

Novel cichlid-dominated fish assemblages in tropical urban reservoirs

Kwik, J.T.B.¹, Lim, B.H.R.¹, Liew, J.H.² and D.C.J. Yeo^{1,3*}

¹Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Singapore

²School of Biological Sciences, The University of Hong Kong, Pok Fu Lam Road, Hong Kong SAR, China

³Lee Kong Chian Natural History Museum, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Singapore

*Corresponding author: dbsyeod@nus.edu.sg

Abstract

Recent biodiversity surveys in the lentic habitats of Singapore revealed that non-native cichlids (at least 14 species from different origins) were the most abundant species in the reservoirs of Singapore. To understand the diversity and distribution patterns in six reservoirs (two inland and four coastal), we investigated the species richness and abundances of these cichlids. We also investigated foodwebs to characterise the trophic relationships of cichlids relative to the aquatic community using stable isotope and gut content analyses in each reservoir. Based on various sampling methods (electrofishing, netting and trapping), a total of 5,675 individual cichlids representing 14 species and two hybrids were caught. The three most abundant species (contributing to 66.8% of all cichlids) included the green chromide, *Etroplus suratensis*, the eartheater cichlid, *Geophagus altifrons*, and the Orinoco Peacock Bass, *Cichla orinocensis*. Based on a canonical correspondence analysis, we found that the distribution and abundances of cichlids appeared to be related to abiotic parameters such as salinity and dissolved oxygen, and that species richness and abundances of cichlids differed between coastal and inland reservoirs. We also found that the trophic positions of different cichlid species varied within and across the reservoirs surveyed, where sympatry between highly specialised as well as generalist cichlid species were commonly observed. This was reflected in both the gut contents as well as the empirical foodwebs generated. While we are unable to determine source and timing of the introductions of these cichlids, we are at least confident that that many of the cichlids have already established in these six reservoirs. We postulate that the establishment success and the co-existence of this non-native group has come about through their ability to adapt to the conditions within each reservoir, and this is related to the life history strategies, feeding and behavioural patterns that these different cichlid species display.

Keywords: Cichlidae, non-native, establishment, freshwater, lentic

Introduction

The Cichlidae are a large family of freshwater fishes (>3,000 species) whose native distribution spans three continents (South America, Africa and Asia), with species originating from many countries (Lowe-McConnell, 1969; De Silva et al., 1984; Chakrabarty, 2004; Lamboj, 2004; Sparks and Smith, 2004; Stauffer Jr et al., 2006). Cichlids are also known invasives that are widely established outside their native range; with some examples including the Mayan cichlid, *Cichlasoma urophthalmus*, and the Nile tilapia, *Oreochromis niloticus*, in the United States (Bergmann and Motta, 2005; Grammer et al., 2012); the pearl cichlid, *Geophagus brasiliensis*, and the Mozambique tilapia, *Oreochromis mossambicus*, in Australia (Arthington and Blühdorn, 1994; Morgan et al., 2004; De Graaf and Coutts, 2010); the chameleon fish, *Australoheros facetus*, in Portugal (Ribeiro et al., 2007); and the mango tilapia, *Sarotherodon galilaeus*, in West Africa (Gbaguidi et al., 2016). Within Southeast Asia, there are records of establishment of the Mayan cichlid, *Cichlasoma*

urophthalmus, in Thailand (Nico et al., 2007), and also the blackchin tilapia, *Sarotherodon melanotheron*, in the Philippines (Ordoñez et al., 2015). In Singapore, a broad-based qualitative biodiversity survey performed between 2006–2010 across 14 reservoirs found that non-native Cichlidae was the most speciose fish family (Ng and Tan, 2010a). In addition, what made this cichlid assemblage unique was that it comprised a mix of 14 species (from 12 genera) from throughout the family's native range including the Neotropics, Afrotropics, and South Asia co-existing in these reservoirs (Ng and Tan, 2010a). Potential modes/sources of these fishes include the release of unwanted aquarium species (Lintermans, 2004) or angling species by recreational fishermen (McDowall, 2004); mercy release by religious devotees (Yeo and Chia, 2010); and escapes of cultured species (Magalhães and Vitule, 2013).

The success of cichlids outside of their native range may be attributed to several factors, including species occupying a range of trophic levels, from piscivores (e.g., peacock basses) (Jepsen et al., 1997) to macroinvertebrates such as the geophagine cichlids (López-Fernández et al., 2012) and herbivorous species such as Tilapia and green chromide (Chapman and Fernando, 1994; Ng and Tan, 2010b). Besides the specialist feeders, several cichlid species are also known to display generalist feeding strategies allowing them to be omnivorous and survive on a broad-based diet (Ribeiro et al., 2007; Beatty et al., 2013; Gbaguidi et al., 2016). Another factor that may be contributing to the large family's success outside its native range are its various parental brooding and reproductive strategies (Carlisle, 1985; Keenleyside, 1991). This includes mouth brooding in tilapia such as *Oreochromis mossambicus* and *O. niloticus* (Oliveira and Almada, 1998; Grammer et al., 2012); having the capacity to lay multiple batches of eggs during single reproductive periods in *Cichla piquiti* and *Mesonauta festivus* (Resende et al., 2008; Pires et al., 2015); and even parental provisioning of nutrition during the early stages of offspring development as found in the discus, *Symphysodon* spp. (Wisenden et al., 1995; Buckley et al., 2010). In addition, some cichlids are euryhaline (e.g., *Oreochromis* spp., *Etroplus suratensis*) (Grammer et al., 2012; Chandrasekar et al., 2014), inhabiting and spreading via coastal waters to freshwater reservoirs and streams (Whitfield and Blaber, 1979; Gamboa-Pérez and Schmitter-Soto, 1999; Langston et al., 2010). Cichlids are also known to be found in varied habitats including areas with both simple (e.g., soft sediment, rocky) and complex habitat types (e.g., vegetated or submerged structures) (Gamboa-Pérez and Schmitter-Soto, 1999; Chávez-López et al., 2005; Stauffer Jr et al., 2006) as well as highly urbanized environments (e.g., concretized canals, urban stormwater ponds and reservoirs) (Liew et al., 2012; Kwik et al., 2013; Liew et al., 2018).

Despite the diversity and popularity of cichlids for human uses in Singapore and elsewhere (aquaculture, fisheries, ornamental trade) (Yeo and Chia, 2010; Liew et al., 2012) as well as their notoriety as invasive species (Langston et al., 2010; Kwik et al., 2013), little is actually understood about the novel cichlid assemblages in Singapore's freshwater reservoirs or how these have successfully established as the dominant group of fishes in these lentic habitats. While we have some ideas about the sources of introductions of these cichlids, it is also interesting that such an apparent diversity of cichlids originating from different countries/regions appears to be able to co-exist in Singapore's reservoirs. Based on what has previously been found, we predict that the cichlid species composition may differ due to the biotic and abiotic parameters in each reservoir. As such, the objectives of this study are to: 1) determine the species diversity of cichlids inhabiting Singapore's reservoirs; 2) investigate whether abiotic parameters might influence/be associated with the species compositions of these cichlids; 3) investigate the trophic relationships and resource utilization patterns between the cichlids species that can be found within each reservoir; and in addition, based on understanding the empirically-derived foodweb relationships and the known biology of the different cichlid species, we discuss possible reasons for the co-existence of cosmopolitan cichlid assemblages in the reservoirs of Singapore.

Material and Methods

Study sites

Six reservoirs, including two inland reservoirs (created through damming of headwaters; Reservoirs 1 and 6) and four coastal reservoirs (i.e. created through damming of estuarine areas/river mouths; Reservoirs 2, 3, 4 and 5), were surveyed in this study (Figure 1; Yeo and Lim, 2011). The smaller Reservoirs 1 to 5 were sampled over periods of two months and included surveys across six zones. To facilitate more representative coverage, the larger Reservoir 6 was divided into eight zones, which necessitated a longer period of three months for sampling. In each sampling zone, electrofishing, cast netting and traps were employed to catch fishes; while plankton nets (80 μm mesh) and invertebrate colonisers (Loke et al., 2010) were used to collect plankton and benthic macroinvertebrates, respectively.

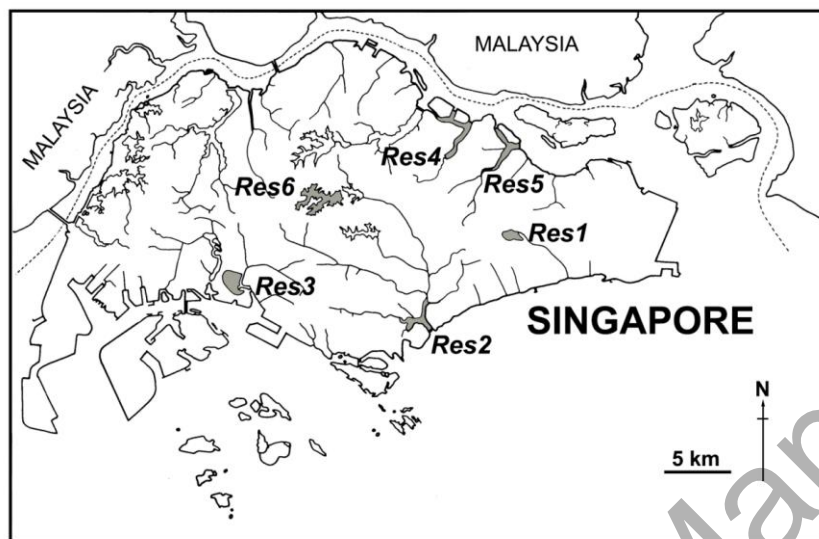


Figure 1. Map of Singapore with the six reservoirs (shaded: Res 1–6) surveyed between December 2014 and May 2016.

Fish sampling

In all reservoirs sampled (with the exception of Reservoir 6), a total of eight electrofishing occasions were conducted over two months, at two electrofishing sessions per week covering all the zones at two-week intervals (increased to 12 occasions in the larger Reservoir 6 over three months). Within each zone, due to restrictions only six physico-chemical parameters (temperature, dissolved oxygen, pH, conductivity, TDS and salinity) were recorded using a YSI-Professional Plus Multiparameter Instrument (Xylem, USA). Each sampling occasion at each zone consisted of 10–20 electrofishing bursts (i.e. five minutes per burst) accompanied by active netting using long-handle nets and visual observation of fishes. In addition to electrofishing, bi-weekly cast netting (7 m diameter, 1 cm mesh) was also performed for two days per week at all reservoirs sampled. During each sampling occasion, 60 to 80 casts were performed across all six (or eight) sampling zones. Lastly, unbaited metal fish traps (80 cm x 40 cm, 2 cm mesh) were also deployed bi-weekly at all reservoirs sampled. 10 traps were deployed haphazardly along the littoral zone (depths of 1–2 m) of the reservoir within each of the six (or eight) zones (total of 60 or 80 traps), and collected after 48 hours. All fish specimens collected using all the methods described above were identified (Baker and Lim, 2008; Ng and Tan, 2010a), measured for standard length (cm) and weighed for total wet weight (g) using precision spring weighing scales (PESOLA, Switzerland). For dietary and stable isotope analyses, a minimum of 18 specimens (where available) for each species were collected from each reservoir, stored in ice and brought back to the laboratory for dissection and tissue collection. A total of 7,612 fish were

caught across all the reservoirs, of which 599 specimens were euthanized for gut content and stable isotope analyses.

Dietary analyses

All fish specimens collected specifically for gut content analysis were dissected, the fore gut excised and the dietary composition for each specimen was quantified as percentage of the total gut content volume ($VO\%$) and frequency of occurrence ($FO\%$) following procedures modified from Kruuk and Parish (1981) and Sá-Oliveira et al. (2014). The dietary items identified under stereoscopic microscope, and were grouped into 11 categories: substrate (i.e. inorganic sediment), unidentifiable animal matter (i.e. highly digested matter of non-fish vertebrates), plant matter (e.g., whole or parts of leaves, flowers, stems), algae (i.e. benthic or encrusting algae), phytoplankton, zooplankton, insect larvae (i.e. whole or parts of aquatic insect larvae), gastropods (i.e. aquatic snails and bivalves), decapod crustaceans (i.e. crab and shrimps), and fish (i.e. whole or remains). The volume ($VO\%$) and frequency of occurrence ($FO\%$) of each dietary item was combined to calculate the feeding index (FI_i) as follows:

$$FI_i = \frac{FO_i \times VO_i}{\sum(FO_i \times VO_i)}$$

where FI_i = feeding index, FO_i = frequency of occurrence of diet item i , and VO_i = volume of diet item i .

Stable isotope analysis

We measured the isotopic profiles of all species of fishes, representative aquatic invertebrate taxa: insect larvae, decapod crustaceans, gastropod molluscs, and zooplankton, and primary producers in the form of riparian vegetation (C_3 and C_4), epiphytic algae and phytoplankton. This was done by sampling the muscle tissue of different fish species (collected during fish sampling), decapods and gastropods specimens, as well as whole zooplankton and insect larvae specimens. Riparian vegetation was represented by leaf clips of the most abundant plants, while epiphytic algae were sampled from hard surfaces in the littoral zones. All samples were oven dried at 70°C for a duration of 48–72 hours, homogenised and weighed (to the nearest 0.0001 g). Processed samples were packed in standard tin capsules and sent to the Stable Isotope Facility at the University of California, Davis, for analyses.

We used $^{13}\text{C}/^{12}\text{C}$ (i.e. $\delta^{13}\text{C}$) and $^{15}\text{N}/^{14}\text{N}$ (i.e. $\delta^{15}\text{N}$) data to assess trophic relationships at our study sites (Liew et al., 2018). This was done using two-source concentration dependent Bayesian mixing models (SIAR) (Parnell and Jackson, 2013), where the dietary analyses were used to validate results of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each prey item to determine their relative contribution. Specifically, we restricted the inclusion of multiple potential food sources (with verification from literature where available) to items found in the gut of the fish species of interest (after Liew et al. 2018). Before the mixing models were run, we corrected our isotope data for trophic discrimination (both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) (Post, 2002; McCutchan Jr et al., 2003; Bunn et al., 2013), as well as lipid enrichment (only $\delta^{13}\text{C}$) (Logan et al., 2008). Trophic discrimination values were taxon-specific for $\delta^{15}\text{N}$ (adopted from McCutchan et al. (2003) and Bunn et al. (2013)), while a fixed value of $0.4 (\pm 1.3)$ was used to correct the $\delta^{13}\text{C}$ value of all consumer taxa analysed (Post 2002). For each consumer taxon, we ran a total of 500,000 iterations (burn-in value of 50,000) of the associated mixing model and the output were expressed in proportion contributions (1–100%) indicating the relative importance of the various potential food items to a consumer taxon. We assumed that food sources with a median source contribution estimate of ≈ 0 are ecologically unimportant (or stochastic), and these were therefore removed from further analyses (after Liew et al., 2018). All remaining interactions were

then tabulated in a predator-prey matrix summarising the presence or absence of trophic relationships between all taxa present in each study site (Liew et al., 2016a).

Foodweb visualisation and interpretation

We visualised the foodwebs of all six sampling sites using the *igraph**1.01 statistical package (Csardi and Nepusz, 2006). All cichlid species in the webs were also highlighted to improve ease of visualisation. To quantify the role cichlids in each foodweb, we calculated the following for all cichlid species using the *NetIndices**1.4.4 statistical package (Kones et al. 2009): (1) trophic position, where (autotrophic) primary producers are assigned a trophic position of 1 and positions greater than or equal to two denote heterotrophy; and (2) omnivory, where a value of ≈ 0 indicates prey specificity while greater values suggests that a consumer feeds on prey from a wider range of trophic levels. As both measures are species-specific, we also calculate the average, as well as the range (minimum and maximum) of trophic position and omnivory values associated with all cichlid species present in the foodweb.

Statistical analyses

A canonical correspondence analysis (CCA) was performed to determine the influence of environmental factors on the distribution of individual fish species found at different zones within each reservoir using the program PC-ORD (McCune and Mefford, 1999). CCA is a constrained ordination technique that incorporates the unimodal response of species to environmental variables. Linear combinations of environmental variables are selected to produce maximum separation of the species distribution in the ordination spaces (Ter Braak and Prentice, 1988; Poulin et al., 1993; Grantham and Hann, 1994). For this analysis, the species data consisted of the abundances of each fish species occurring within each of the six (or eight) zones for each reservoir. The environmental data consisted of the six physico-chemical parameters (temperature, dissolved oxygen, pH, conductivity, TDS and salinity) that we were allowed to collect at each site. Overall CCA model significance was tested using Monte Carlo permutation tests (1,000 iterations) and by evaluating canonical coefficients (Ter Braak, 1986). As a complement to the CCA, a correspondence analysis (CA) was performed using PC-ORD (McCune and Mefford, 1999) based on presence/absence data for each species occurring within each of the six (or eight) zones for each reservoir in the absence of environmental correlations.

In addition, to analyse fish communities of the reservoirs for similarities and differences, Bray-Curtis similarities in relative abundances among fish species were used to construct a two-dimensional non-metric multi-dimensional scaling (NMDS) in PRIMER 6.0 (Clarke and Gorley, 2006) plots to determine if any overlaps between fish communities occurred. In addition, two-dimensional bubble plots representing abundances of each cichlid species within each reservoir zone are also presented. The stress values associated with NMDS plots included indicate the magnitude of distortion (for group distances) between original ordination and the 2-dimensional graphs (Clarke, 1993). The values presented within the graphs indicate whether they are adequate for interpretation (where Stress < 0.1 indicates “no real prospect of misleading interpretation,” stress < 0.2 gives a “useful” two dimensional picture, and stress > 0.2 “should be treated with a great deal of scepticism” (Clarke and Warwick, 2001).

Dietary overlap

The dietary niche breadth of each species was calculated using the standardized Levin's (1968) index:

$$B_i = \frac{1}{(n-1)} \left(\frac{1}{(\sum_j P_{ij}^2)} - 1 \right)$$

where B_i = standardized Levin's niche breadth; P_{ij} = proportion of diet of consumer i consisting of resource j ; and n = total number of resources. The standardized niche breadth index ranges from a scale of 0 (i.e. species consuming only a one item) to 1 (i.e. species consuming all available items in equal proportion). The dietary niche overlap was measured for each co-occurring species-pair using the Pianka's index based on the following formula:

$$O_{jk} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}$$

where O_{jk} = Pianka's niche overlap index between species j and species k ; P_{ij} = proportion of food item i consumed by species j ; P_{ik} = proportion of food item i consumed by species k ; and n = total number of overlapped dietary items between species j and species k (Winemiller and Pianka, 1990). The Pianka's index values ranges from 0 (i.e. indicating no niche overlap) and 1 (i.e. complete niche overlap). Variance of the Pianka's overlap for each cichlid community was determined based on the pairwise overlap of all cichlids in each reservoir. To improve our understanding of the niche breadth and overlap results, values greater than 0.6 are considered high, values between 0.4–0.6 are regarded as intermediate, and values less than 0.4 are considered low (Novakowski et al., 2008; Bonato and Fialho, 2014; Sá-Oliveira et al., 2014).

Additionally, the significance of Pianka's overlap for each reservoir cichlid assemblage was evaluated using null models generated using the package "EcoSimR" in R (Gotelli et al., 2015; R Core Team, 2018). The null models consisted of a set of randomized diet for the cichlid community in each reservoir where the columns represent the diet categories, and each row represents a cichlid species. These null matrices were iterated 10,000 times using the RA3 (scrambled zeros) and RA4 (conserved zeros) algorithms which preserve the row totals of the observed data, thus maintaining the species' niche breadth and the degree of trophic specialization in the simulated null models (Albrecht and Gotelli, 2001). Under the RA3 algorithm, all the feeding coefficients were reshuffled for each row in the null matrices, thus assuming that each species could potentially use other resources (i.e. prey-switching). However for the RA4 algorithm, only the non-zero coefficients were reshuffled for each row in the null matrices, therefore assuming that each species could only feed on what had been observed based on the original data. The two-tailed statistical significance of the comparison between observed and randomly generated null model was evaluated by considering significance at $\alpha = 0.05$.

Significant lower observed diet overlap than expected by chance might indicate resource partitioning (i.e. competition) while observed values significantly higher than expected by chance suggests greater resource sharing within the cichlid assemblage. Additionally, patterns in the variance were also evaluated where significantly higher observed variance than expected by chance suggests presence of trophic guild organisation in the cichlid assemblage. This is because species-pairs within guild will have greater overlaps while species-pairs from different guilds have lower overlaps, leading to large variances (Inger and Colwell, 1977). Although the RA4 algorithm is more conservative (Albrecht and Gotelli, 2001), RA4 is a stronger test for nonrandom patterns of resource partitioning while RA3 is more ideal as a test of guild structure (Winemiller and Pianka, 1990).

Results

A total of 7,612 individual fish representing 43 species from 17 families were captured in the six freshwater reservoirs by electrofishing, netting and trapping (Table 1). The most abundant family was the Cichlidae (including 14 species and two potential hybrids) which contributed to 74.5% of the total fish abundance in the six reservoirs. The three most abundant cichlid species recorded were the green chromide, *Etroplus suratensis* (2,056 individuals or 27% of total fish captured), the eartheater cichlid, *Geophagus altifrons* (972 individuals or 12.8% of total fish captured), and the Orinoco peacock bass, *Cichla orinocensis* (762 individuals or 10% of total fish captured).

Table 1. Abundances of all fishes caught in six reservoirs in Singapore using electrofishing, cast netting and trapping during surveys.

Family	Species	Status	Native range	Abundance	Abbreviation
Adrianichthyidae	<i>Oryzias javanicus</i>	native	Southeast Asia	2	OJ
Ambassidae	<i>Parambassis siamensis</i>	non-native	Thailand	5	PS
Anabantidae	<i>Anabas testudineus</i>	native	Southeast Asia	1	AT
Ariidae	<i>Hexanemichthys sagor</i>	native	Southeast Asia	1	HS
Channidae	<i>Channa micropeltes</i>	non-native	Southeast Asia	154	CM
Channidae	<i>Channa striata</i>	native	Southeast Asia	114	CS
Cichlidae	<i>Acarichthys heckelii</i>	non-native	South America	31	AH
Cichlidae	<i>Amphilophus citrinellus</i>	non-native	South America	235	AC
Cichlidae	<i>Cichla kelberi</i>	non-native	South America	7	CK
Cichlidae	<i>Cichla orinocensis</i>	non-native	South America	762	CO
Cichlidae	<i>Cichla piquiti</i>	non-native	South America	1	CP
Cichlidae	<i>Cichla temensis</i>	non-native	South America	293	CT
Cichlidae	<i>Cichlasoma urophthalmum</i>	non-native	Central America	372	CU
Cichlidae	<i>Cichlasoma x Paratheraps</i> hybrid	non-native	Artificial hybrid	1	CH
Cichlidae	<i>Etroplus suratensis</i>	non-native	India	2,056	ES
Cichlidae	<i>Geophagus altifrons</i>	non-native	South America	972	GA
Cichlidae	<i>Heterotilapia buttkoferi</i>	non-native	West Africa	171	HB
Cichlidae	<i>Oreochromis mossambicus</i>	non-native	Africa	446	OMos
Cichlidae	<i>Oreochromis niloticus</i>	non-native	Africa	60	ON
Cichlidae	<i>Oreochromis</i> 'Pink Tilapia' hybrid	non-native	Africa	6	OH
Cichlidae	<i>Parachromis managuensis</i>	non-native	South America	7	PMan
Cichlidae	<i>Vieja melanura</i>	non-native	South America	255	VM
Clariidae	<i>Clarias gariepinus</i>	non-native	Africa	36	CG
Cyprinidae	<i>Barbonymus schwanenfeldii</i>	non-native	Asia	31	BS
Cyprinidae	<i>Crossocheilus oblongus</i>	non-native	Southeast Asia	1	COb
Cyprinidae	<i>Cyprinus carpio</i>	non-native	Europe, Asia	1	CC
Cyprinidae	<i>Gyrinocheilus aymonieri</i>	non-native	Thailand	1	GAy
Cyprinidae	<i>Leptobarbus rubripinna</i>	non-native	Southeast Asia	1	LH
Cyprinidae	<i>Morulius chrysophekadion</i>	non-native	Southeast Asia	1	MC
Datnoididae	<i>Datnoides microlepis</i>	non-native	Southeast Asia	2	DM
Eleotridae	<i>Oxyeleotris marmorata</i>	native	Southeast Asia	981	OMa
Gobiidae	<i>Glossogobius aureus</i>	native	Southeast Asia	377	GAu
Gobiidae	<i>Rhinogobius giurinus</i>	native	Southeast Asia	1	RG
Hemiramphidae	<i>Hyporhamphus quoyi</i>	native	Southeast Asia	16	HQ
Loricariidae	<i>Pterygoplichthys disjunctivus</i>	non-native	South America	19	PD

Loricariidae	<i>Pterygoplichthys pardalis</i>	non-native	South America	26	PP
Loricariidae	<i>Pterygoplichthys</i> sp.	non-native	South America	11	P
Notopteridae	<i>Chitala ornata</i>	non-native	Thailand, Vietnam	9	CO _r
Notopteridae	<i>Notopterus notopterus</i>	non-native	Southeast Asia	4	NN
Osphronemidae	<i>Osphronemus goramy</i>	non-native	Southeast Asia	32	OG
Osteoglossidae	<i>Scleropages formosus</i>	non-native	Southeast Asia	44	SF
Serrasalminidae	<i>Piaractus brachypomus</i>	non-native	South America	1	PB
Synbranchidae	<i>Monopterus javanensis</i>	native	Asia	65	MJ

In the canonical correspondence analysis (CCA), Axis 1 and Axis 2 contributed to more than 56% of the variance explained, and that the Monte Carlo permutation tests for fish species-environment variables found both the first two axes highly significant ($P < 0.05$). Based on the CCA, we also found that the green chromide, *Etroplus suratensis*, the Mayan cichlid, *Cichlasoma urophthalmum*, and Mozambique tilapia, *Oreochromis mossambicus*, were most strongly associated with reservoirs (Reservoirs 4 and 5) characterized by relatively higher salinities (all six reservoirs recorded salinities < 0.05 ppt), conductivity, pH and dissolved oxygen (Figure 2A). Reservoirs 2 and 3 while similarly characterized by increased salinities, conductivity and pH, had lower levels of dissolved oxygen, and were instead dominated by the Orinoco peacock bass, *Cichla orinocensis*, the Quetzal cichlid, *Vieja melanura*, the zebra tilapia, *Heterotilapia buttkoferi*, the Midas cichlid, *Amphilophus citrinellus*, the threadfin acara, *Acarichthys heckleii*, the Azul peacock bass, *Cichla piquiti*, the jaguar cichlid, *Parachromis managuensis*, and the *Oreochromis* ‘Pink Tilapia’ hybrid (Figure 2A). Reservoirs 2 to 5 included all the coastal reservoirs in this study (Figure 1). Cichlids that were more associated to the inland reservoirs of lower salinities (Reservoirs 1 and 6), included the Nile tilapia, *Oreochromis niloticus*, the Kelberi peacock bass, *Cichla kelberi*, the eartheater cichlid, *Geophagus altifrons* and the speckled peacock bass, *Cichla temensis* (Figure 2A). The cichlid species that were found at the six reservoirs observed in the CCA were similar to the results in the correspondence analysis (CA) which was based on presence/absence data and without the environmental parameters (Figure 2B).

The non-metric multidimensional scaling (NMDS) of the fish communities found in each of the zones at each reservoir indicated two clusters were apparent at 25% similarity, and included an inland reservoirs cluster (Reservoirs 1 and 6) and a coastal reservoir cluster (Reservoirs 2, 3, 4 and 5) (Figure 3). At 50% similarity, with the exception of reservoirs 2 and 5 which were clustered together, all the other remaining reservoirs had unique fish assemblages (Figure 3). The more detailed two-dimensional bubble plots based on each of the cichlid species during the NMDS analysis also showed that there was no one cichlid species that was found in all six reservoirs surveyed. The most common species, found in five reservoirs, included *Cichla orinocensis* and *H. buttkoferi*; while species that could only be found in single reservoirs included *Cichla kelberi*, *Cichla piquiti*, the *Cichlasoma* hybrid, the *Oreochromis* “pink tilapia” and *Parachromis managuensis* (Figure 4).

Among the four species of peacock bass (genus *Cichla*), the more abundant *Cichla orinocensis* was found mainly in the slightly more saline (as compared to the inland reservoirs which recorded very low salinities) coastal reservoirs (Reservoirs 2–5) while *Cichla temensis* was primarily found in the less saline inland reservoirs (Reservoirs 1 and 6). For the tilapiine cichlids (*Oreochromis*), high numbers of *Oreochromis mossambicus* and with lower numbers of *Oreochromis niloticus* could be found co-occurring in both reservoirs 2 and 5 (which are clustered together based on a 50% similarity in fish communities in the NMDS, Figure 3). Similarly, the most abundant cichlid (green chromide, *Etroplus suratensis*) was found in three of the coastal reservoirs (Reservoirs 2, 4 and 5), and also in one of the inland reservoirs (Reservoir 1) (Figure 4). In comparison, the second most abundant cichlid, the eartheater cichlid, *Geophagus altifrons*, was more abundantly found in the inland reservoirs (Reservoirs 1 and 6), and with lower numbers in the coastal reservoirs (Reservoirs 2 and 5) (Figure 4).

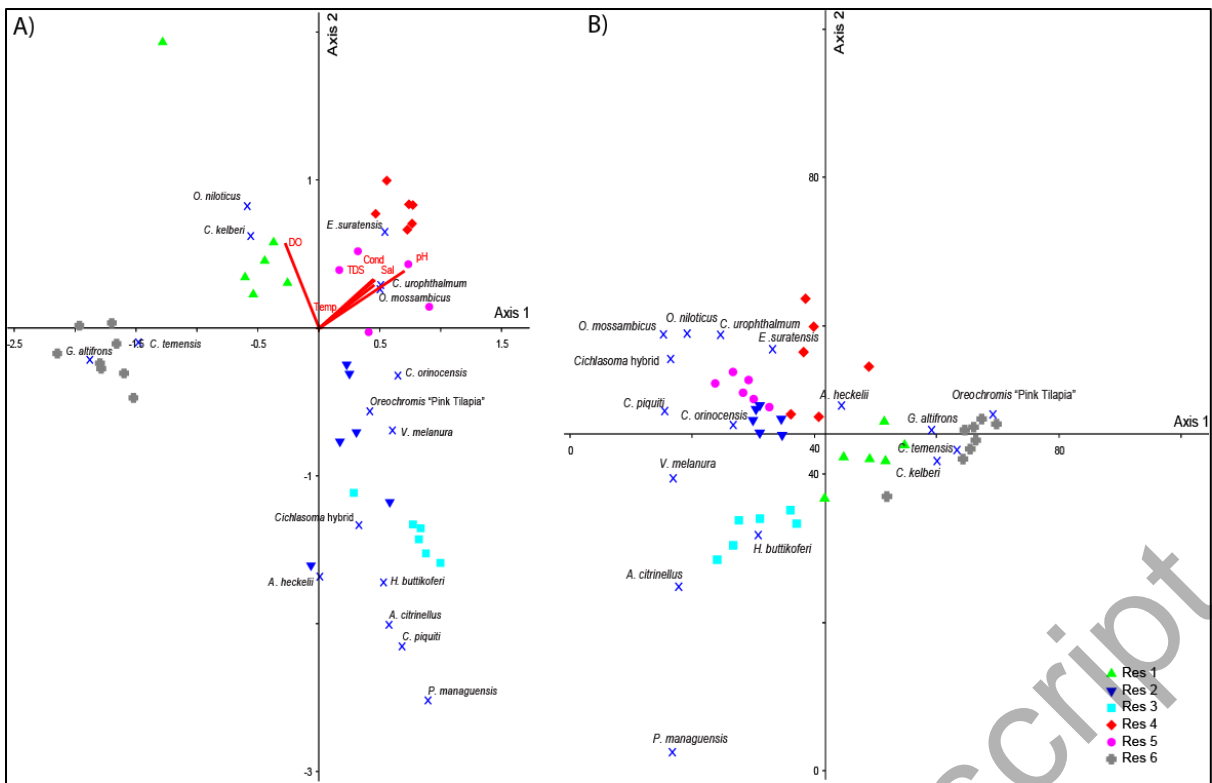


Figure 2. A) Canonical correspondence analysis (CCA) of abundances of each fish species and six associated environmental measures where the eigenvalues of Axis 1 (39.9%) and Axis 2 (16.2%) are 0.776 and 0.16 respectively; and B) Correspondence analysis of abundance of each fish species (based on presence/absence data) found at six reservoirs in Singapore surveyed between December 2014 and May 2016.

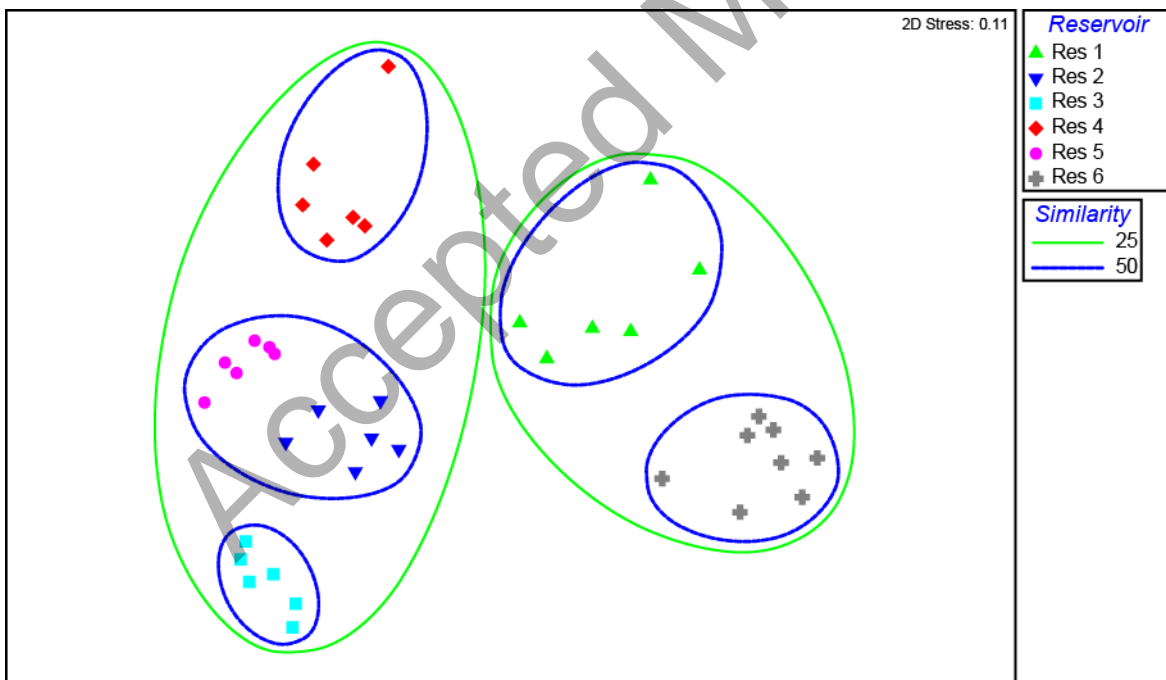


Figure 3. Non-metric dimensional scaling (NMDS) of fish communities (43 species) found in six reservoirs of Singapore surveyed between December 2014 and May 2016.

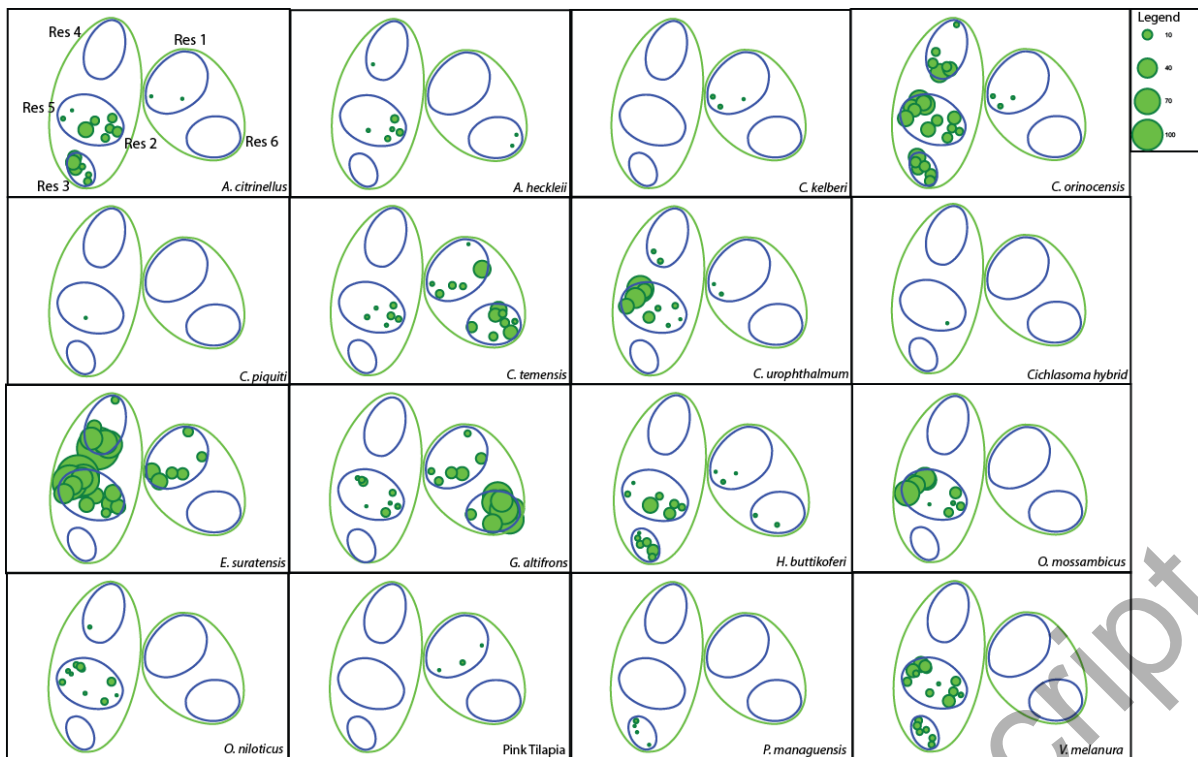


Figure 4. Bubble plots based on non-metric dimensional scaling for each of the 16 cichlid species found in the six reservoirs surveyed between December 2014 and May 2016 (where size of circles represent relative abundances of each species found in each zone for each reservoir, and with stress values of 0.11).

From the 599 digestive tracts examined, 457 belonging to 11 cichlid species contained stomach contents. The remaining five cichlid species were excluded from the diet analysis due to low sample sizes ($N < 5$). Based on the diet accumulation curve, all species with the exception for *Acarichthys heckelii* reached an asymptote (Figure 5). The feeding index of the dietary items, trophic guild, and niche breadth for the 11 cichlid species are presented in Table 2. Overall, fish, animal matter, gastropods, and detritus were the most exploited food resources representing of 75% of the total food items ingested by all the cichlid species. The majority of cichlid species (7 of 11 species) had a carnivorous or piscivorous diet. Niche breadth (B) values varied from 0.14 to 0.65 (Table 2), where approximately 63% of the cichlid species were trophic specialists such as *Cichla* spp. (piscivores) and *Oreochromis* spp. (detritivores) with relatively low niche breadth ($B < 0.4$).

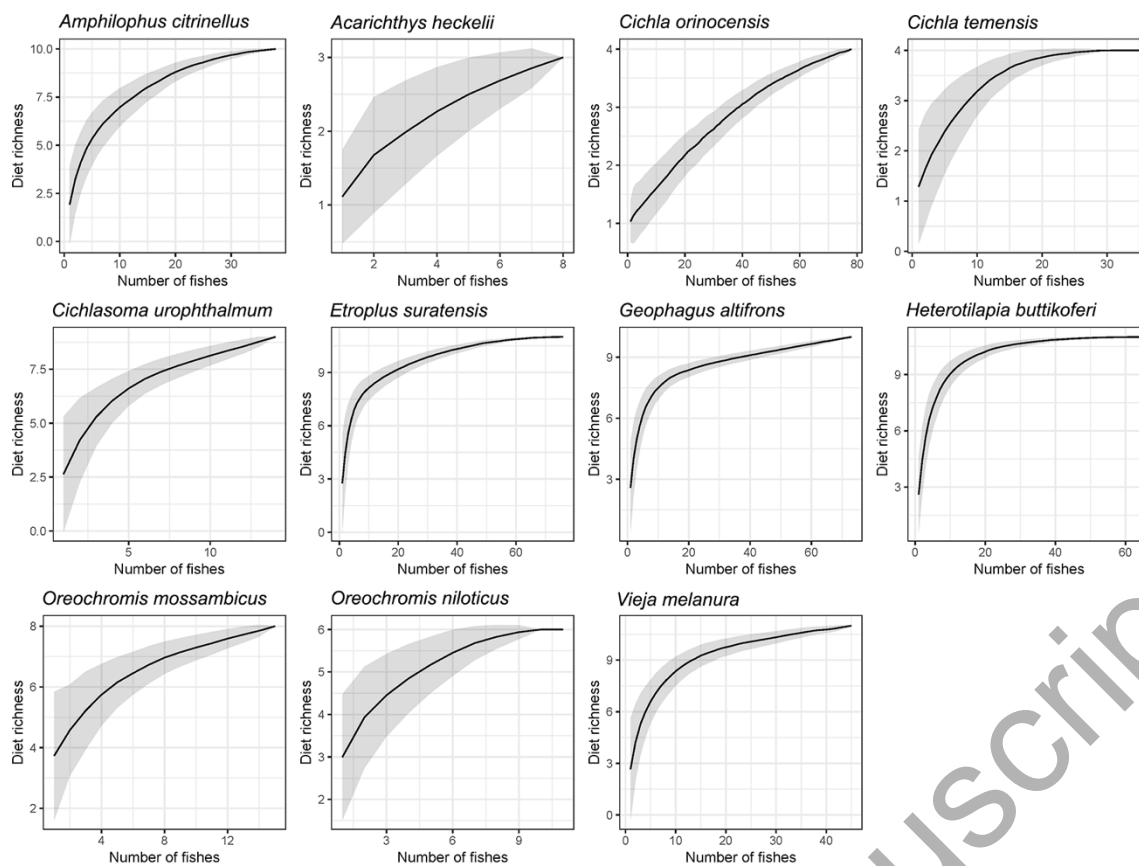


Figure 5. Observed accumulation curve of diet by cichlid species sampled in our study. Solid line represents the mean diet richness and shading indicates the 95% confidence interval.

The mean dietary niche overlap observed for the cichlid communities in each reservoir were relatively low, ranging from 0.16–0.41 (Table 3). Cichlid communities in the inland reservoirs (Reservoirs 1 and 6) had the lowest feeding overlap values (0.17 and 0.29) while the coastal reservoirs (Reservoirs 2 and 5) which shared the greatest similarity in their cichlid assemblage had the highest niche overlap values (0.39 and 0.41). Comparisons with null communities generated using RA3 and RA4 algorithms found that the observed niche overlaps were significantly higher than expected by chance in Reservoirs 2 and 5 but also for Reservoir 1 using the RA3 algorithm only (Table 3). This suggests similar foraging patterns and greater resource sharing in these reservoirs. Similarly, patterns of variance were observed to be significantly higher than expected by chance for Reservoir 2 and 5 using both RA3 and RA4 algorithms (Table 3), suggesting the presence of trophic guild organization in the cichlid communities.

Table 2. Feeding index values and trophic guild classification of the 11 cichlid species included for the gut content analysis (and where species abbreviations can be found in Table 1).

Species	Diet categories											Trophic guild	Standardized Levin's niche breadth (B)	
	Substrate	Animal matter	Plant	Periphyton	Phytoplankton	Zooplankton	Insect	Decapod	Gastropod	Fish	Detritus			
AH		0.905					0.069				0.026		Carnivorous	0.653
AC	0.009	0.195	0.099		0.002	0.001	0.001		0.317		0.361	0.016	Carnivorous	0.349
CO		0.001									0.999		Piscivorous	0.140
CT			0.011					0.003			0.985	0.001	Piscivorous	0.206

CU	0.005	0.63 2	0.0 18	0.007			0.1 35	0.002	0.08	0.12 1		Carnivorou s	0.531
ES	0.027	0.12 8	0.2 67	0.357	0.001		0.0 69		0.058		0.093	Omnivorou s	0.366
GA	0.024	0.47 2	0.0 51	0.082			0.3 18		0.025	0.02 1	0.007	Carnivorou s	0.479
HB	0.042	0.14 5	0.1 38	0.344	0.04	0.002	0.0 05	0.001	0.011	0.00 7	0.265	Herbivorou s	0.398
OM os	0.007		0.0 05		0.231	0.046	0.0 02				0.709	Detritivoro us	0.238
ON	0.003		0.0 02	0.028	0.077	0.014					0.877	Detritivoro us	0.161
VM	0.008	0.21	0.0 84	0.015			0.0 89	0.008	0.55	0.03	0.006	Carnivorou s	0.423

Table 3. Observed and simulated mean dietary niche overlap (Pianka's index) for the cichlid assemblage in each reservoir using the RA3 (scrambled zeros) and RA4 (conserved zeros) algorithms. $P_{obs.}$ refers to the P-value where the mean observed overlap is greater than simulated values, $P_{var.}$ refers to the P-value where the variance of observed overlap is greater than variance of simulated overlap. Significant P-values are indicated in bold.

	Mean observed	Variance observed	RA3 algorithm				RA4 algorithm			
			Mean simulated	Variance simulated	$P_{obs.}$	$P_{var.}$	Mean simulated	Variance simulated	$P_{obs.}$	$P_{var.}$
Res 1	0.288	0.116	0.18	0.069	0.043	0.069	0.264	0.099	0.314	0.288
Res 2	0.387	0.102	0.219	0.065	<0.01	0.011	0.300	0.085	0.036	0.126
Res 3	0.321	0.094	0.261	0.059	0.212	0.241	0.236	0.063	0.122	0.317
Res 4	0.341	0.092	0.166	0.067	0.101	0.354	0.371	0.099	0.585	0.411
Res 5	0.414	0.127	0.252	0.061	<0.01	<0.01	0.270	0.065	<0.01	<0.01
Res 6	0.166	0.063	0.179	0.068	0.511	0.475	0.119	0.052	0.291	0.337

There were no clear trends in the trophic positions occupied by cichlids across the surveyed reservoirs (Figure 6). The average trophic position of cichlids for all foodwebs was ≈ 3 , corresponding with trophic positions typically occupied by secondary consumers. Across all the reservoirs, at least one cichlid species, most often from the genus *Cichla*, occupied the apex of the foodweb (trophic position >4). Further, we did not observe any strictly herbivorous cichlids (trophic position=2). Instead, the lowest trophic position attributed to a cichlid species (*Oreochromis niloticus*) was 2.1 in Res 5. The average omnivory of cichlid species varied greatly within each reservoir, commonly ranging from ≈ 0 to ≈ 1 (Table 4). This suggests that sympatry of highly specialised and generalist cichlid species were common in the reservoirs surveyed.

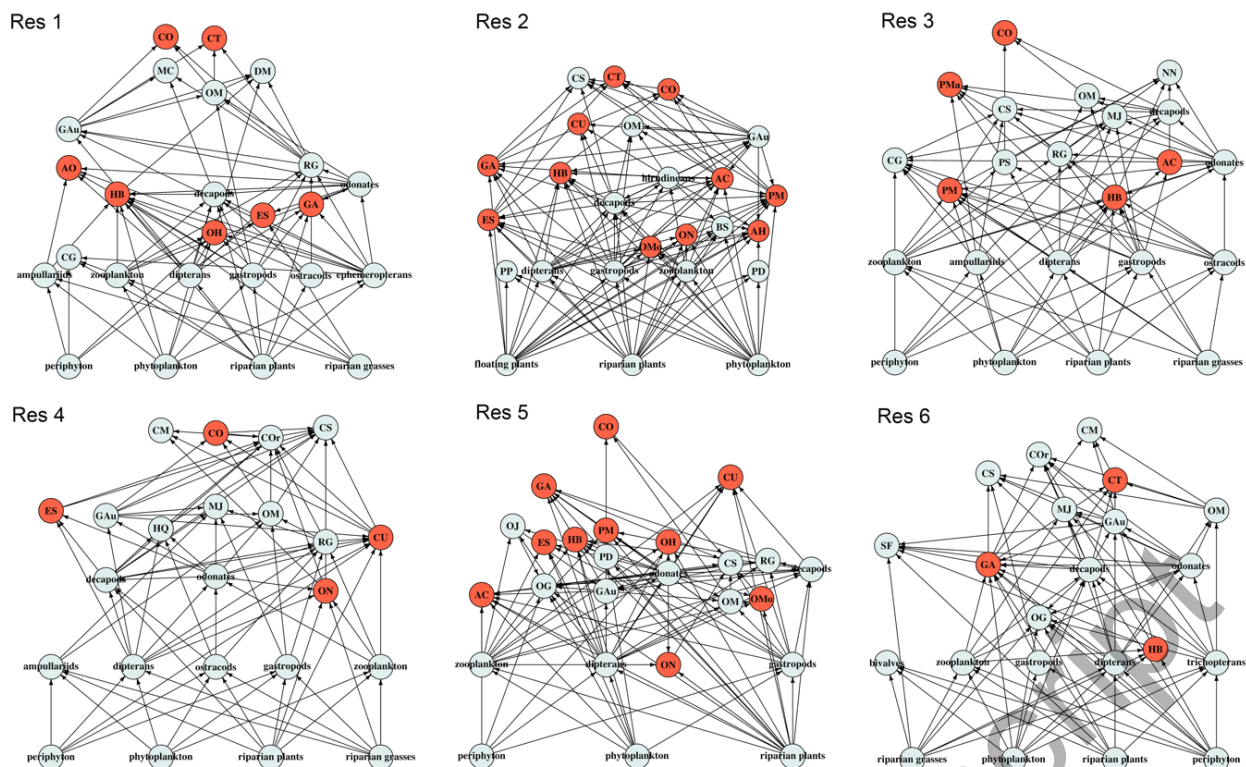


Figure 6. Empirical foodwebs of six reservoirs surveyed in this study. Nodes in the foodweb represent individual taxa, while links between the nodes are indicative of trophic relationships. Trophic positions of all taxa are reflected by the position of their nodes along the vertical axis of the foodwebs where primary producers (trophic position=1) occupy the base of webs. Nodes associated with cichlid species are highlighted in red (and where species abbreviations can be found in Table 1).

Table 4. Summary of indices describing the trophic roles of cichlids in all six reservoirs surveyed.

Trophic index	Sites					
	Res 1	Res 2	Res 3	Res 4	Res 5	Res 6
Average trophic position	3.3	3.0	3.3	3.6	3.1	3.3
Maximum trophic position	4.6	4.1	4.3	4.6	4.6	4.1
Minimum trophic position	2.5	2.3	2.7	2.8	2.7	2.1
Average omnivory	0.3	0.4	0.2	0.4	0.6	0.4
Maximum omnivory	0.9	0.8	0.4	1.1	1.3	0.8
Minimum omnivory	0.1	0.1	≈ 0.0	≈ 0.0	≈ 0.0	0.1

Discussion

In general, we found that regardless of their origins (i.e. native ranges and introduction pathways), the cichlids that occur in Singapore appear to have adapted to the conditions that can be found in the six reservoirs surveyed. However, certain species appeared better adapted to certain reservoirs compared to others; these included several more euryhaline species (e.g., *Oreochromis mossambicus*, and *Etroplus suratensis*) which were more abundant in the coastal reservoirs, and several more

freshwater-adapted species (e.g., *Cichla temensis*), which have established in the inland reservoirs where water salinities are lower as compared to the coastal reservoirs. The dominance of these fish species in certain reservoirs might be explained by these fishes adapting to the abiotic and biotic conditions specific in each reservoir and thus being able to establish themselves successfully over time; or in the case of the euryhaline species, it is also possible that these fishes already being dominant prior to the damming of the coastal catchment areas in Singapore (Ng and Tan, 2013; Liew et al., 2016b). As each reservoir appears to be unique in its aquatic community (Liew et al., 2018), these cichlids have also managed to successfully occupy the various available trophic niches. The success of these cichlids could also be explained by the variety of feeding and reproductive strategies of these cichlids (Lowe-McConnell, 1969; Keenleyside, 1991; Chakrabarty, 2004; Chávez-López et al., 2005; Stauffer Jr et al., 2006). Importantly, however, the introduction sources and the effects of propagule pressure, which are currently not known, are also likely to have an important impact of these assemblages. The information presented here can nevertheless still be useful as a baseline database for future population and community studies

Based on the results from this study, the establishment of reservoir-specific cichlid species in at least these six freshwater reservoirs in Singapore could be attributed to both abiotic and biotic conditions. This might provide an increased adaptive advantage in inhabiting certain reservoirs, or even a competitive advantage between fish taxa within a reservoir (Moyle and Light, 1996; Bomford et al., 2010). For example in the tilapiine cichlids, high numbers of *Oreochromis mossambicus* and lower numbers of *Oreochromis niloticus* could be found co-occurring in two of the coastal reservoirs, which might be explained in part by the higher salinity tolerance of this genus (Whitfield and Blaber, 1979; Uchida et al., 2000). Yet another example is the most widespread cichlid (green chromide, *Etroplus suratensis*) which has a broad range in salinity tolerance (De Silva et al., 1984; Chandrasekar et al., 2014) and was abundantly found in three of the coastal reservoirs, but in low numbers in one of the inland reservoirs. Similarly, the second most abundant cichlid was the eartheater cichlid, *Geophagus altifrons*, which is known to be a blackwater species (i.e. preferring stained, soft and acidic waters) in its native ranges (Saint-Paul et al., 2000); was more commonly found in the less saline inland reservoirs. In addition to the water conditions, the vegetation and maturity of the reservoirs may also play an important role in the establishment of freshwater fishes (Pusey and Arthington, 2003). The inland Reservoir 6, for example, which is older (created in 1970s) than the other reservoirs surveyed (created between 1980s to 2010s) (Ng et al., 2011) and situated within a nature reserve, and has denser riparian vegetation including mature secondary forests along its periphery as compared to the younger reservoirs surveyed (pers. observ.). This reservoir also features specific riparian habitats that are more suitable for certain cichlid species (e.g., coarse woody debris, i.e. large branches of submerged broken trees for cichlids such as *Cichla temensis* or *Cichla orinocensis*) (Jepsen et al., 1997; Winemiller et al., 1997; Gois et al., 2012). In contrast, the more recently constructed reservoirs usually contain more rocky bunds (i.e. embankments) and sparser woody vegetation (mainly grasses) along the banks (pers. obs.), and could be more suitable for substrate-brooding cichlid species (Ng and Tan, 2010a; Liew et al., 2012; Kwik et al., 2013).

Besides environmental conditions, the dietary adaptations displayed by cichlids may also play an important role for their establishment success in Singapore's reservoirs. The diets of the cichlids encountered in Singapore's reservoir were generally similar to those recorded in their native ranges; these included primarily piscivores such as the peacock basses (*Cichla* spp.) (Jepsen et al., 1997); to invertivores such as *Veija melanura* and *Geophagus altifrons* (López-Fernández et al., 2012); and herbivores such as *Etroplus suratensis* and *Heterotilapia buttikoferi* (Chapman and Fernando, 1994; Ng and Tan, 2010b). We also found, however, that while diets could be specialised, many of the cichlids still fed on a wide range of food types (albeit in lower proportions); such opportunistic feeding habits potentially playing an important role in rapid colonisation and establishment success of cichlids (Bergmann and Motta, 2005). It is also possible that the relatively high abundances of smaller prey fish species (i.e. smaller than 5 cm) and in these reservoirs afford the predators opportunities to shift from one resource to another (depending on their requirements), instead of

utilising the full diversity of food types available to them (Gerking, 1994). The overall cichlid communities within Singapore's reservoirs exploited a wide variety of food items comprising species with varying degree of trophic specialisation. Species that can be considered as specialist with low niche breadth values and omnivory index include those that consumed exclusively on fish, plants or detritus (i.e. *Cichla* spp. and *Oreochromis* spp.) while omnivorous/generalist species tend to feed on a greater variety of resources and/or from differing trophic groups (i.e. *Cichlasoma urophthalmum* and *Geophagus altifrons*). Despite the overall low niche overlap values observed, foraging patterns within the cichlid communities based on the comparisons with null models revealed evidence of significant resource sharing and presence of trophic guild organization for the coastal reservoirs (Reservoirs 2 and 5). This suggests that resource competition is not the primary driver for the cichlid assemblage within these coastal reservoirs even though there were significant higher niche overlaps than expected by chance. Although the competitive exclusion principle states that species competing for the same resource cannot coexist (Hardin, 1960), coexistence of competing species may still occur when resources are not limiting which alleviates competition and allows resource sharing (Corrêa et al., 2011; Bonato and Fialho, 2014). We note that the cichlid species assemblage in the coastal reservoirs were similar to each other and also had the greatest diversity of cichlid species. Furthermore, the assemblages observed for the coastal reservoirs were dominated by a mixture of specialist (i.e. *Cichla* spp. and *Oreochromis* spp.) and generalist species (i.e. *Cichlasoma urophthalmum* and *Epiplatys suratensis*) each occupying different trophic guilds while having strong intra-guild niche overlaps between the piscivorous or detritivorous species.

Finally, and as mentioned earlier, other important considerations when assessing the cichlid species diversity that are currently recorded in each of these reservoirs is the specific time at which these cichlid species were first introduced into the reservoirs; as well as data on pre-existing cichlid assemblages prior to coastal reservoir construction/damplings. Such information might explain the current dominance of certain cichlid species within each reservoir, and possibly provide a temporal understanding on the trends in abundances observed for each cichlid species. Unfortunately, only rough approximations of introduction timeframes are available in the literature for certain cichlid species introduced in Singapore. For example, Alfred (1966) could only postulate that *Oreochromis mossambicus* was introduced by the Japanese from Java sometime between 1942 and 1945. Similarly, the first records of *Epiplatys suratensis* was based on collection records from 1995 (Ng and Tan, 2010b), and it could only be assumed that this was within the initial introduction period as there were no records of the species prior to 1993 (Japar et al., 1994). For some other cichlids, such as *Cichla orinocensis* and *Cichlia temensis*, definitive information on their introduction is limited to when they were first recorded (as recorded by Ng and Tan, 2010a), although they were assumed to be introduced sometime in the early 1990s by recreational fishermen (Ng et al., 2011). As such, the quantitative data reported in this paper on cichlid species richness and abundances will be useful as the baseline quantitative information for these fishes. Besides the timing of introductions, the pathways (i.e. sources) of introduction also play an important role in the cichlid species that could potentially be found in reservoirs (Yeo and Chia, 2010), and include the ornamental trade and aquaculture/live food trade (Savini et al., 2010; Strecker et al., 2011). The introduction pathways through which cichlids enter reservoirs or waterways involve activities such as mercy release (Yeo and Chia, 2010); releases of unwanted aquaria-purchased pets (Ng and Tan, 2010a; Kwik et al., 2013); escapees from aquaculture (Ng and Tan, 2010a; Liew et al., 2012) and more recently due to releases for recreational fishing activities (Ng and Tan, 2010a) (e.g., peacock basses which are highly sought after by recreational anglers). While there are legislations regulating the release of animals into reservoirs and waterways (Yeo and Chia, 2010), enforcement of these regulations is challenging (Heng, 2016; Hong, 2018).

Conclusions

Based on our observations and the known biology of the group, we found that the distribution and species diversity of cichlids appear to be influenced by the biotic and abiotic conditions that can be

found within each reservoir. We also feel that that the establishment success of these cichlids is also owed to the various biological and behavioural adaptations that cichlids display. Factors such as these have also provided better opportunities for the co-existence of these many different species of cichlids from different origins. While some ecological succession may occur (e.g., switch in dominance between tilapiines and the green chromide in certain reservoirs (pers. obs.)), the cichlids will likely remain as the most species rich and abundant taxa in Singapore's reservoirs. Given their prominence in Singapore's ornamental pet trade, which is a major national industry (Cheong, 1996; Liew et al., 2012), is not inconceivable that the number of species of cichlids in the reservoirs of Singapore may increase further through additional introductions, although as the reservoir communities begin to accumulate, successful new species establishments would probably depend on their ability to co-exist or to replace the currently established cichlids.

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References

- Albrecht, M., Gotelli, N.J., 2001. Spatial and temporal niche partitioning in grassland ants. *Oecologia* 126(1), 134–141.
- Arthington, A.H., Blühdorn, D.R., 1994. Distribution, genetics, ecology and status of the introduced cichlid, *Oreochromis mossambicus*, in Australia. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen* 24(1), 53-62.
- Baker, N., Lim, K., 2008. *Wild Animals of Singapore: A Photographic Guide to Mammals, Reptiles, Amphibians and Freshwater Fishes*, Draco and Nature Society (Singapore).
- Beatty, S.J., Morgan, D.L., Keleher, J., Allen, M.G., Sarre, G.A., 2013. The tropical South American cichlid, *Geophagus brasiliensis* in Mediterranean climatic south-western Australia. *Aquat. Invasions* 8(1), 21-36.
- Bergmann, G.T., Motta, P.J., 2005. Diet and morphology through ontogeny of the nonindigenous Mayan cichlid '*Cichlasoma (Nandopsis) urophthalmus* (Günther 1862) in southern Florida. *Environ. Biol. Fishes* 72(2), 205-211.
- Bomford, M., Barry, S.C., Lawrence, E., 2010. Predicting establishment success for introduced freshwater fishes: a role for climate matching. *Biol. Invasions* 12(8), 2559-2571.
- Bonato, K.O., Fialho, C.B., 2014. Evidence of niche partitioning under ontogenetic influences among three morphologically similar Siluriformes in small subtropical streams. *PLoS ONE* 9(10), e110999.
- Buckley, J., Maunder, R.J., Foey, A., Pearce, J., Val, A.L., Sloman, K.A., 2010. Biparental mucus feeding: a unique example of parental care in an Amazonian cichlid. *J. Exp. Biol.* 213(22), 3787-3795.

- Bunn, S.E., Leigh, C., Jardine, T.D., 2013. Diet-tissue fractionation of $\delta^{15}\text{N}$ by consumers from streams and rivers. *Limnol. Oceanogr.* 58(3), 765-773.
- Carlisle, T.R., 1985. Parental response to brood size in a cichlid fish. *Anim. Behav.* 33(1), 234-238.
- Chakrabarty, P., 2004. Cichlid biogeography: comment and review. *Fish Fish.* 5(2), 97-119.
- Chandrasekar, S., Nich, T., Tripathi, G., Sahu, N., Pal, A., Dasgupta, S., 2014. Acclimation of brackish water pearl spot (*Etroplus suratensis*) to various salinities: relative changes in abundance of branchial Na^+/K^+ -ATPase and $\text{Na}^+/\text{K}^+/\text{2Cl}^-$ co-transporter in relation to osmoregulatory parameters. *Fish Physiol. Biochem.* 40(3), 983-996.
- Chapman, G., Fernando, C.H., 1994. The diets and related aspects of feeding of Nile tilapia (*Oreochromis niloticus* L.) and common carp (*Cyprinus carpio* L.) in lowland rice fields in northeast Thailand. *Aquaculture* 123(3-4), 281-307.
- Chávez-López, R., Peterson, M.S., Brown-Peterson, N.J., Morales-Gomez, A.A., Franco-Lopez, J., 2005. Ecology of the mayan cichlid, *Cichlasoma urophthalmus* Günther, in the Alvarado lagoonal system, Veracruz, Mexico. *Gulf Caribb. Res.* 17(1), 123-131.
- Cheong, L., 1996. Overview of the current international trade in ornamental fish, with special reference to Singapore. *Rev. Sci. and Tech.* 15(2), 445-481.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18 117-143.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial (Plymouth Routines in Multivariate Ecological Research). PRIMER-E, Plymouth.
- Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd Edition ed. Plymouth Marine Laboratory, Plymouth.
- Corrêa, C.E., Albrecht, M.P., Hahn, N.S., 2011. Patterns of niche breadth and feeding overlap of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin. *Neotrop. Ichthyol.* 9(3), 637-646.
- De Graaf, M., Coutts, T., 2010. Invasive potential of a South-American fish species, *Geophagus brasiliensis*, in the Swan River, Western Australia: based on tolerance to instantaneous and gradual changes in salinity. *J. R. Soc. West. Aust.* 93(3), 147.
- De Silva, S.S., Maitipe, P., Cumarantunge, R.T., 1984. Aspects of the biology of the euryhaline Asian cichlid, *Etroplus suratensis*. *Environ. Biol. Fishes* 10(1-2), 77-87.
- Gamboa-Pérez, H.C., Schmitter-Soto, J.J., 1999. Distribution of cichlid fishes in the littoral of Lake Bacalar, Yucatan Peninsula. *Environ. Biol. Fishes* 54(1), 35-43.
- Gbaguidi, H.M., Adite, A., Sossoukpe, E., 2016. Feeding Ecology and Establishment of the Naturally-Colonized Freshwater Cichlid, *Sarotherodon galilaeus* (Pisces: Actinopterygii: Perciformes) from a Man-Made Lake, South-Benin, West Africa. *Nat. Res.* 7(06), 337.
- Gerking, S.D., 1994. Feeding ecology of Fish. Academic Press, San Diego, California.

- Gois, K.S., Antonio, R.R., Gomes, L.C., Pelicice, F.M., Agostinho, A.A., 2012. The role of submerged trees in structuring fish assemblages in reservoirs: two case studies in South America. *Hydrobiologia* 685(1), 109-119.
- Gotelli, N.J., Hard, E.M., Ellison, A.M., 2015. *EcoSimR: Null model analysis for ecological data*.
- Grammer, G.L., Slack, W.T., Peterson, M.S., Dugo, M.A., 2012. Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) establishment in temperate Mississippi, USA: multi-year survival confirmed by otolith ages. *Aquat. Invasions* 7(3).
- Grantham, B.A., Hann, B.J., 1994. Leeches (Annelida: Hirudinea) in the experimental lakes area, northwestern Ontario, Canada: Patterns of species composition in relation to environment. *Can. J. Fish. Aquat. Sci.* 51(7), 1600-1607.
- Hardin, G., 1960. The competitive exclusion principle. *Science* 131(3409), 1292-1297.
- Heng, L. 2016, May 22. Vesak Day practice of releasing animals harms ecosystems. *The New Paper*. Retrieved from <https://www.tnp.sg/news/singapore/vesak-day-practice-releasing-animals-harms-ecosystems>.
- Hong, J. 2018, September 24. More non-native fish in Singapore waterways. *The Straits Times*. Retrieved from <https://www.straitstimes.com/singapore/more-non-native-fish-in-spore-waterways>.
- Inger, R.F., Colwell, R.K., 1977. Organization of Contiguous Communities of Amphibians and Reptiles in Thailand. *Ecol. Monogr.* 47(3), 229–253.
- Japar, S.B., Sasekumar, A., Chong, V.C., Low, J.K.Y., 1994. Mangrove fish resources in ASEAN region, In: Sudara, S., Wilkinson, C.R., Chou, L.M. (Eds.), *Third ASEAN-Australia Symposium on Living Coastal Resources: Chulalongkorn University, Bangkok*, pp. 179-200.
- Jepsen, D.B., Winemiller, K.O., Taphorn, D.C., 1997. Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. *J. Fish Biol.* 51(6), 1085-1108.
- Keenleyside, M.H., 1991. *Cichlid fishes: behaviour, ecology and evolution*. Springer Science & Business Media.
- Kruuk, H., Parish, T., 1981. Feeding Specialization of the European Badger *Meles meles* in Scotland. *J. Anim. Ecol.* 50(3), 773–788.
- Kwik, J.T.B., Kho, Z.Y., Quek, B.S., Tan, H.H., Yeo, D.C.J., 2013. Urban stormwater ponds in Singapore: potential pathways for spread of alien freshwater fishes. *BioInvasion Records* 2(3), 239-345.
- Lamboj, A., 2004. *The cichlid fishes of western Africa*. Birgit Schmettkamp Verlag.
- Langston, J.N., Schofield, P.J., Hill, J.E., Loftus, W.F., 2010. Salinity tolerance of the African jewelfish *Hemichromis letourneuxi*, a non-native cichlid in south Florida (USA). *Copeia* 2010(3), 475-480.
- Levins, R., 1968. *Evolution in changing environments: Some theoretical explorations*. Princeton University Press, Princeton, NJ.

- Liew, J.H., Carrasco, L., Tan, H.H., Yeo, D.C.J., 2016a. Native richness and species level trophic traits predict establishment of alien freshwater fishes. *Biol. Invasions* 18(12), 3495-3512.
- Liew, J.H., Jardine, T., Lim, R., Kwik, J.T.B., Tan, H.H., Kho, Z., Yeo, D.C.J., 2018. Bottom-up influences on tropical freshwater foodweb structure support the “environmental filtering” hypothesis. *Limnol. Oceanogr.* 63(5), 1877-1890.
- Liew, J.H., Tan, H.H., Yeo, D.C.J., 2012. Some cichlid fishes recorded in Singapore. *Nature in Singapore* 5 229-236.
- Liew, J.H., Tan, H.H., Yeo, D.C.J., 2016b. Dammed rivers: impoundments facilitate fish invasions. *Freshw. Biol.* 61(9), 1421-1429.
- Lintermans, M., 2004. Human-assisted dispersal of alien freshwater fish in Australia. *NZ J. Mar. Freshw. Res.* 38(3), 481-501.
- Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., Lutcavage, M.E., 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J. Anim. Ecol.* 77(4), 838-846.
- Loke, L.H., Clews, E., Low, E.-w., Belle, C.C., Todd, P.A., Eikaas, H.S., Ng, P.K., 2010. Methods for sampling benthic macroinvertebrates in tropical lentic systems. *Aquat. Biol.* 10(2), 119-130.
- López-Fernández, H., Winemiller, K.O., Montaña, C., Honeycutt, R.L., 2012. Diet-morphology correlations in the radiation of South American geophagine cichlids (Perciformes: Cichlidae: Cichlinae). *PLoS ONE* 7(4), e33997.
- Lowe-McConnell, R.H., 1969. The cichlid fishes of Guyana, South America, with notes on their ecology and breeding behaviour. *Zool. J. Linn. Soc.* 48(2), 255-302.
- Magalhães, A.L.B., Vitule, J.R.S., 2013. Aquarium industry threatens biodiversity. *Science* 341(6145), 457-457.
- McCune, B., Mefford, M.J., 1999. *PC-ORD Multivariate Analysis of Ecological Data*, Version 4 ed: Glenden Beach, Oregon, USA, p. MjM Software Design.
- McCutchan Jr, J.H., Lewis Jr, W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102(2), 378-390.
- McDowall, R., 2004. Shoot first, and then ask questions: a look at aquarium fish imports and invasiveness in New Zealand. *NZ J. Mar. Freshw. Res.* 38(3), 503-510.
- Morgan, D.L., Gill, H.S., Maddern, M.G., Beatty, S.J., 2004. Distribution and impacts of introduced freshwater fishes in Western Australia. *NZ J. Mar. Freshw. Res.* 38(3), 511-523.
- Moyle, P.B., Light, T., 1996. Fish invasions in California: do abiotic factors determine success? *Ecology* 77(6), 1666-1670.
- Ng, H.H., Tan, H.H., 2010a. An annotated checklist of the non-native freshwater fish species in the reservoirs of Singapore. *COSMOS* 6(1), 96-116.

- Ng, P.K.L., Corlett, R.C., Tan, H.T.W., 2011. Singapore biodiversity: an encyclopedia of the natural environment and sustainable development. Editions Didier Millet.
- Ng, P.X., Tan, H.H., 2013. Fish diversity before and after construction of the Punggol and Serangoon reservoirs, Singapore. *Nature in Singapore* 6 19-24.
- Ng, T.H., Tan, H.H., 2010b. The introduction, origin and life-history attributes of the non-native cichlid *Etroplus suratensis* in the coastal waters of Singapore. *J. Fish Biol.* 76(9), 2238-2260.
- Nico, L.G., Beamish, W.H., Musikasinthorn, P., 2007. Discovery of the invasive Mayan Cichlid fish "*Cichlasoma*" *urophthalmus* (Günther 1862) in Thailand, with comments on other introductions and potential impacts. *Aquat. Invasions* 2(3), 197-214.
- Novakowski, G.C., Hahn, N.S., Fugi, R., 2008. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotrop. Ichthyol.* 6 567-576.
- Oliveira, R.F., Almada, V.C., 1998. Maternal aggression during the mouthbrooding cycle in the cichlid fish, *Oreochromis mossambicus*. *Aggressive Behavior: Official Journal of the International Society for Research on Aggression* 24(3), 187-196.
- Ordoñez, J.F.F., Asis, A.M.J.M., Catacutan, B.J., Santos, M.D., 2015. First report on the occurrence of invasive black-chin tilapia *Sarotherodon melanotheron* (Ruppell, 1852) in Manila Bay and of Mayan cichlid *Cichlasoma urophthalmus* (Gunther, 1892) in the Philippines. *BioInvasions Record* 4(2).
- Parnell, A., Jackson, A., 2013. siar: Stable Isotope Analysis in R. R package version 4.2, Available from: Available from: <http://CRAN.R-project.org/package=siar>. (23 March 2014).
- Pires, T.H., Campos, D.F., Röpke, C.P., Sodr e, J., Amadio, S., Zuanon, J., 2015. Ecology and life-history of *Mesonauta festivus*: biological traits of a broad ranged and abundant Neotropical cichlid. *Environ. Biol. Fishes* 98(3), 789-799.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83(3), 703-718.
- Poulin, B., Lefebvre, G., McNeil, R., 1993. Variations in bird abundance in tropical arid and semi-arid habitats. *Ibis* 135(4), 432-441.
- Pusey, B.J., Arthington, A.H., 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Mar. Freshw. Res.* 54(1), 1-16.
- R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria.
- Resende, E.d., Marques, D., Ferreira, L., 2008. A successful case of biological invasion: the fish *Cichla piquiti*, an Amazonian species introduced into the Pantanal, Brazil. *Braz. J. Biol.* 68(4), 799-805.
- Ribeiro, F., Orjuela, R., Magalhães, M., Collares-Pereira, M., 2007. Variability in feeding ecology of a South American cichlid: a reason for successful invasion in mediterranean-type rivers? *Ecol. Freshwat. Fish* 16(4), 559-569.

- Sá-Oliveira, J.C., Angelini, R., Isaac-Nahum, V.J., 2014. Diet and niche breadth and overlap in fish communities within the area affected by an Amazonian reservoir (Amapá, Brazil). *An Acad Bras Cienc* 86(1), 383–405.
- Saint-Paul, U., Zuanon, J., Correa, M.A.V., García, M., Fabr e, N.N., Berger, U., Junk, W.J., 2000. Fish communities in central Amazonian white-and blackwater floodplains. *Environ. Biol. Fishes* 57(3), 235-250.
- Savini, D., Occhipinti–Ambrogi, A., Marchini, A., Tricarico, E., Gherardi, F., Olenin, S., Gollasch, S., 2010. The top 27 animal alien species introduced into Europe for aquaculture and related activities. *J. Appl. Ichthyol.* 26 1-7.
- Sefc, K.M., 2011. Mating and Parental Care in Lake Tanganyika's Cichlids. *International Journal of Evolutionary Biology* 2011 20.
- Sparks, J.S., Smith, W.L., 2004. Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). *Cladistics* 20(6), 501-517.
- Stauffer Jr, J., Black, K., Geerts, M., Konings, A., McKaye, K., 2006. 14 Cichlid Fish Diversity, In: Hodkinson, T., Parnell, J. (Eds.), *Reconstructing the Tree of Life: Taxonomy and Systematics of Species Rich Taxa*. CRC Press, pp. 213-227.
- Strecker, A.L., Campbell, P.M., Olden, J.D., 2011. The aquarium trade as an invasion pathway in the Pacific Northwest. *Fisheries* 36(2), 74-85.
- Ter Braak, C.J., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67(5), 1167-1179.
- Ter Braak, C.J., Prentice, I.C., 1988. A theory of gradient analysis, *Adv. Ecol. Res.* Elsevier, pp. 271-317.
- Uchida, K., Kaneko, T., Miyazaki, H., Hasegawa, S., Hirano, T., 2000. Excellent salinity tolerance of Mozambique tilapia (*Oreochromis mossambicus*): elevated chloride cell activity in the branchial and opercular epithelia of the fish adapted to concentrated seawater. *Zool. Sci.* 17(2), 149-160.
- Whitfield, A.K., Blaber, S.J., 1979. The distribution of the freshwater cichlid *Sarotherodon mossambicus* in estuarine systems. *Environ. Biol. Fishes* 4(1), 77-81.
- Winemiller, K.O., Pianka, E.R., 1990. Organization in Natural Assemblages of Desert Lizards and Tropical Fishes. *Ecol. Monogr.* 60(1), 27–55.
- Winemiller, K.O., Taphorn, D.C., Barbarino-Duque, A., 1997. Ecology of Cichla (Cichlidae) in two blackwater rivers of southern Venezuela. *Copeia* 690-696.
- Wisenden, B.D., Lanfranconi-Izawa, T.L., Keenleyside, M.H., 1995. Fin digging and leaf lifting by the convict cichlid, *Cichlasoma nigrofasciatum*: examples of parental food provisioning. *Anim. Behav.* 49(3), 623-631.
- Yeo, D.C.J., Chia, C.S.W., 2010. Introduced Species in Singapore: An Overview. *Cosmos* 06(01), 23-37.

Yeo, D.C.J., Lim, K.K.P., 2011. Freshwater Ecosystems. In: Ng, P.K.L., Corlett, R.C., Tan, H.T.W. (eds.), Singapore Biodiversity: An Encyclopedia of the Natural Environment and Sustainable Development. Editions Didier Millet. Pp 52–63.

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