amazon River basin)	this study
Osphronemidae	*Trichopodus* (*Trichogaster*) *pectoralis* Regan, 1910	snakeskin gourami	Sepat Siam, Janggo	Thailand	this study
Osphronemidae	*Trichopodus* (*Trichogaster*) *trichopterus* Pallas, 1770	three spot gourami	Sepat	Sundaland, Indochina	this study
Poecilidae	*Poecilia reticulata* Peters, 1859	guppy	Seribu	Northern South America	this study
Synbranchidae	*Ophisternon* cf. *bengalense* McClelland, 1844	swamp eel	Belut	Indo-Malaysian region to New Guinea	this study
Serrasalmidae	*Colossoma macropomum* (Cuvier, 1816)	blackfin pacu	Ikan bawal hitam	South America	this study