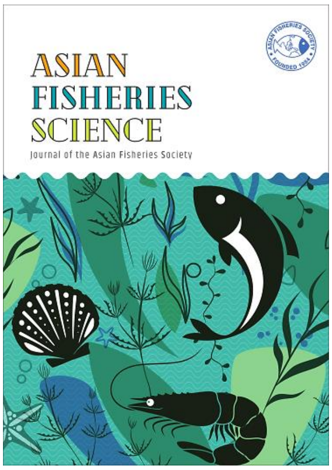

Diet of Exotic Pirapitinga *Piaractus brachypomus* (Cuvier, 1818) From Vembanad-Kole Wetland, India, as Inferred From Gut Content Analysis and DNA Barcoding

VINOD SREEDEVI ANUPAMA, SMRITHY RAJ, SUVARNA S. DEVI, APPUKUTTANNAIR BIJU KUMAR*
Department of Aquatic Biology and Fisheries, Faculty of Science, University of Kerala, Thiruvananthapuram 695581, India

*E-mail: bijukumar@keralauniversity.ac.in | Received: 06/09/2020; Accepted: 15/03/2021

ISSN: 0116-6514
E-ISSN: 2073-3720
https://doi.org/10.33997/j.afs.2021.34.1.005

Abstract

Gut contents of the exotic characid fish *Piaractus brachypomus* (Cuvier, 1818) that escaped into the Vembanad-Kole Wetland, India, during the floods were examined for their gut food spectrum. The qualitative analysis of gut contents showed that the fish is an omnivore with detritus (27 %) as the most dominant food item followed by, plant matter (25 %), crabs (16 %), molluscs (12 %), fish (11 %) and insects (7 %), respectively. DNA barcoding of the gut contents revealed taxa such as *Puntius mahecola* (Valenciennes, 1844) (Cyprinid fish), *Bellamaya* sp. (Mollusca, Gastropoda, Viviparidae), *Spiralothelphusa* sp. (Crustacea, Brachyura, Gecarcinucidae) and *Ictinogomphus* sp. (Insecta, Odonata, Gomphidae) among diet contents. Ontogenic diet shift was not recorded, and none of the fishes showed empty guts, indicating the higher feeding rate and abundance of food in the habitat. The most predominant food item of *P. brachypomus* in the Vembanad-Kol wetland system is crabs in terms of percentage occurrence, percentage number, percentage volume, index of preponderance, and index of relative importance. *Piaractus brachypomus* showed greater variations in diet spectrum from their frugivorous nature in the home range (Amazon basin) to a more generalist heterogeneous feeding nature in the introduced ecosystem. The study found that in a highly biodiverse ecosystem, the introduced alien fish may compete with native fish and feed on native organisms. The paper suggests a precautionary approach in flood plain aquaculture, especially with the increase in extreme climatic events and holistic studies on invasion biology to manage invasive species.

Keywords: red-bellied pacu, food spectrum, relative gut length, gastro-somatic index, invasive species

Introduction

Species invasion is a global phenomenon exacerbated by human interventions (Ricciardi, 2007) and is pronounced in freshwater ecosystems (Flitcroft et al., 2019). The invasion by alien species may lead to biotic homogenisation, extinction of endemic species (Olden et al., 2004; Clavero and Garcia-Berthou, 2005), food web disruption (Angeler et al., 2003; Simberloff et al., 2013), economic loss (Pimentel et al., 2000), biodiversity loss (Wilcove et al., 1998), competition with native fish species (Meffe et al., 1983; Simon and Townsend, 2003), predation (Zaret and Paine, 1973; Meffe, 1985; Crowl and Boxrucker, 1990) and habitat alteration (Mitchell, 1986). Introduced species forms 5 % and 27 % of cultivated fish globally (Gozlan, 2017), and many of the species have established in the wild, including in India (Sandilyan et al., 2018).

Depletion of the local fishery due to species invasion has also been reported from many parts of India, including Kerala (Krishnakumar et al., 2011; Singh, 2014; Sandilyan et al., 2018). The streams and rivers draining the southern region of the Western Ghats (WG) mountain ranges are globally recognised for their exceptional diversity of freshwater-dependent fauna (Kottelat and Whitten, 1996; Molur et al., 2011), with many species showing 'point endemism' (Dahanukar et al., 2011). The massive flood event in August 2018 in the state of Kerala, India, due to extreme climatic events, resulted in 498 human deaths, displacement of millions, altering the morphology and flow patterns of major rivers (Anonymous, 2019). The flood also resulted in the release of many exotic fish species kept in aquaculture farms and ornamental fish ponds along the river flood plains, including predators such as arapaima, *Arapaima gigas* (Schinz, 1822) and alligator gar, *Atractosteus spatula* (Lacepède, 1803) into various water bodies of Kerala (Kumar et al., 2019). Pirapitinga or red-bellied pacu, *Piaractus brachypomus* (Cuvier, 1818), native to the Amazon River basin (Escobar et al., 2019), has been unofficially introduced into India for aquaculture and has been reported from various natural water bodies (Chatterjee and Mazumdar, 2009; Singh et al. 2010a; Singh and Lakra, 2011; Roshni et al., 2014; Laxmappa, 2016; Dharan and Sherly, 2017; Singh, 2018). *Piaractus brachypomus* is a preferred fish for aquaculture since it can be cultivated in high density, readily shifting dietary habits (Singh, 2018) and superior meat quality (Fresneda et al., 2004; Ghosh and Datta, 2014). Food and feeding habits of fishes define the prey-predator relationship in an ecosystem and also affects the population dynamics and community structure in varied habitats and provides information about the food web, food resources and its competitors (Cardone et al., 2006; Hargrave et al., 2006; Vander et al., 2006). Quantitative dietary analyses are important to assess the direct and indirect ecological impacts of non-native species because it helps in elucidating the functional ecology of the introduced species (Ricciardi et al., 2013). Liew et al. (2016) studied the native richness and species level trophic traits and concluded that alien fish generally feed lower down the food web.

The diet content analysis of exotic fishes provides information on its food spectrum, niche overlap and facilitates developing strategies and management measures (Zanden et al., 2003). *Piaractus brachypomus* is reported to feed on fishes, eggs and fry and has diet plasticity (Correa et al., 2014). They are also found to exploit various floodplain resources, where they feed on fruits and seeds, which form the dominant items in juveniles and adults (Knab-Vispo et al., 2003; Lucas, 2008).

The entry of large numbers of *P. brachypomus* into the natural water bodies during the flood leads to the hypothesis that the fish may exhibit diet plasticity due to the non-availability of their natural food. In order to prove this hypothesis, the specimens of *P. brachypomus* were collected from Vembanad Lake to study their gut content.

Materials and Methods

Sampling area

Piaractus brachypomus were collected from various regions along Vembanad-Kole Wetland, Kerala (Latitude 9.26-10.6°N; Longitude 76.01-76.58°E), a Ramsar site and is the largest brackishwater system in southwest India, covering an area of 151250 ha (WISA, 2013) (Fig. 1). The wetland is drained by seven small rivers, Chalakkudy, Periyar, Muvattupuzha, Meenachil, Manimala, Pamba and Achankovil, originating from the Western Ghats. For this study, collections were made from Kumarakom (Lat. 9.597645°N; Long. 76.42478°E), Thottapalli (Lat. 9.323137°N; Long. 76.388657°E), Thannermukkam (Lat. 9.675054°N; Long. 76.397619°E), and Kolathumkadavu (Lat. 9.754658°N; Long. 76.388267°E) during 2018–2019 period.

The gut contents of 123 specimens of *P. brachypomus*, ranging in size from 16.0 cm to 30.0 cm, were examined for the study. Fishes were collected employing fishers cast net and gill net. Standard length (SL) and total length (TL) were measured for 0.1 cm length with digital caliper (1112-150, Insize, Taiwan) and weighed to 0.01 g using analytical balance (AUW120D, Shimadzu, Japan). Fish were injected and preserved with 10 % buffered formalin. The gut contents of selected partially digested and unknown food items available were preserved in 100 % ethanol for DNA barcoding. At the lab, the fishes were dissected, the length and weight of the gut of each fish were recorded, and the gut contents were preserved in 5 % formalin and later examined under stereo microscope (EZ4, Leica, Germany) and compound microscope (BX43, Olympus, Japan).

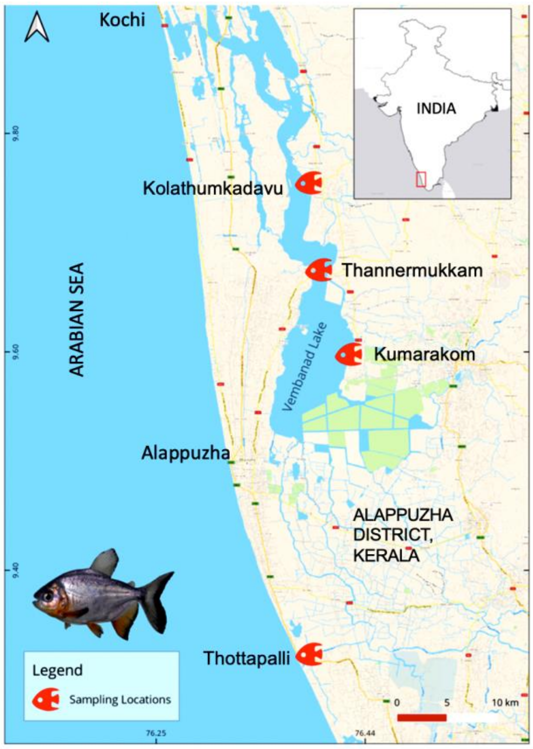

Fig. 1. Map of Vembanad-Kole Wetland, southwest coast of India, showing sampling locations of *Piaractus brachypomus* to study its gut contents.

Methods for gut content analysis

Points method

In this method, based on the fullness of the stomach, the points were provided based on eye estimation following Kow (1950) and Windel and Bowen (1974). The sum of the points obtained for each food item was then converted to a percentage to show the percentage composition of the food items in the stomach of fish.

Frequency of occurrence method

Each stomach was analysed to identify the presence of food items. Each food item was identified and sorted, and the number of stomachs with each food item was recorded and expressed as a percentage of all stomachs containing food (Hyslop, 1980):

Frequency of occurrence $\%Oi = Ni \div N \times 100$

where Ni is the number of stomachs containing specific food item and N is the number of stomachs examined.

Index of relative importance (IRI)

The percentage of frequency of occurrence of each food item (%O) is multiplied by the sum of the percentage by volume (%V) and percentage by number (%N) to assess the relationship of the various food items in the stomach (Pinkas et al., 1971):

$$IRI = \%Oi(Ni + Vi)$$

where Ni, Vi and Oi represents the percentage of number, volume and frequency of occurrence of the prey "i", respectively.

Relative gut length (RGL)

The relative gut length was determined using the method described by Al-Hussaini (1949):

$$RGL = GL/TL$$

where, GL is the gut length and TL is the total length.

Gastro-somatic index (GaSI)

It is the percentage of gut weight to the total body weight of the fish (Khan et al., 1998):

GaSI = Weight of gut ÷ Weight of fish × 100 g

DNA barcoding

A total of four unknown food samples collected from twenty-five fish were used for molecular studies; they were preserved in ethanol and sequenced to confirm the species identity of food organisms. DNA extraction was done using Qiagen's DNeasy Tissue kit (USA), and CO1 gene was amplified using the Universal Invertebrate Primer set LCO1490 (5′-GTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al., 1994). PCR amplification was done following the standard procedures, and Sanger sequencing was done at Rajiv Gandhi Centre for Biotechnology (RGCB), Trivandrum, India and the sequences were visualised in Bioedit (Hall, 1999). DNA sequences obtained from the gut contents were blasted to find closely allied sequences from the NCBI, thus identifying the species to the closest taxa (https://blast.ncbi.nlm.nih.gov/Blast.cgi).

Results

Qualitative analyses of food contents of *P. brachypomus* showed that it is an omnivore, feeding on phytoplankton, aquatic plants, fish, brachyuran crabs, insects, molluscs, detritus and miscellaneous items, which includes sand, mud and microplastics (Fig. 2).

Four unknown food samples obtained from the gut of various *P. brachypomus* were subjected to DNA

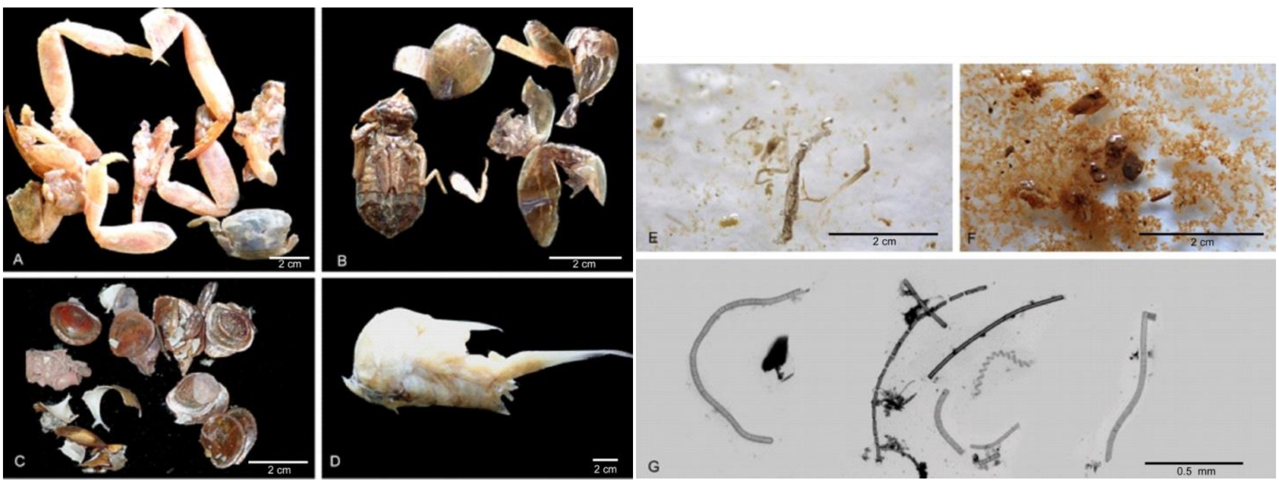

Fig. 2. Selected food contents isolated from the gut of *Piaractus brachypomus*, A. Crabs; B. Insects; C. Molluscs; D. Fish; E. Plant remains; F. Detritus; G. Phytoplankton.

barcoding, revealed taxa such as *Puntius mahecola* (Valenciennes, 1844) (Cyprinid fish), *Bellamaya* sp. (Mollusca, Gastropoda, Viviparidae), *Spiralothelphusa* sp. (Crustacea, Brachyura, Gecarcinucidae) and *Ictinogomphus* sp. (Insecta, Odonata, Gomphidae) (Table 1).

The percentage composition of the diet of *P. brachypomus* revealed the major dominant items as detritus (27 %) and plant matter (25 %); the other items include crabs (16%), followed by molluscs (12 %), fish (11 %) and insects (7 %) (Fig. 3). Miscellaneous items constituted 2 % of the gut contents, represented by plastic fibres, fragments, mud and sand particles. The study indicates the broad food spectrum of *P. brachypomus*, with more than half of the contents represented by detritus and plant matter.

The fish were categorised into three different size ranges (16.0–20.0, 21.0–25.0 and 26.0–30.0 cm) based on their length. In all the length groups, detritus and plant matter constitute the major percentage of food items (Fig. 4). The smaller length groups (young fish) preferred molluscs and insects, while medium and higher length groups fed on crabs, molluscs and fishes compared to the other animal matter. This indicates no ontogenic diet shifts in *P. brachypomus*, and the fish consumes whatever food is available.

The relative gut length of *P. brachypomus* in smaller (15.0–20.0 cm), medium (21.0–25 cm) and largest (26–30 cm) length groups are 17.1 cm, 24.9 cm and 31.04 cm, respectively, revealing a gradual increase in various size groups.

The frequency of occurrence of food items in the gut

Table 1. Percentage similarity of nucleotide sequences in unknown samples from the gut of *Piaractus brachypomus* with sequences from NCBI.

Group	Organism	Percentage similarity from NCBI sequences (In brackets)
Crabs	*Spiralothelphusa* sp.	96.77 % similarity with *Spiralothelphusa fernandoi* Ng, 1994 (GQ289667.1)
Insecta	Order: Odonata, Family: Gomphidae – *Ictinogomphus* sp.	93.06 % similarity with *Ictinogomphus* sp. (MF358742.1)
Fish	Unidentified fish body parts *Puntius mahecola* (Valenciennes, 1844)	99.80 % similarity with *Puntius mahecola* (Valenciennes, 1844)(MT835272.1)
Mollusca	Gastropods – *Bellamaya* sp.	95.35 % similarity with *Bellamya dissimilis* (Mueller, 1774)(KU179510.1)

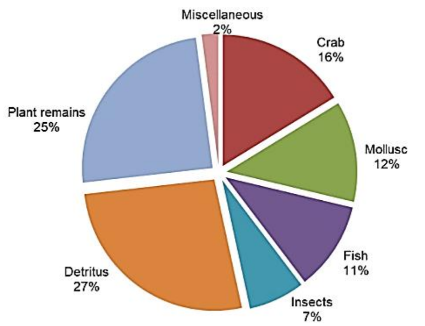

Fig. 3. Percentage composition of the diet of *Piaractus brachypomus*

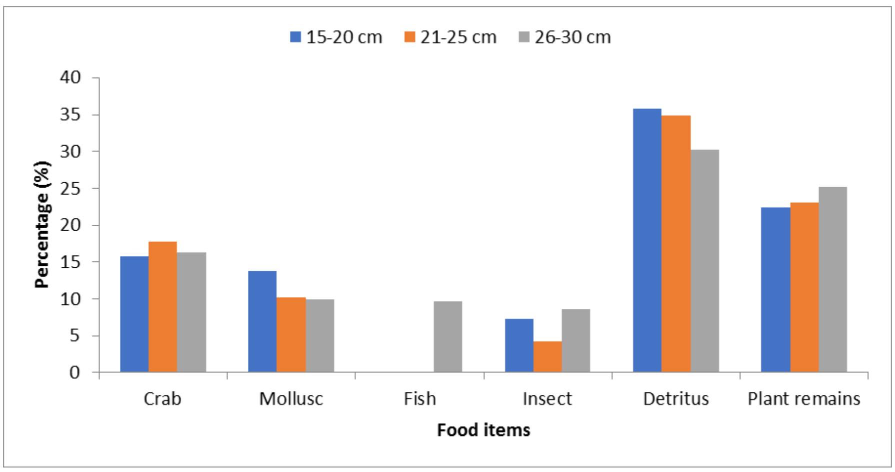

Fig. 4. Size-based (in cm) food preferences of *Piaractus brachypomus* indicating no particular ontogenic diet shifts.

of *P. brachypomus* shows a distinct predominance of detritus and plant matter with 27 % and 24 %, very closely followed by crabs (21 %) and molluscs (12 %) over other animal matter in the food spectrum (Fig. 5). Insects formed 7 %, fish 6 % and miscellaneous items including sand, mud, plastic fibres, fragments and films constituted 3 %.

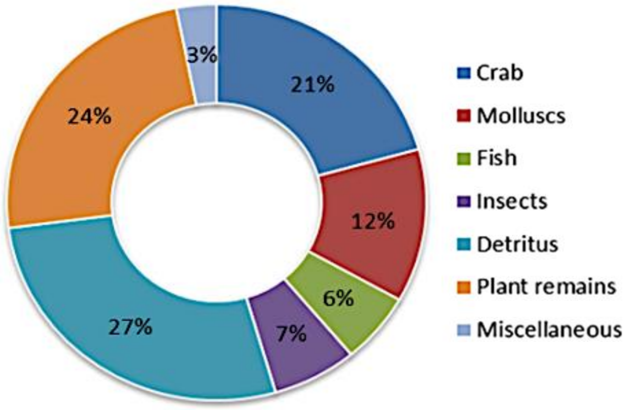

Fig. 5. Frequency of occurrence of food items in the gut contents of *Piaractus brachypomus* denoting detritus and plant remains as the major component.

The feeding intensity of *P. brachypomus* revealed that 33.3 % of the fishes had gorged stomach, 22.91 % with good, 17.7 % with poor and 15.62 % with full stomachs. None of the fish showed empty guts, indicating the higher feeding rate and abundance of food in the habitat. The feeding intensity recorded for *P. brachypomus* of different size groups recorded maximum intensity for the larger size group and minimum for the smallest size group, and a large number of poor stomachs was also noticed in the larger size group fishes with least in the smaller size group (Fig. 6). The gastro somatic index (GaSI) of *P. brachypomus* shows a slight decrease in value with an increase in the size of the fish (Fig. 7). The most predominant food item of *P. brachypomus* in Vembanad-Kole wetland is crabs in terms of percentage occurrence (% O), percentage number (% N), percentage volume (% V), index of preponderance (IP), and index of relative importance (IRI) (Table 2).

Discussion

The pirapatinga *P. brachypomus* is considered a 'flood plain specialist' and a fast-growing frugivorous fish with a strong preference for plant food (Anderson et al. 2009). The analysis of the food spectrum of *P. brachypomus* from Vembanad Lake by quantitative, qualitative and DNA based approaches revealed a broad food spectrum, indicating it as a generalist/opportunistic feeder, consuming a variety of food from the ecosystem, with a strong preference towards detritus and plant matter. Percentage composition of the gut contents of the fish showed detritus and plant remains in almost equal quantities, followed by crabs (*Spiralothelphusa* sp.), molluscs (*Bellamya* sp.), fish (*Puntius mahecola* (Valenciennes, 1844)) and insects. However, in terms of frequency of occurrence, the most common item in the food was plant matter, including phytoplankton and detritus, closely followed by crabs and molluscs. Index of relative importance (IRI) revealed the crab *Spiralothelphusa* sp. as the most abundant food item followed by molluscs, insects and fish remains. The genus *Piaractus* has the ability to crush hard shells of seeds in their natural habitats, with their strong dentition and jaws (Correa et al., 2014) with cusped teeth resembling human molars. The present study reported several molluscs and crabs in the gut contents of this exotic fish, and their natural adaption to feed on hard-shelled food items may prove advantageous in feeding on molluscs and crustaceans in the introduced ecosystem.

Being an omnivore, *P. brachypomus* shows several predatory impacts on the native species of fishes upon which they feed. Similar cases of impacts of

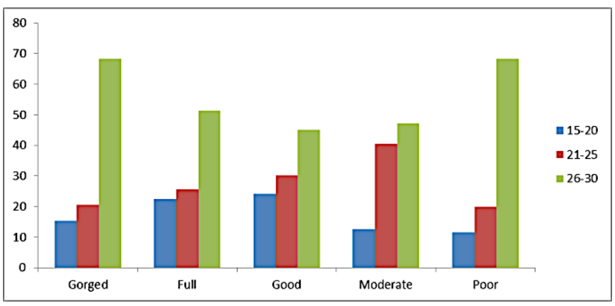

Fig. 6. Feeding intensity of *Piaractus brachypomus* represented by the condition of the stomach in different size (15-30 cm) groups.

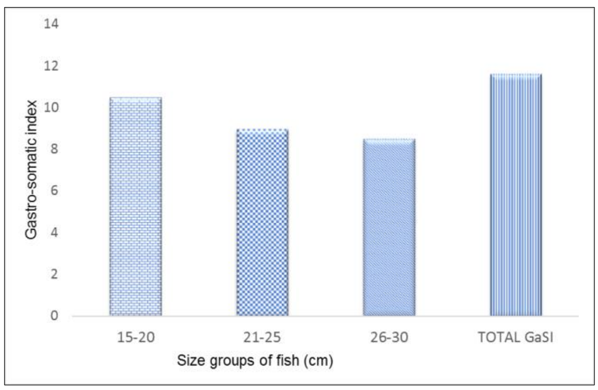

Fig. 7. Gastro somatic index (GaSI) of *Piaractus brachypomus* for different size (in cm) groups.

Table 2. Percentage occurrence (%O), percentage number (%N), percentage volume (%V), and index of relative importance (IRI) of various food items in the diet of *Piaractus brachypomus*.

Food items	%O	%N	%V	IRI (Pinkas et al., 1971 method)
Crabs	45	45.94	40.35	1861.69
Molluscs	36.37	27.02	23.35	1006.0
Fishes	12.10	16.21	21.1	217.2
Insects	6.05	0.65	15.13	19.06

invasive flathead catfish *Pylodictus olivaris* (Rafinesque, 1818) on native species from Chesapeake Bay tributaries were reported by Schmitt et al. (2017). Correa et al. (2014) gave an explanation for the presence of fish remains as carrion behaviour of the fish. But the present study recorded tissues and body parts of several fishes in the gut, indicating that they may also feed on fishes, besides other animal food items available in the wetlands, including molluscs, crabs and insects, which is pointed towards the high diet plasticity of the exotic fish in the introduced ecosystem.

Size-based food preference of *P. brachypomus* did not show much variation except for the item of fish consumed in less quantity by the small-sized group; hence no ontogenic diet shifts were observed.

Accordingly, the gut length among different size groups showed a proportional rise with an increase in the length of the fish. The feeding intensity of the fish for the collection period showed no empty guts, denoting the abundance of food resources in the Vembanad wetland system. The gut content of the analysis of *P. brachypomus* from the Amazon waters using the stable isotope method showed that they did not change their diet between the floods (Santos, 2009). In contrast, Dabrowski and Portella (2005) stated that the fish exhibited plasticity in feeding habit. *Piaractus brachypomus* from Vembanad-Kole wetland seems to feed on plant matter, crabs, molluscs, insects, detritus, and miscellaneous items in the present study. The gut contents of juvenile *P. brachypomus* from Sepik River, Papua New Guinea, constitute plant matter and fish remains (Correa et al., 2014). The present study also recorded several very small stem and leaf parts of plants and medium-sized fishes among the diet contents, though juveniles were not collected. According to Goulding (1980) and Knab-Vispo et al. (2003), native populations of *P. brachypomus* feed very little on aquatic plants. Feeding patterns of *P. brachypomus* and *Colossoma macropomum* (Cuvier, 1816) which are considered as frugivorous habits was studied for three years in the Peruvian Amazon and could not find any evidence for selective feeding, and the fishes consumed only 35% of the fruits and seeds available at the site (Anderson et al., 2009). The studies by Gehrke et al. (2011) claimed that *P. brachypomus* consuming plant matter might have led to the decline of native floodplain fish populations, as a reduction in aquatic plants may, in turn, affect the habitat of aquatic invertebrates which form the native food for the native floodplain fishes. The adults and juveniles of *P. brachypomus* prefer terrestrial plants as food because of their adaptability to live in varied environmental conditions (Knab-Vispo et al., 2003; Lucas, 2008). The juvenile and sub-adults of *P. brachypomus* from the Sepik- Ramu River Basin, Papua New Guinea showed dietary shifts to a more generalised diet when compared to individuals in the native population (Correa et al., 2014) as they could not identify any fruits or seeds from the river. Dietary shifts due to changes in food availability were also noticed for the fish by de Mérona et al. (2001) in Tucuruí Reservoir. The present study did not record any fruits or seeds from the gut contents of *P. brachypomus* from the Vembanad-Kole wetland system, as the brackishwater ecosystem are ecologically different from the natural ranges (floodplains of rivers).

The studies on food and feeding habits of invasive species such as *Cyprinus carpio* Linnaeus, 1758 (Singh et al. (2010b) and *Oreochromis niloticus* (Linnaeus, 1758) (Alam et al., 2015) established in the river Ganga of India have shown that both the fishes are omnivorous. Though there are no reports on the invasive nature of *P. brachypomus* in the water bodies of India, the broader food spectrum of the species, including Arthropoda, Mollusca and Pisces, is a matter of concern and therefore demands a greater precautionary approach in their aquaculture, which takes into account management measures to prevent their entry into natural water bodies.

In general, the observation in this study is in corroboration with the findings of Correa et al. (2014), which established "an inherently plastic diet that can be adjusted when displaced to a novel geographic area". The hypothesis in the present study is also proved correct, as *P. brachypomus* introduced into the Vembanad-Kole wetland shows greater variations in diet spectrum from their frugivorous nature in the home range to a more generalist heterogeneous feeding nature in the introduced ecosystem. Thus, it can be concluded that the exotic *P. brachypomus* make use of locally available resources like food and extreme plasticity with regard to food choices. The

Vembanad Lake is the largest brackishwater system on the southwest coast of India and with its highly diverse and commercially valuable resources like fishes, shrimps, crabs and clams, support commercial fishery and livelihood of hundreds of fishers (CICFRI, 2001; Krishnakumar and Rajan, 2012). The introduced *P. brachypomus* may compete with indigenous fauna for food and feed upon the species in the wetland. This also demands a more precautionary approach in aquaculture operations in the flood plains of rivers and management interventions that might prevent the escape of cultivated fish into natural water bodies (Kumar et al., 2019)..

Conclusion

This study on the gut contents of alien *Piaractus brachypomus* from Vembanad-Kole wetland of south-west India shows that the fish is omnivorous, with detritus (27 %), plant matter (25 %), crabs (16 %), molluscs (12 %), fish (11 %) and insects (7 %) forming the major food elements. The presence of molluscs and crabs in the gut contents and their natural adaption to feed on hard-shelled food items coupled with broader food spectrum including fish and insects may prove disadvantageous to indigenous biodiversity. This study unequivocally proved the plasticity in the feeding behaviour of exotic red-bellied pacu *P. brachypomus*. While the fish in their natural range are frugivorous and prefer food, including leaves, fruits and seeds, in the introduced ecosystem, they become heterogeneous in their food habits, feeding on whatever comes in their way as food material. This may pose threats to indigenous biodiversity and reduce food availability for the indigenous fauna available in the ecosystem. Extensive study is needed on the environmental impact of *P. brachypomus* in various natural aquatic ecosystems by a holistic approach based on invasion ecology under different climatic and water quality scenarios.

References

Alam, A., Chadha, N.K., Joshi, K.D., Chakraborty, S.K., Sawant, P.B., Kumar, T., Srivastava, K., Das, S.C.S., Sharma, A.P. 2015. Food and feeding ecology of the non-native Nile Tilapia *Oreochromis niloticus* (Linnaeus, 1758) in the River Yamuna, India. Proceedings of the National Academy of Sciences, India Section B: Biological Sciences 85:167–174. https://doi.org/10.1007/s40011-014-0338-3

Al-Hussaini, A.H. 1949. On the functional morphology of the alimentary tract of some fishes in relation to differences in their feeding habits: Anatomy and histology. Quarterly Journal of Microscopical Science 90: 109-139.

Anderson, J.T., Saldaña-Rojas, J., Flecker, A.S. 2009. High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. Oecologia 161:279–290. https://doi.org/10.1007/s00442-009-1371-4

Angeler, D.G., Chow-Fraser, P., Hanson, M.A., Sanchez-Carrillo, S., Zimmer, K.D. 2003. Biomanipulation: a useful tool for freshwater wetland mitigation? Freshwater Biology 48:2203–2213. https://doi.org/10.1046/j.1365-2427.2003.01156.x

Anonymous, 2019. Rebuild Kerala development programme. A resilient recovery policy framework and action plan for shaping Kerala's resilient, risk-informed development and recovery from 2018 Floods. Rebuild Kerala Initiative, Government of Kerala, India. https://impactkerala.com/sites/default/files/DRAFT_RKDP_12_March_2019.pdf (Accessed 27 July 2020).

Cardone, I.B., Lima, J.S.E., Goitein, R. 2006. Diet and capture of *Hypostomus strigaticeps* (Siluriformes, Loricariidae) in a small Brazilian stream: relationship with limnological aspects. Brazilian Journal of Biology 66:25–33. https://doi.org/10.1590/S1519-69842006000100005

Chattarjee, N.R., Mazumdar, B. 2009. Induced breeding of pacu (*Piaractus brachypomus*) in captivity with pituitary extract. Aquaculture Asia Magazine 14:23.

CICFRI (Central Inland Capture Fisheries Research Institute). 2001. Ecology and fisheries investigations in Vembanad Lake. Central Inland Capture Fisheries Research Institute, Barrackpore, India. 121 pp.

Clavero, M., García-Berthou, E. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution 20:110. https://doi.org/10.1016/j.tree.2005.01.003

Correa, S.B., Ricardo, B., Bernard, D.M., Jonathan, W. 2014. Diet shift of Red Belly Pacu *Piaractus brachypomus* (Cuvier, 1818) (Characiformes: Serrasalmidae), a Neotropical fish, in the Sepik-Ramu River Basin, Papua New Guinea. Neotropical Ichthyology 12:827–833. https://doi.org/10.1590/1982-0224-20130212

Crowl, T.A., Boxrucker, E. 1990. Effects of crayfish size, orientation, and movement on the reactive distance of largemouth bass foraging in clear and turbid water. Hydrobiologia 183:133–40. https://doi.org/10.1007/BF00018718

Dabrowski, K., Portella, M.C. 2005. Feeding plasticity and nutritional physiology in tropical fishes. Fish Physiology 21:155-224. https://doi.org/10.1016/S1546-5098(05)21005-1

Dahanukar, N., Raghavan, R., Ali, A., Abraham, A., Shaji, C.P. 2011. The status and distribution of freshwater fishes of the Western Ghats. In: The status and distribution of freshwater biodiversity in the Western Ghats, India, Molur, S., Smith, K.G., Daniel, B.A. and Darwall, W.R.T. (Compilers). IUCN, Cambridge, UK and Gland, Switzerland, Zoo Outreach Organisation, Coimbatore, India. 116 pp.

de Mérona, B., Santos G.M., Almeida, R.G. 2001. Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. Environmental Biology of Fishes 60:375–392. https://doi.org/10.1023/A:1011033025706

Dharan, R.S.E., Sherly, W. 2017. First record of the pirapitinga *Piaractus brachypomus*, Cuvier, 1818 (Actinopterygii: Serrasalmidae) in Pamba river Kerala, India. The Bioscan 2:121–124.

Escobar, M.D., Ota, R.P., Machado-Allison, A., Farias, I.P., Hrbek, T. 2019. A new species of *Piaractus* (Characiformes: Serrasalmidae) from the Orinoco Basin with a redescription of *Piaractus brachypomus*. Journal of Fish Biology 95: 411–427. https://doi.org/10.1111/jfb.13990

Flitcroft, R., Cooperman, M.S., Harrison, I.J., Juffe-Bignoli, D., Boon, P.J. 2019. Theory and practice to conserve freshwater biodiversity in the Anthropocene. Aquatic Conservation: Marine and Freshwater Ecosystem. 29:1013–1021 https://doi.org/10.1002/aqc.3187

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3:294–299.

Fresneda, A., Lenis, G., Agudelo, E., Olivera, A.M. 2004. Espermiacion inducida y crioconservacion de semen de cachama blanca (*Piaractus brachypomus*). Revista Colombiana de Ciencias Pecuarias 17:46-52.

Gehrke, P.C., Sheaves M.J., Boseto, D., Figa, B.S., Wani, J. 2011. Vulnerability of freshwater and estuarine fisheries in the tropical Pacific to climate change. In: Vulnerability of tropical Pacific fisheries and aquaculture to climate change. Bell, J.D., Johnson, J. E., Hobday, A.J. (Eds.). Secretariat of the Pacific Community, Noumea, New Caledonia, pp. 577–646.

Ghosh, S., Datta, M.K. 2014. Farming of red-bellied pacu (*Piaractus brachypomus*) in India with special reference to West Bengal. Fishing Chimes 34:32–39.

Goulding, M. 1980. The fishes and the forest: Explorations in Amazonian natural history. University of California Press, Berkeley. 280 pp.

Gozlan, R.E. 2017. Interference of non-native species with fisheries and aquaculture. impact of biological invasions on ecosystem services. In: Impact of biological invasions on ecosystem services, invading nature, Vilà, M., Hulme, P.E. (Eds.). Springer International Publishing, Switzerland, pp. 119–137. https://doi.org/10.1007/978-3-319-45121-3_8

Hall, T.A. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series 41:95–98.

Hargrave, C.W., Ramirez, R., Brooks, M., Eggleton, M.A., Sutherland, K., Deaton. R., Galbraith, H. 2006. Indirect food web interactions increase growth of an algivorous stream fish. Freshwater Biology 51:1901–1910. https://doi.org/10.1111/j.1365-2427.2006.01625.x

Hyslop, E.J. 1980. Stomach contents analysis-a review of methods and their application. Journal of Fish Biology 17:411–429. https://doi.org/10.1111/j.1095-8649.1980.tb02775.x

Khan, T.A., Wilson, M.E., Khan, M.I. 1998. Evidence for invasive carp mediated trophic cascade in shallow lakes of western Victoria, Australia. Hydrobiologia 506:465–472. https://doi.org/10.1023/B:HYDR.0000008558.48008.63

Knab-Vispo, C., Daza, F., Vispo, C., González, N. 2003. The diet of Morocoto (*Piaractus brachypomus*) in the lower Rio Caura in relation to its ecological role and its conservation. Scientia Guaianæ 12:367–391.

Kottelat, M., Whitten, T. 1996. Freshwater biodiversity in Asia: with special reference to fish. World Bank technical paper No. WTP 343. World Bank Group, Washington, D.C. 59 pp. https://doi.org/10.1596/0-8213-3808-0

Kow, T.A. 1950. The food and feeding relationship of the fishes of Singapore Straits. His Majesty's Stationery Office, London. 35 pp.

Krishnakumar, K., Ali, A., Pereira, B., Raghavan, R. 2011. Unregulated aquaculture and invasive alien species: a case study of the African Catfish *Clarias gariepinus* in Vembanad Lake (Ramsar Wetland), Kerala, India. Journal of Threatened Taxa 3:1737–1744. https://doi.org/10.11609/JoTT.o2378.1737-44

Krishnakumar, K., Rajan, P.D. 2012. Fish and fisheries in Vembanad Lake. Consolidated report of Vembanad fish count 2008–2011. Community environment resource centre and Ashoka trust for research in ecology and the environment, Alappuzha, Kerala, India. 126 pp.

Kumar, A.B., Raj, S., Arjun, C.P., Katwate, U., Raghavan, R. 2019. Jurassic invaders: flood-associated occurrence of arapaima and alligator gar in the rivers of Kerala. Current Science 116:1628–1630.

Laxmappa, B. 2016. Exotic fish species in aquaculture and aquatic ecosystem in Telangana State, India. Journal of Aquatic Biology & Fisheries 4:1–7.

Liew, J.H., Carrasco, L.R., Tan, H.H., Yeo, D.C.Y. 2016. Native richness and species level trophic traits predict establishment of alien freshwater fishes. Biological Invasions 18:3495–3512. https://doi.org/10.1007/s10530-016-1241-z

Lucas, C.M. 2008. Within flood season variation in fruit consumption and seed dispersal by two characin fishes of the Amazon. Biotropica 40:581–589. https://doi.org/10.1111/j.1744-7429.2008.00415.x

Meffe, G.K. 1985.Predation and species replacement in American southwestern fishes: a case study. Southwestern Naturalist 30:173–87. https://doi.org/10.2307/3670732

Meffe, G.K., Hendrickson, D.A., Minckley, W.L., Rinne, J.N. 1983. Factors resulting in decline of the endangered Sonoran top minnow (Atheriniformes: Poeciliidae) in the United States. Biological Conservation 25:135–159. https://doi.org/10.1016/0006-3207(83)90057-5

Mitchell, C.P. 1986. Effects of introducing grass carp on populations of two species of native fish in a small lake. New Zealand Journal of Marine and Freshwater Research 20:219–30. https://doi.org/10.1080/00288330.1986.9516146

Molur, S., Smith, K.G., Daniel, B.A., Darwall, W.R.T. 2011. The status and distribution of freshwater biodiversity in the Western Ghats, India. International Union for Conservation of Nature (IUCN), Gland, Switzerland and Zoo Outreach Organization (ZOO), Coimbatore, India, 116 pp.

Olden, J.D., Poff, N.L., Douglas, M.R., Douglas, M.E., Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19:18–24. https://doi.org/10.1016/j.tree.2003.09.010

Pimentel, D., Lach, L., Zuniga, R., Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65. https://doi.org/10.1641/0006-3568(2000)050[0053:EAECON]2.3.CO;2

Pinkas, L., Oliphant, M.S., Iverson, I.L.K. 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. Fish Bulletin 152. State of California, Department of Fish and Game, USA. 105 pp.

Ricciardi, A. 2007. Are modern biological invasions an unprecedented form of global change? Conservation Biology 21:329–336. https://doi.org/10.1111/j.1523-1739.2006.00615.x

Ricciardi, A., Hoopes, M.F., Marchetti, M.P., Lockwood, J.L. 2013. Progress toward understanding the ecological impacts of non-native species. Ecological Monographs 83:263–282. https://doi.org/10.1890/13-0183.1

Roshni, K., Renjithkumar, C.B., Kurup, B.M. 2014. Record of a newly introduced fish, red-bellied pacu *Piaractus brachypomus* (Cuvier, 1818) (Characiformes, Serrasalmidae), in a tropical wetland system, India. Journal of Applied Ichthyology 30:1037–1038. https://doi.org/10.1111/jai.12462

Sandilyan, S., Meenakumari, B., Biju Kumar, A., Mandal, R. 2018. A review on impacts of invasive alien species on Indian inland aquatic ecosystems. National Biodiversity Authority, Chennai. 103 pp.

Santos, F.A. 2009. Estrutura trofica de peixes do Lago Grande, Manacapuru, AM com base nos isotopos estaveis de C e N (Determination of fish trophic structure in the Great Lake Manacapuru, AM, Brazil using stable isotopes of C and N). M.Sc. Dissertation, Ciencias Pesqueiras nos Tropicos, UFAM, Manaus. 74 pp.

Schmitt, J.D., Emmel, J.A., Bunch, A.J., Hilling, C.D., Orth, D.J. 2017. Feeding ecology and distribution of an invasive apex predator: flathead catfish in sub-estuaries of the Chesapeake Bay, Virginia. North American Journal of Fisheries Management 39:390–402. https://doi.org/10.1002/nafm.10279

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., Pysek, P., Sousa, R., Tabacchi, E., Vila, M. 2013. Impacts of biological invasions: what's what and the way forward. Trends in Ecology and Evolution 28:58–66. https://doi.org/10.1016/j.tree.2012.07.013

Simon, K.S, Townsend, C.R. 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. Freshwater Biology 48:982–994. https://doi.org/10.1046/j.1365-2427.2003.01069.x

Singh A.K., Pathak A.K., Lakra W.S. 2010b. Invasion of an exotic fish—common carp, *Cyprinus carpio* L. (Actinopterygii: Cypriniformes: Cyprinidae) in the Ganga River, India and its impacts. Acta Ichthyologica Et Piscatoria 40:11–19. https://doi.org/10.3750/AIP2010.40.1.02

Singh, A.K. 2014. Emerging alien species in India aquaculture: prospects and threats. Journal of Aquatic Biology & Fisheries 2:32–41.

Singh, A.K. 2018. Environmental issues of exotic fish culture in Uttar Pradesh. Journal of Environmental Biology 22:205–208.

Singh, A.K., Dinesh, K., Abubakar, A. 2010a. Commercial farming of the redbelly pacu. Aquaculture Asia-Pacific 8(4):48-49.

Singh, A.K., Lakra, W.S. 2011. Risk and benefit assessment of alien fish species of the aquaculture and aquarium trade into India. Reviews in Aquaculture 3:3–18. https://doi.org/10.1111/j.1753-5131.2010.01039.x

Vander, Z.M.J., Olden, J.D., Gratton, C. 2006. Food-web approaches in restoration ecology. In: Foundations of restoration ecology, Falk, D.A., Palmer, M.A., Zedler, J.B. (Eds.). Island Press, Washington DC, pp. 165–189.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E. 1998. Quantifying threats to imperilled species in the United States. Bioscience 48:607–615. https://doi.org/10.2307/1313420

Windel, V., Bowen, K. 1974. Ornamental fish farming-successful small-scale aqua business in India. Aquaculture Asia 8:14–16.

WISA 2013. Vembanad – Kol wetlands – An integrated management planning framework for conservation and wise use. Wetlands International-South Asia, New Delhi, India. 138 pp.

Zanden, M.J.V., Chandra, S., Allen, B.C., Reuter, J.E., Goldman, C.R. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California–Nevada) basin. Ecosystems 6:274–288. https://doi.org/10.1007/s10021-002-0204-7

Zaret, T.M., Paine, R.T. 1973. Species introduction in a tropical lake. Science 182:449-455. https://doi.org/10.1126/science.182.4111.449