# Feeding and Trophic Interaction of Fishes in a Newly Impounded Irrigation Reservoir in the Central Plain of Thailand

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## ABSTRACT

This study examines diet composition, diet overlap, and trophic interactions of fishes in Khlong Luang Rachalothorn Reservoir, which was impounded and first operated in 2015. Fish were sampled from four zones, namely upstream, transition zone, reservoir, and downstream. Samples were collected monthly from September 2017 to August 2018 using multi-mesh gill nets and seines. Stomach contents were examined, and food items were classified and scored by trophic weighting point scores. There was a total of 1,031 fish specimens, belonging to 46 species, sampled in this study. The highest number of species (n = 36) was collected from the reservoir zone. Results depict the important food items and feeding guilds in each area. Macroalgae was the most important diet category, followed by oligochaetes and aquatic insects in all areas. Each area has a distinctive community of fish that feed differently. Common fish species found at all stations showed high trophic feeding plasticity, as evident by diverse food items that differed spatio-temporally within a species, and by the wide diet breadth of these fishes. Fish species with trophic index less than 1.50 and greater than 2.50 tended to choose a unique diet, whereas fishes with trophic index in the range of 1.51-2.49 showed a wide range of food preferences. Low diet overlap (0.00-0.39) was observed in all study areas. The results reveal the importance of various food resources along each section of the reservoir and ability in resource utilization of fish species in Khlong Luang Rachalothorn Reservoir.

Keywords: Diet breadth, Khlong Luang Rachalothorn, Stomach content, Trophic level

## INTRODUCTION

The creation of a dam across a river interrupts the natural continuum of biotic and abiotic features. It also transforms the river into at least three distinct sections: (i) the upper reach, where the river flows naturally, (ii) the reservoir, where flow is minimal, and (iii) the downstream reach, where the flow is regulated and may not follow seasonal patterns (Marmulla, 2001; Miranda *et al*., 2019; Seanghong *et al*., 2021). Impacts of river damming have been well reported, with most of the focus on the aquatic environment, fishes and fisheries as independent issues, or on the relationships among them (e.g., McCartney, 2009; Dugan *et al*., 2010). A link among these three issues reflects the availability of food resources. The environment determines the diversity and abundance of food resources, while growth, survival and abundance of fishes, which determine fishery production, depend on food (Marmulla, 2001; Dugan *et al*., 2010). The trophic structure of fishes is associated with the habitat diversity and food availability along the river continuum (Miranda *et al*., 2019; De Oliveira *et al*., 2020). Fish communities in the upper reach of a dammed river depend primarily on allochthonous resources for energy contributed by riparian flora and fauna in the aquatic-terrestrial transition zone,

which are highly related to hydrological regime. Meanwhile, communities in lower reaches rely more on autochthonous resources from the reservoir *per se*, which are regulated mostly by dam operation (Johnson *et al.*, 1995; Marmulla, 2001; Miranda *et al.*, 2019; De Oliveira *et al.*, 2020). Within the reservoir, there is an increasing importance of autochthonous resources in fish diets, which are highly related to season and fluctuation in water levels (De Mérona *et al.*, 2003; Amarasinghe *et al.*, 2014).

Classification of fish feeding guilds is commonly based on the major food items found in the stomach, and guilds can be roughly divided into herbivore, zooplanktivore, zoobenthivore, piscivore, omnivore and detritivore (Elliott *et al.*, 2007). Nevertheless, most freshwater fishes are suspected to have dietary flexibility (i.e., due to the abundance and accessibility of each resource), which is related to fish size, season, and location within the system, or a combination of these factors (Welcomme *et al.*, 2006; Saowakoon *et al.*, 2021). In the reservoir, fishes present in each zone (upstream/inlet, reservoir, and downstream/outlet) may modify their diet according to the characteristics of foods available; individuals may adopt different diets and feed on specific organisms depending on their energetic benefit relative to handling time costs (i.e., optimal foraging theory), and seek less resource competition for their survival (Agostinho *et al.*, 1995; Amarasinghe *et al.*, 2014; Cachera *et al.*, 2017). Feeding competition is, indeed, regarded as one of the factors that drive species to either occur in allopatry or sympatry (i.e., to avoid or minimize competition) (Kadye and Booth, 2020). The spatio-temporal differences in fish communities in each zone of a reservoir, therefore, not only reflect their behavioral adaptation to the reservoir and flow preferences, but also diet competition (Jutagate *et al.*, 2012; Amarasinghe *et al.*, 2014).

In complex fish communities such as those found in tropical Asian reservoirs, the diversity of food resources and composition of fish species result in both resource partitioning and overlap (Gammanpila *et al.*, 2019). Food resource competition may vary according to habitat characteristics, integrity of the environment, physical (e.g., temperature and turbidity) and chemical (e.g., dissolved oxygen levels and dissolved minerals) variables, and seasonality (De Mérona *et al.*, 2003; Novakowski *et al.*, 2008; Sá-Oliveira *et al.*, 2014). Hydrological seasonality of the waterbody also affects the abundance, availability and accessibility of food resources (Winemiller and Jepsen, 1998). Fish species with narrow breadth are relative specialists, whereas species with broad diet breadth are generalists (Sá-Oliveira *et al.*, 2014).

Impoundments potentially change the dynamics of river flow as well as nutrient transport and storage in the system (i.e., river continuum concept), which then alter environmental conditions along the longitudinal axis of the reservoir and eventually affect fish assemblages and their feeds (Marmulla, 2001; Miranda *et al.*, 2019). An understanding of the feeding behavior of fishes in each zone of a reservoir can be further used to determine the food web, predator-prey relationships, and carrying capacity in the system. Appropriate management of tropical fish stocks and aquatic ecosystems also requires greater knowledge of feeding and food web ecology, in particular for ecosystem-based management. This knowledge includes, for example, predator-prey interactions and availability of food resources (Winemiller and Jepsen, 1998; Braga *et al.*, 2012; Gammanpila *et al.*, 2019). In this study, it is hypothesized that diets differ spatially and temporally among the sampled fish species. The objectives are, therefore, to examine diet composition of sampled fish species, identify diet overlap that occurs among fish species within the same reservoir zone, and evaluate the diet breadth of sampled species by applying the concept of trophic guilds.

## MATERIALS AND METHODS

*Study area and fish sampling*

Khlong Luang Rachalothorn Reservoir (KLR; 13°22'N; 101°21'E) is a multipurpose reservoir located in Chonburi Province, eastern Thailand (Figure 1), which began impoundment in 2015. This region experiences four seasons, based on precipitation: dry season (D; January-April),

dry to wet transition (T1; May-June), wet season (W; July-October), and wet to dry transition (T2; November-December). The KLR was built by damming the Khlong Luang River, thereby creating three distinct zones: the upstream inlet, the reservoir, and the downstream outlet. The surface area of the KLR is approximately 25.6 km$^2$ at full capacity and contains at least 50 fish species, based on combined results of surveys conducted after impoundment (Inland Fisheries Research and Development Division, 2012; Bureau of Project Management, 2017). Environmental impact studies of the river before impoundment revealed that the most abundant species were riverine cyprinids, including *Cyclocheilichthys armatus*, *Labiobarbus siamensis*, and *Henicorhynchus siamensis* (Inland Fisheries Research and Development Division, 2012; Bureau of Project Management, 2017).

Fish sampling was conducted monthly during September 2017 to August 2018 at four (4) sampling stations (Figure 1), which reflect the longitudinal transition (i.e., from upstream of the inlet upstream to downstream of the outlet, as detailed in Table 1). Fish were sampled by beach seines (2 hauls per station), and three double-panel monofilament gillnets, with panels of 20 and 30 mm,

40 and 55 mm, and 70 and 90 mm stretched mesh. Gill nets were set for 12 h during the night time (6.00 p.m.-6.00 a.m.), whereas beach seine hauls were made during daytime. All live fish specimens were sacrificed by ice-slurry immersion. Fish specimens were then identified (Nelson, 2006), measured (total length, cm) and weighed (g) *in situ*. Their stomachs were removed from the visceral cavity and assessed visually for fullness. The fullness was visually rated from 1 to 4, whereby 1 = empty; 2 = <50 % filled; 3 = >50 % filled; and 4 = bursting (Chittapalapong *et al.*, 2014). Only stomachs rated between 2 and 4 by this scale were selected and preserved in 10% buffered formalin. The stomachs of each fish species were grouped by season (4 seasons).

*Stomach content analysis*

Each stomach was spread open in a petri dish, and contents were separated by items under a stereomicroscope. Food items in the stomach were identified into 13 categories with point scores for trophic weighting (Table 2, Hynes, 1950; Chittapalapong *et al.*, 2014). Percentage weight (pw$_{ij}$) of each food item in the stomachs of the ith sample (i.e., species i within a season) was
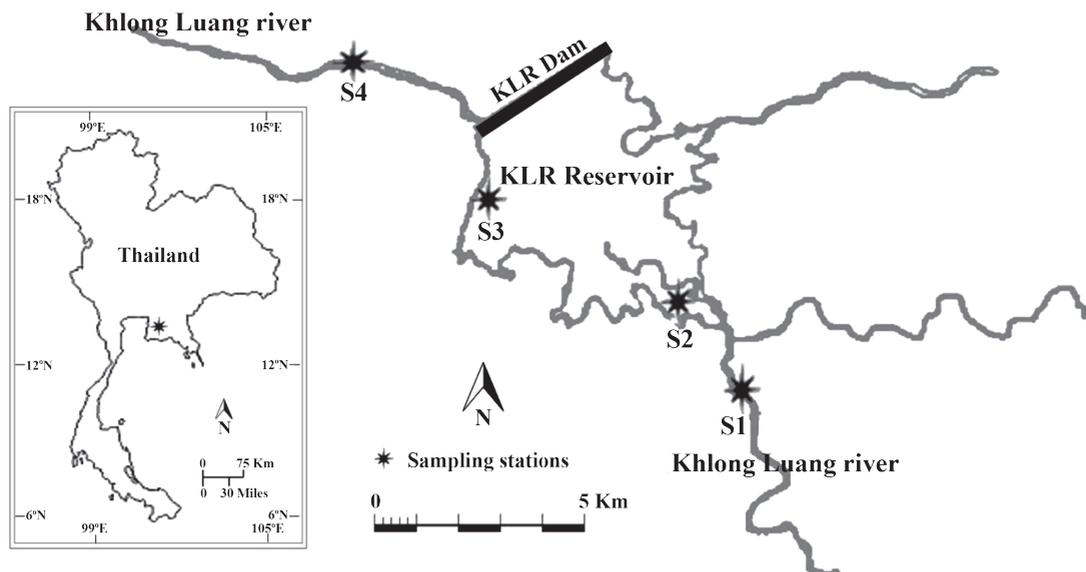


Figure 1. Location (✳) and map of Khlong Luang Rachalothorn (KLR) Reservoir, where sampling stations are indicated by stars (✳).

Table 1. Detail and location of the sampling stations in Khlong Luang Rachalothorn Reservoir used for this study.

| Station | Detail | Location |
|---|---|---|
| S1: Upstream | Upstream area: the river zone at 8.5 km upstream of the dam site | 13° 19' 48.8" N 101° 24' 29.2" E |
| S2: Transition | Transition area: the inlet zone connected to the reservoir, located 5.0 km upstream of the dam site | 13° 20' 49.6" N 101° 23' 16.3" E |
| S3: Reservoir | Reservoir area: lake-like conditions, located 1.5 km downstream of the dam site | 13° 22' 16.5" N 101° 20' 51.2" E |
| S4: Downstream | Downstream area: the outlet zone, which is influenced by the dam's operation, located 2.5 km downstream of the dam site | 13° 24' 33.4" N 101° 19' 52.8" E |

Table 2. The main diet items, point score and trophic class of each category used in this study (Chittapalapong et al., 2014).

| Diet category | Diet items | Point score | Trophic class |
|---|---|---|---|
| Phytoplankton | Diatoms, blue green algae, green algae and filamentous algae | 0.01 | 0 |
| Detritus | Fine organic materials | 0.1 | 0 |
| Plants | Stems and leaves | 0.3 | 0 |
| Macroalgae | Stonewort and water thyme | 0.3 | 0 |
| Sponges | Spicules | 0.4 | 1 |
| Bryozoans | Statoblasts | 0.4 | 1 |
| Molluscs | Bivalves and gastropods | 0.5 | 1 |
| Zooplankton | Cladocerans, copepods, ostracods and rotifers | 0.2 | 1.5 |
| Aquatic insects | Mayfly larvae, dragonfly larvae, midge larvae, water bugs | 0.5 | 1.5 |
| Terrestrial insects | Insects and ants (whole or remains) | 0.5 | 1.5 |
| Oligochaetes | Setae | 0.6 | 1.5 |
| Crustaceans | Crabs and shrimps (whole or remains) | 0.7 | 1.5 |
| Fish | Whole animals or remains, including scales, fins, and bones | 1.0 | 2 |

estimated by the proportion of the point score of food item j ($p_j$) to the total point score ($\sum_{j=1}^{n} p_j$), multiplied by the average weight of all diet items in the stomachs ($W_i$).

$$pwij = \sum_{j=1}^{n} p_j \, W_i \qquad \text{-------- (1)}$$

The percentage weight of each food item for each species ($pw_{ij}$) was also further used for cluster analysis as well as for estimating trophic index and diet overlap.

Food items were classified into trophic categories and scored as presented in Table 2 (Amarasinghe et al., 2014; Gammanpila et al., 2019). By multiplying these trophic scores by the proportions of food items, the trophic index ($T_i$) of any given fish collected during a sampling trip was then calculated as

$$T_i = 1.0 + \sum_{j=1}^{n} T_j \, (pw_{ij}) \qquad \text{-------- (2)}$$

where $T_j$ is the trophic class of prey item j.

Diet breadth ($B_i$) of fish species i was calculated according to Levins' niche breadth index (Levins, 1968) to determine the relative level of diet specialization as

$$B_i = \ 1/\sum_{j=1}^{n} pw_{ij}^2 \qquad \text{-------- (3)}$$

where n is the total number of food items in the diet. The values of $T_i$ and $B_i$ were presented as a species within a season for each station. The value of $B_i$ ranges between 0 (i.e., species that favor a specific food) and 1 (i.e., generalist species that can feed on a variety of foods equally). The Pianka index, $O_{ik}$ (Pianka, 1973) was used to compare overlap in food resources (i.e., diet overlap) between trophic levels in each station.

$$O_{ik} = \frac{\sum_{j=1}^{n} pw_{ij} pw_{kj}}{\sqrt{\sum_{j=1}^{n} pw_{ij}^2 \ \sum_{j=1}^{n} pw_{kj}^2}} \qquad \text{-------- (4)}$$

where $pw_{kj}$ is the percentage weight of each food item j in the diet of fish species k. The overlap values range from 0 to 1 (i.e., null to complete overlap) and are defined as low (0.00-0.39), intermediate (0.40-0.60), or high (0.61-1.00) (de Oliveira et al., 2020).

*Data analyses*

To examine the spatio-temporal variation in fish feeding in each station, dendrogram cluster analysis was used to group "species×season" samples, using Euclidean dissimilarity and Ward agglomeration methods. Analysis of similarity (ANOSIM) was used to test for significant differences among clusters. The relationship between trophic index and diet breadth was examined by curvilinear regression model. All statistical analyses were performed by using R (R Core Team, 2021) and package "vegan" for dendrogram cluster analysis (Oksanen et al., 2020).

**RESULTS**

A total of 1,031 individual fishes belonging to 46 species of 19 families were sampled and used for the dietary analysis (Table 3). Seventeen of the species were sampled in every station; seven of these were represented by 50 or more individuals: *Cyclocheilichthys armatus, Oreochromis niloticus, Labiobarbus siamensis, Puntioplites proctozysron, Barbonymus gonionotus, Osteochilus hasselti* and *Henicorhynchus siamensis*. The highest number of species (36) was collected from the reservoir zone (S3). In terms of season, the dry season sampling yielded the highest number of species (37) (Table 3). The overall diet composition of all specimens and diet compositions by zone are presented in Figure 2. The results show that macroalgae (19.2 %) was the most important diet category, followed by oligochaetes (18.0 %), and aquatic insects (13.7 %). Together, these three food items contributed over 50 % to the total stomach contents by weight; similar patterns were found for the upstream (S1) and downstream (S4) stations. Macroalgae and oligochaetes were also the two most important food items, by weight, for fishes in the transition zone (S2), but zooplankton was ranked third at this station. Meanwhile, oligochaetes, fishes and macroalgae accounted for over 50 % of the stomach contents, by weight, from fish sampled in the reservoir station (S3).

Cluster dendrogram analysis based on stomach contents, which were first condensed into 13 broad categories, presented a significant grouping by dominant prey for all four stations (Figure 3; ANOSIM, p<0.05). A maximum of nine groups was obtained from the reservoir station (S3) and eight groups from each of the remaining three stations. Sixty-four (64) "species×season" samples containing 33 fish species were from the upstream station (S1) (Table 4a), and one-third of these samples were based primarily on oligochaetes in

## S1: Upstream



## S2: Transition



## S3: Reservoir
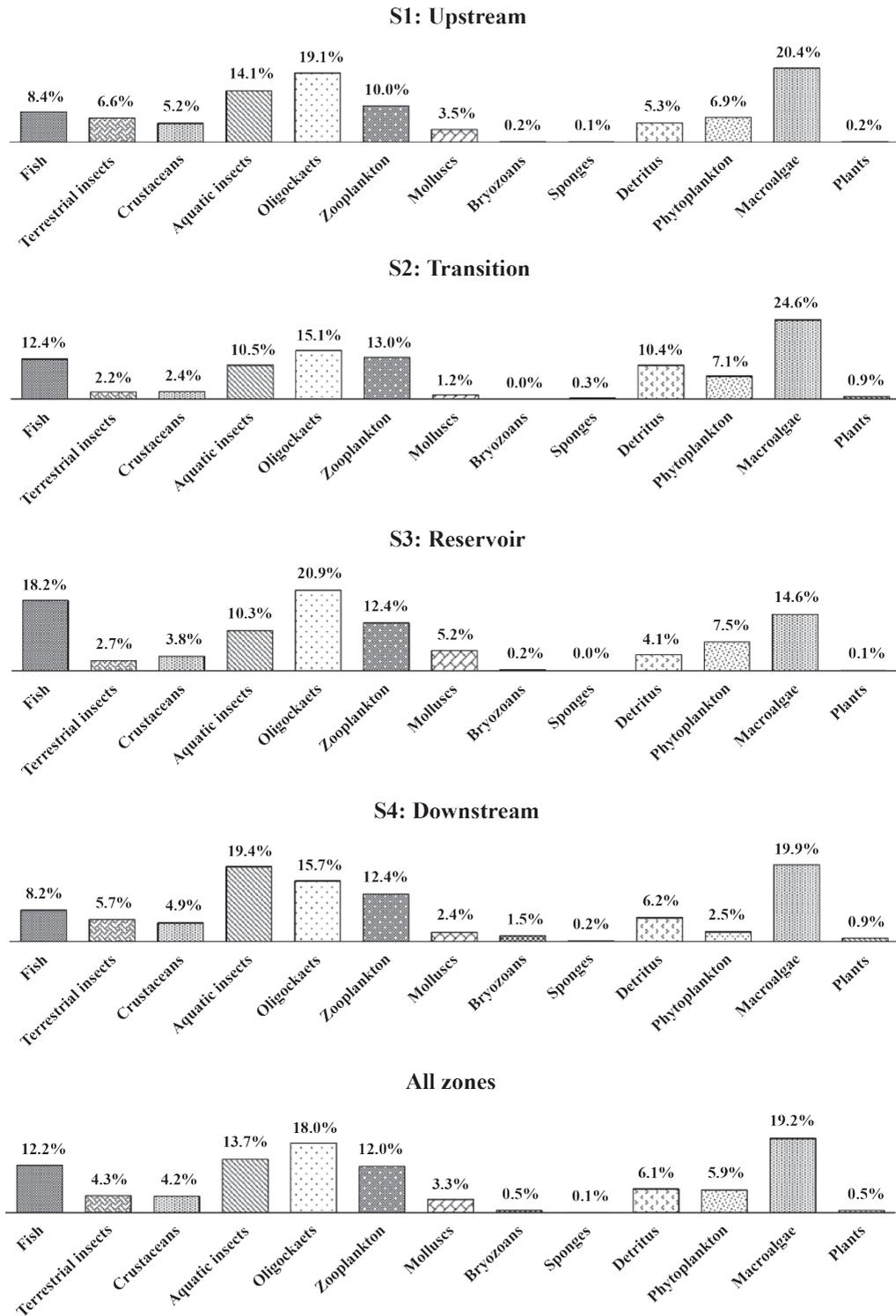


## S4: Downstream



## All zones



Figure 2. Percentage weight of diet composition, from all fish specimens from Khlong Luang  Rachalothorn Reservoir, separated by sampling stations and for all zones, between September 2017 and August 2018.

Table 3. List of fish species found in each station and season (+) between September 2017 and August 2018, with abbreviation (Abv), number of stomachs examined (N) and size range of specimens.

| Scientific name | Abv | Stations | | | | Stations | | | | N | Size range (cm TL) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | S1 | S2 | S3 | S4 | D | T1 | W | T2 | | |
| **Family Notopteridae** | | | | | | | | | | | |
| *Chitala ornata* | Co | | + | + | + | + | | + | + | 14 | 14.2-45.5 |
| *Notopterus notopterus* | Nn | + | + | + | + | + | + | + | + | 38 | 11.4-28.9 |
| **Family Cyprinidae** | | | | | | | | | | | |
| *Barbonymus gonionotus* | Bg | + | + | + | + | + | + | + | + | 63 | 8.5-41.9 |
| *Cyclocheilichthys armatus* | Ca | + | + | + | + | + | + | + | + | 80 | 9.6-19.5 |
| *Cirrhinus cirrhosus* | Cc | | | + | | + | | | | 1 | 60.4-60.4 |
| *Esomus metallicus* | Em | + | + | + | + | + | + | | | 16 | 4.7-7.3 |
| *Henicorhynchus siamensis* | Hs | + | + | + | + | + | + | + | + | 50 | 11.9-20.7 |
| *Leptobarbus hoeveni* | Lh | + | | + | | + | | | + | 4 | 20.5-33.0 |
| *Labeo rohita* | Lr | + | | + | | + | | + | | 9 | 15.0-61.0 |
| *Labiobarbus siamensis* | Ls | + | + | + | + | + | + | + | + | 71 | 8.6-27.0 |
| *Osteochilus hasselti* | Oh | + | + | + | + | + | + | + | + | 55 | 11.0-23.1 |
| *Puntioplites proctozysron* | Pp | + | + | + | + | + | + | + | + | 70 | 9.5-31.5 |
| *Parachela siamensis* | Pr | + | + | | + | + | + | + | | 16 | 6.0-8.2 |
| *Paralaubuca typus* | Pt | | + | + | | | + | | | 4 | 10.7-13.6 |
| *Rasbora borapetensis* | Rb | + | | | + | + | | | | 5 | 4.0-5.5 |
| *Rasbora paviei* | Rp | + | | | + | + | | + | | 4 | 6.8-9.8 |
| **Family Cobitidae** | | | | | | | | | | | |
| *Acantopsis* sp. | Ac | + | | | | | + | | + | 12 | 8.8-16.0 |
| **Family Loricariidae** | | | | | | | | | | | |
| *Hypostomus plecostomus* | Hp | + | + | | | | + | + | + | 7 | 7.1-35.8 |
| **Family Bagridae** | | | | | | | | | | | |
| *Hemibagrus nemurus* | Hn | + | | + | + | + | + | + | + | 20 | 8.4-39.0 |
| *Hemibagrus wyckii* | Hw | | | + | | | | | + | 1 | 27.0-27.0 |
| *Mystus multiradiatus* | Mm | + | + | + | + | + | + | + | + | 45 | 10.5-18.5 |
| *Pseudomystus siamensis* | Pi | | + | | | | | + | | 1 | 16.1-16.1 |
| **Family Siluridae** | | | | | | | | | | | |
| *Ompok bimaculatus* | Ob | | | + | + | + | + | | + | 6 | 16.0-27.5 |
| **Family Pangasiidae** | | | | | | | | | | | |
| *Pangasianodon hypophthalmus* | Ph | | | + | + | | | + | | 4 | 7.1-18.2 |
| **Family Clariidae** | | | | | | | | | | | |
| *Clarias batrachus* | Cb | | | + | + | | | + | + | 3 | 18.2-27.7 |
| *Clarias macrocephalus*× *Clarias gariepinus* | Cl | | | + | | + | | | + | 2 | 22.7-32.5 |
| *Clarias macrocephalus* | Cm | + | | + | | | | + | | 2 | 24.5-27.3 |
| **Family Belonidae** | | | | | | | | | | | |
| *Xenentodon cancila* | Xc | + | + | + | + | + | + | + | + | 53 | 9.4-29.5 |
| **Family Hemiramphidae** | | | | | | | | | | | |
| *Dermogenys pusilla* | Dp | + | | | + | + | | | | 3 | 4.8-5.3 |
| **Family Synbranchidae** | | | | | | | | | | | |
| *Monopterus albus* | Ma | | | + | | | | + | | 1 | 43.2-43.2 |

Table 3. (Cont.)

| Scientific name | Abv | Stations | | | | Stations | | | | N | Size range (cm TL) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | S1 | S2 | S3 | S4 | D | T1 | W | T2 | | |
| **Family Mastacembelidae** | | | | | | | | | | | |
| *Mastacembelus favus* | Mf | + | | + | + | + | | + | + | 5 | 23.3-38.6 |
| *Macrognathus siamensis* | Ms | | + | | | | | + | | 1 | 14.4-14.4 |
| *Mastacembelus favus* | Mf | + | | + | + | + | | + | + | 5 | 23.3-38.6 |
| **Family Ambassidae** | | | | | | | | | | | |
| *Parambassis siamensis* | Ps | + | + | + | + | + | + | + | + | 27 | 4.5-6.3 |
| *Parambassis apogonoides* | Pa | + | + | + | + | + | + | + | | 34 | 4.5-6.3 |
| *Puntius brevis* | Pb | + | + | + | + | + | + | + | + | 31 | 7.8-11.5 |
| **Family Cichlidae** | | | | | | | | | | | |
| *Oreochromis niloticus* × | On | + | | | | + | | | | 1 | 19.4-19.4 |
| *Oreochromis mossambicus* | | | | | | | | | | | |
| *Oreochromis niloticus* | Or | + | + | + | + | + | + | + | + | 76 | 5.5-39.0 |
| **Family Nandidae** | | | | | | | | | | | |
| *Pristolepis fasciata* | Pf | + | | | + | + | | + | + | 23 | 7.8-11.5 |
| **Family Channidae** | | | | | | | | | | | |
| *Channa striata* | Cs | + | | | + | + | + | + | + | 16 | 1.0-44.4 |
| *Channa micropeltes* | Ch | | + | + | | + | + | | + | 9 | 22.4-41.5 |
| **Family Anabantidae** | | | | | | | | | | | |
| *Anabas testudineus* | At | + | | | + | + | | + | + | 11 | 8.4-20.0 |
| **Family Osphronemidae** | | | | | | | | | | | |
| *Trichogaster microlepis* | Tm | + | + | + | + | + | + | + | + | 39 | 8.3-13.7 |
| *Trichogaster pectoralis* | Tp | + | + | + | + | + | | + | + | 24 | 8.3-19.8 |
| *Trichogaster trichopterus* | Tt | + | + | + | + | + | + | + | + | 39 | 6.1-11.1 |
| *Trichopsis vittata* | Tv | | + | + | + | + | + | | | 18 | 4.4-6.0 |
| **Family Eleotridae** | | | | | | | | | | | |
| *Oxyeleotris marmorata* | Om | + | + | + | + | + | | + | + | 17 | 5.5-26.8 |
| | **Total** | 33 | 26 | 36 | 32 | 37 | 24 | 34 | 29 | | |

**Note:** S1-S4 are sampling stations as detailed in Table 1; Abbreviations for season; D = dry season; T1 = dry to wet transition; W = wet season; T2 = wet to dry transition

the diet. Only two species from different seasons were grouped into the same cluster (*Channa striata* [Cs] and *C. armatus* [Ca]); these fed exclusively on fishes or oligochaetes, respectively. The remaining species, in contrast, showed the potential to switch primary food items from season to season. For example, *H. siamensis* (Hs) and *Trichogaster microlepis* (Tm) switched among phytoplankton, macroalgae and aquatic insects as their main diet item. Oligochaetes and macroalgae were both main diets of samples at the transition station (S2), as they are found in most samples with high percentage

weight (Table 4b); each represented about one-fourth of the 50 samples, containing 26 fish species. In this station, *Xenentodon cancila* (Xc) and *Parambassis siamensis* (Ps) did not change their main food items (fishes and zooplankton, respectively) throughout the study period. In the reservoir station (S3) (Table 4c), *C. striata* (Cs) and *C. armatus* (Ca) fed chiefly on fishes, similar to the samples from the upstream station. From the 92 samples representing 36 fish species in the reservoir station (Table 4c), the samples in the oligochaete group showed more diversity of

Table 4. Samples (Species×Season) that were grouped together based on similarity in percentage weight (pw) of diet composition, and the mean pw in each group. The first two letters in each sample name indicate species, followed by the abbreviation for the season of collection (see Table 3).

**a: S1-Upstream**

| Group | Species×Season | Phy | Det | Pla | Mac | Spo | Bry | Mol | Zoo | Aqu | Ter | Oli | Cru | Fis |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | XcT2, MfD, PsW, HsT2, TmT2, PrT1, TtD | 4.2 | 9.1 | 2.0 | 39.8 | NA | 2.5 | 4.7 | 15.1 | 4.5 | 1.6 | 16.1 | NA | NA |
| 2 | TtW, HsD, TmD, TmW, OrD, OnD, OrW | NA | NA | NA | 9.3 | NA | NA | NA | 7.6 | 8.2 | 74.5 | NA | NA | NA |
| 3 | HnT2, PpT2 | 1.1 | 4.5 | NA | 14.9 | NA | NA | NA | 7.0 | 23.8 | NA | 45.1 | 2.3 | 0.6 |
| 4 | EmD, HpW, TrT1, HsW, OhT2, LsW, TmT1, HsT1, OhW | 2.4 | 1.3 | NA | 3.9 | NA | NA | 2.8 | 7.8 | 71.1 | 1.0 | 3.5 | 5.2 | 0.9 |
| 5 | HnD, CsT1, CsW, MmT2, PaD | NA | NA | 1.2 | 2.8 | NA | 5.5 | 1.6 | NA | 6.8 | 1.7 | 2.9 | NA | 76.4 |
| 6 | DpD, RbD, BgW, PrD, PsD, LhT2, RpD | 2.7 | 10.8 | NA | NA | NA | NA | NA | 86.6 | NA | NA | NA | NA | NA |
| 7 | XcD, OmW, XcT1, AcT1, PfT2 | 9.1 | 90.9 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 8 | MmD, AcD, PpD, PpW, CaW, CaT2, BgT1, CmW, NnW, AtW, CaD, OrT2, LsT2, LsD, OhD, AcT2, BgT2, TpD, LrD, PbW, MmW, PbD | NA | NA | NA | NA | NA | NA | NA | 0.7 | 6.5 | NA | 0.7 | 69.6 | 22.2 |

**b: S2-Transition**

| Group | Species×Season | Phy | Det | Pla | Mac | Spo | Bry | Mol | Zoo | Aqu | Ter | Oli | Cru | Fis |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | PsD, PrW, PsT1, PsW | 7.5 | NA | NA | 5.9 | NA | NA | NA | 74.3 | NA | 12.3 | NA | NA | NA |
| 2 | OmW | NA | NA | NA | NA | NA | NA | NA | NA | NA | 0.2 | NA | 99.8 | NA |
| 3 | PrW, PbW, PiW, MmT1, TvD | NA | NA | NA | 5.0 | NA | NA | NA | 11.0 | 82.4 | NA | 1.6 | NA | NA |
| 4 | EmT1, HpT1 TmD | 78.8 | 4.8 | NA | 8.1 | NA | NA | NA | 8.3 | NA | NA | NA | NA | NA |
| 5 | LsT1, OhT1 HsD, PpT1 | 5.7 | 57.9 | NA | 1.6 | NA | NA | NA | 16.5 | NA | NA | 18.3 | NA | NA |
| 6 | OrW, TmT1, TmW, LsW, BgW, HsW, OhW, PbT1, HpW, TtW, PrD, TvT1 | 1.8 | 17.6 | 2.0 | 64.3 | 1.1 | NA | NA | 9.1 | 1.7 | 1.3 | 1.1 | NA | NA |
| 7 | XcW, XcD, XcT1, PaD, ChT1, CoW, BgD, NnT1 | NA | 0.7 | 1.5 | 7.1 | NA | NA | NA | 2.8 | 1.9 | NA | 4.1 | 2.6 | 79.3 |
| 8 | MsW, BgT, MmW, CaW, CaD, PpW, TrT1, OrT1, TpD, TtD, NnW, OrD, CaT1, PaT1 | 3.6 | 5.0 | 0.5 | 24.7 | NA | NA | 4.3 | 6.5 | 6.1 | 3.4 | 45.9 | NA | NA |

Table 4. (Cont.)

c: S3-Reservoir

| Group | Species×Season | Phy | Det | Pla | Mac | Spo | Bry | Mol | Zoo | Aqu | Ter | Oli | Cru | Fis |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | MfW | NA | NA | NA | NA | NA | NA | NA | NA | NA | 100.0 | NA | NA | NA |
| 2 | LhD, TtW, HsT1, HsW, HsD, OrT1 | 71.6 | 8.3 | NA | 8.0 | NA | NA | NA | 2.9 | 0.2 | NA | 9.0 | NA | NA |
| 3 | LrW, TpW, EmT1 HsT2, TtT2 | 1.9 | 8.4 | NA | 69.7 | NA | 3.5 | NA | 16.5 | NA | NA | NA | NA | NA |
| 4 | NnT2, MmT2, ObT2, PaD, PaW, XcT1, XcD, XcW, OmD, CsD, CoW, ChT2, CoD, CsW, HnW, CsT2, HnD, HnT2, CoT2, OmT2 | NA | NA | NA | 1.2 | NA | NA | 5.3 | 1.6 | 6.6 | 0.7 | 1.6 | 6.3 | 76.7 |
| 5 | ChD, OmW | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | 79.7 | 20.3 |
| 6 | PbT2, PsT1, CcD, MmT1, OrD, LsT1, TmW | 18.5 | 6.0 | NA | 4.3 | NA | NA | NA | 71.1 | NA | NA | 0.1 | NA | NA |
| 7 | AtT2, ClD, HwT2, BgW, PhW | 4.8 | 0.9 | 1.7 | 10.4 | NA | NA | 63.4 | 5.3 | 4.4 | NA | 6.5 | 2.6 | NA |
| 8 | NnD, ClT2, PbT1, AtD, PsT2, TvT1, PaT1, PsD | 0.2 | NA | NA | 9.4 | NA | NA | 0.6 | 3.1 | 75.0 | NA | 5.2 | 5.1 | 1.4 |
| 9 | CaW, MaW, ObD, LrD, TvD, CmW, LhT2, CaT1, CaT2, PpW, AtW, PbW, CbT2, NnW, MmD, MmW, EmD, OhD, CaD, LsT2, PpD, PbD, LsD, TtD, PtW, BgT1, TpD, TpT2, OhW, OrW, BgD, BgT2, LsW, PpT2, OrT2, PpT1, TmT2 | 2.2 | 6.4 | 0.1 | 20.4 | NA | NA | 1.2 | 12.0 | 5.0 | 3.6 | 47.0 | 0.2 | 1.9 |

d: S4-Downstream

| Group | Species×Season | Phy | Det | Pla | Mac | Spo | Bry | Mol | Zoo | Aqu | Ter | Oli | Cru | Fis |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | OmW, PaT1, OmT2, PaD | NA | NA | NA | 0.1 | NA | NA | NA | 0.7 | 6.5 | NA | 0.7 | 69.6 | 22.4 |
| 2 | HsT2 | 9.1 | 90.9 | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA | NA |
| 3 | HsD, PsW, RbD | 2.7 | 10.8 | NA | NA | NA | NA | NA | 86.5 | NA | NA | NA | NA | NA |
| 4 | HnW, PfD, TtT2, XcD, ObT1, CsT2, HnT2 | NA | NA | 1.2 | 2.8 | NA | 5.5 | 1.6 | 0.5 | 6.8 | 1.7 | 3.0 | 0.5 | 76.4 |
| 5 | MmW, PrD, PsD, CaT2, MfW, MfT2, CsT1, HnT1, PbT1, TvD, PsT1, NnT2, PfT2 | 2.4 | 1.3 | NA | 4.0 | NA | NA | 2.8 | 7.8 | 71.1 | 1.0 | 3.5 | 5.2 | 0.9 |
| 6 | CaT1, EmD, PfW, MmD, PbW, NnW, NnD, CaD, CaW, PpT1, PpD, PpT2, OhD, NnT1, PbT2 | 1.1 | 4.5 | 0.1 | 14.9 | 0.4 | 0.2 | NA | 7.0 | 23.8 | 0.1 | 45.0 | 2.3 | 0.6 |
| 7 | CbW, RpW, AtT2, AtW, DpD | 0.3 | NA | NA | 9.3 | NA | NA | NA | 7.6 | 8.2 | 74.6 | NA | NA | NA |
| 8 | OrT1, OrW, BgT2, OhW, OhT2, HsW, LsD, MmT2, CoW, TtW, OrD, PpW, TpT2, LsT2, TmD, BgD, BgW, LsW, TmT2, OhT1, T1T1, CsW, PhW, TtD, MmT1, PbD, XcW, OmD, TmW, BgT1, TpW | 4.2 | 9.1 | 2.0 | 39.7 | 0.3 | 2.5 | 4.7 | 15.1 | 4.5 | 1.6 | 16.1 | 0.1 | 0.1 |

**Note:** NA = not available; Abbreviations of diet items: Phy = Phytoplankton; Det = Detritus; Pla = Plants; Mac = Macroalgae; Spo = Sponges; Bry = Bryozoans; Mol = Molluscs; Zoo = Zooplankton; Aqu = Aquatic insects; Ter = Terrestrial insects; Oli = Oligochaetes; Cru = Crustaceans; Fis = Fish

other food items in the stomachs than the other feeding groups. Meanwhile, the macroalgae group showed the most varied stomach contents in the downstream station, in contrast to the aquatic insect group, which was less diverse in diet (Table 4d). Among the 32 fish species from 79 samples in the downstream station (S4), species such as *B. gonionotus* (Bg), *O. hasselti* (Oh), *O. niloticus* (Or) and *T. microlepis* (Tm) fed mainly on macroalgae throughout the year.

By examining some common species, it can be seen that trophic level fluctuated less than diet breadth (Figure 4). This implies that although a variety of food items were found in the stomachs, each species tended to have its own diet preference. However, exceptions were found in strict carnivores, such as *P. siamensis* (Ps), *Trichogaster trichopterus* (Tt) and *X. cancila* (Xc). It is also worth noting that diet breadth tended to narrow in the transition station compared to other stations. No clear pattern was seen across seasons since the selected species were not available in this station during the entire year.

Relationships between trophic index and diet breadth in all four stations tended to be parabolic (Figure 5), indicating that the fish species with trophic index between 1.50 and 2.50 had a wide range of food items (i.e., generalists), but species above or below this range consumed a more limited diet (i.e., specialists). Most of the samples are clustered between 1.50 and 2.50 on the x-axis (trophic index), implying that most of the fish species from the study had a variety food items in their stomach. Also, a high degree of overlap in food resources ($O_i$) was found in this range of trophic levels (i.e., 1.51-2.00 vs 2.01-2.50) (Figure 6). Interestingly, high $O_i$ was also observed at lower trophic levels (1.00-1.50 vs 1.51-2.00), but not for more carnivorous groups (2.01-2.50 vs 2.51-3.00).
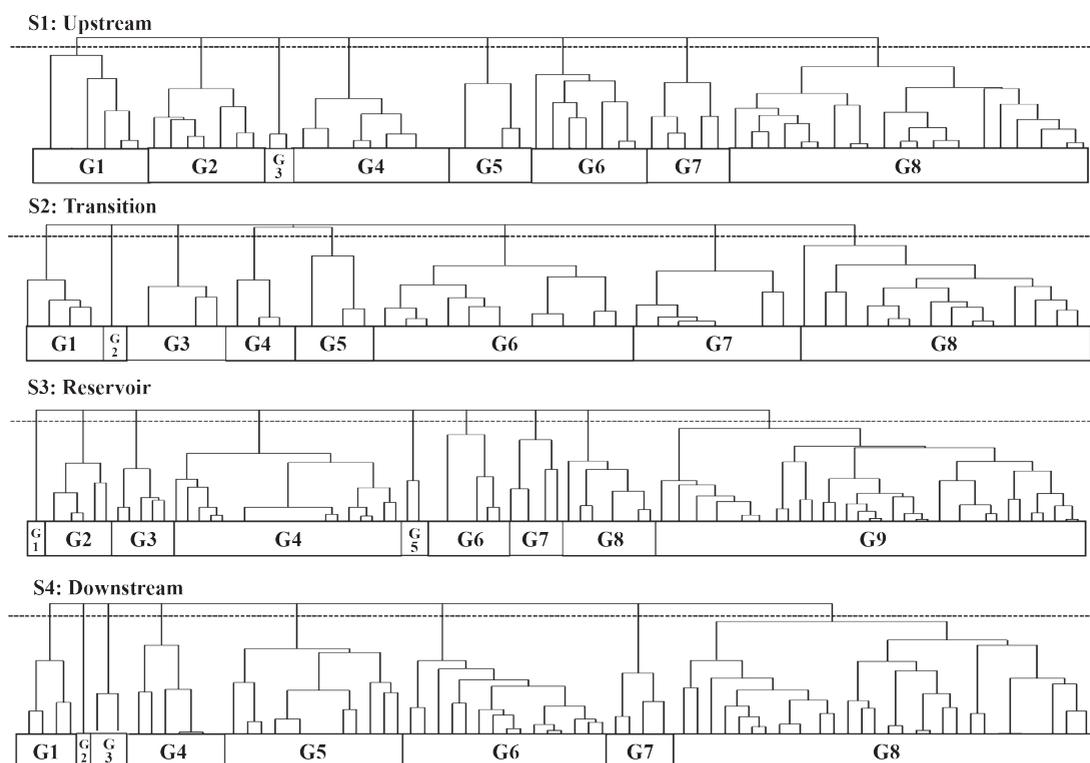


Figure 3. Cluster dendrogram of the samples, i.e., species×season, from Khlong Luang Rachalothorn Reservoir, between September 2017 and August 2018, based on similarity in percentage weight of diet composition. Each cluster is represented by letter "G" followed by the cluster number.
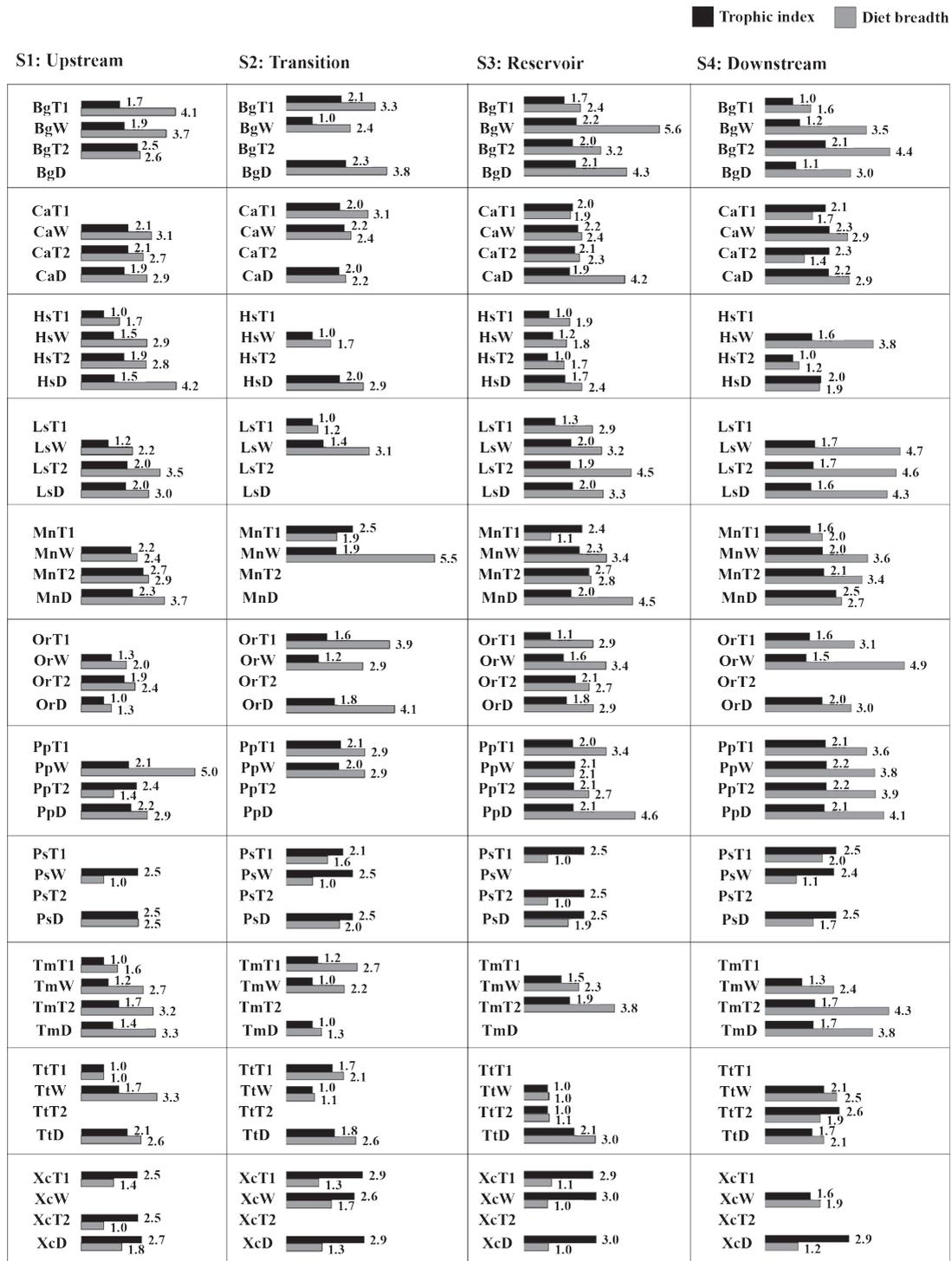
Figure 4.  Trophic index and diet breadth of selected samples (i.e., species×season) from Khlong Luang Rachalothorn Reservoir, between September 2017 and August 2018. The first two letters in each sample indicate species, followed by the abbreviation for season (see Table 3).
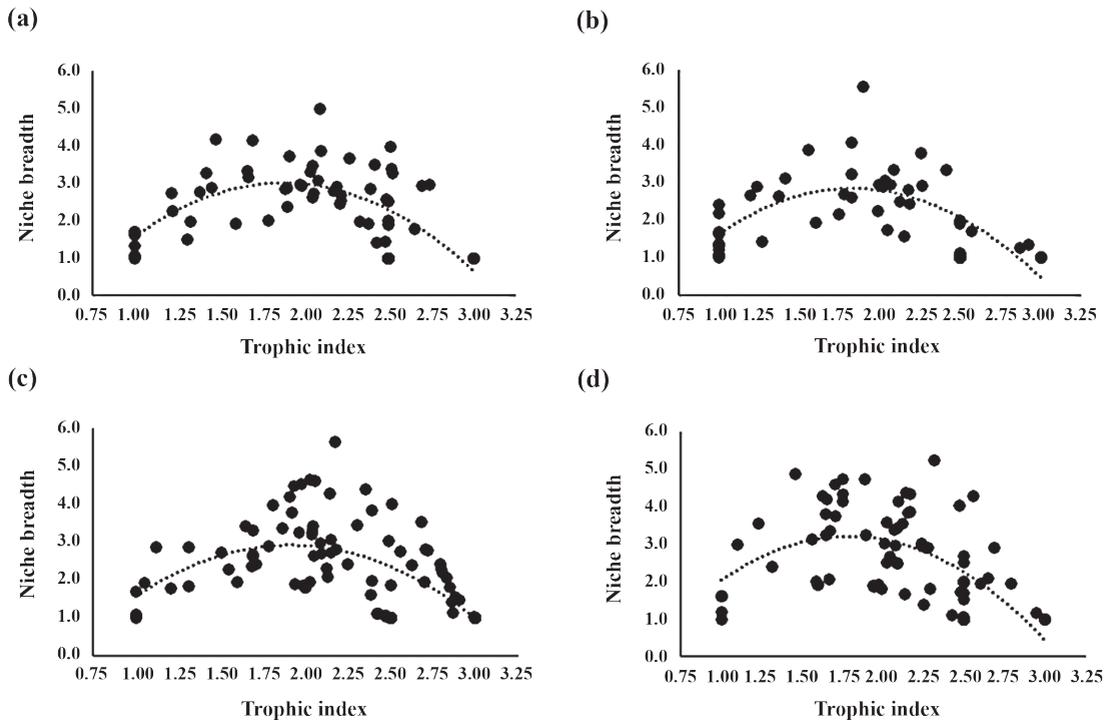
**(a)**

**(b)**

**(c)**

**(d)**

Figure 5.  Relationship between trophic index and diet breadth of samples (i.e., species×season) from Khlong Luang Rachalothorn Reservoir, between September 2017 and August 2018, in (a) S1: Upstream, (b) S2: Transition, (c) S3: Reservoir and (d) S4: Downstream.

Legend:
- 1.00-1.50 & 1.51-2.00
- 1.00-1.50 & 2.01-2.50
- 1.00-1.50 & 2.51-3.00
- 1.51-2.00 & 2.01-2.50
- 1.51-2.00 & 2.51-3.00
- 2.01-2.50 & 2.51-3.00
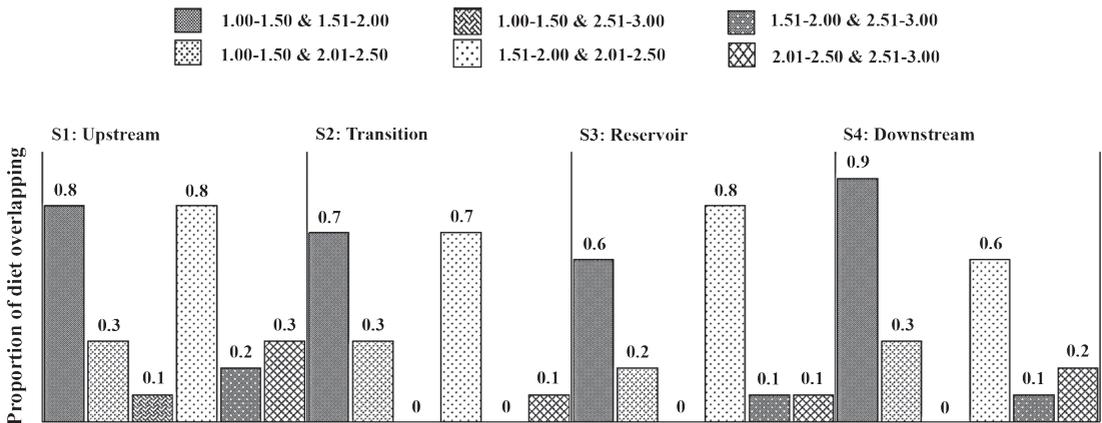
Figure 6.  Proportion of diet overlapping between trophic index groups, based on percentage weight of diet composition, in Khlong Luang Rachalothorn Reservoir.

## DISCUSSION

Fluctuation in diet composition of fishes in the newly impounded reservoir was studied to examine their potential for trophic plasticity. There was no clear fish assemblage pattern found among the four habitats chosen for sampling. This could be explained by the age of this reservoir, since it normally takes more than five years to clearly observe differentiation in fish communities, based on experience from other reservoirs in Thailand (Jutagate *et al*., 2012). Fish specimens in this study included species recognized as carnivores, such as *Channa striata, Clarias macrocephalus* and *Hemibagrus nemurus* as well as herbivores, such as *Labeo rohita, Leptobarbus hoeveni* and *Henicorhynchus siamensis* (Froese and Pauly, 2021). However, the contribution of other food items in the diets of these species, as found in this study, suggests the intraspecific feeding plasticity and variety of food resources in the system. Together, these factors tend to widen the trophic niches of these fishes, implying that they can survive in various freshwater systems (Dabrowski and Portella, 2005).

The higher numbers of species and specimens found at the reservoir station (S3) compared to the others could be due to its more stable and balanced environment (Vehanen *et al*., 2005). Meanwhile, the concentration of fishes into a smaller area during the dry season made them more vulnerable to capture, likely leading to the higher number of species and specimens collected than in other seasons (Cerdier *et al*., 2000). Overall dominance by the macroalgae and oligochaetes found in diets can be explained by impacts from land uses. Run-off from agricultural activities in the surrounding area, such as cattle and crops, becomes a nutrient-rich sediment for aquatic plants and various benthic fauna, including oligochaetes (Edwards, 2004; Suriani-Affonso *et al*., 2011). De Mérona *et al*. (2003) reported that terrestrial and aquatic insects constitute the main foods of fishes in newly impounded rivers. In our study, insects were important in diets of fish in the upstream (S1) and downstream (S4) stations. The transition zone (S2) between lotic and lentic

environments in the reservoir system supports a high density of plankton, since the mass of water expands into the terrestrial zone, where nutrients from soil nourish phytoplankton and subsequently zooplankton (Meksumpun, 2020). The inundating water also generates dead plant material and detritus (Fonseca *et al*., 2016), which support the detritus-dominant group in this station. Interestingly, a detritus-dominant group of fishes was not found in the reservoir station (S3); in many other reservoirs, detritus and sediment were among the food resources most consumed (Amarasinghe *et al*., 2014; De Oliveira *et al*., 2020). The most likely explanation for the difference is that our survey was conducted only two years after impoundment of the river, and it would take longer than this for significant amounts of sediment to accumulate (Marmulla, 2001; De Oliveira *et al*., 2020). Therefore, another examination of diet composition should be conducted in the future, after fish populations have become more fully established. Buckland *et al*. (2017) suggested that prey condition should be also reported, as it significantly influences prey volume or weight. Meanwhile, frequency of occurrence and point score methods as a nested hierarchy of taxonomic levels or diet groups are also beneficial for making comparisons among fish species or feeding guilds.

The complex and varied diets observed in stomach contents reflected the ability of fishes in this reservoir to shift their diets. This behavior implies that besides their preferred food items, fishes try to utilize all available resources in the system to supplement their diets and to avoid competition with other species (Pettit-Wade *et al*., 2015). Our findings also support the hypothesis that most freshwater fishes tend towards omnivory when challenged by seasonal and stochastic fluctuations in the environment (Figure 4) (De Mérona *et al*., 2003). Miranda *et al*. (2019) revealed that the complexity in feeding increases with catchment area along a reservoir cascade. Wolff *et al*. (2013) mentioned that a decrease in proportion of diet items in a given river section could be linked to resource availability, which could explain the different proportions of foods found for the same species sampled in different stations and seasons.

Although there is still no consensus whether the diversity of food resources in a system determines whether the niche of a fish species is broad or narrow (Quirino *et al*., 2017), fishes examined in each station of this study displayed large shifts in diet (Table 4 and Figure 4) and relatively broad diet breadth. Diet breadth was particularly large for the fishes with trophic level between 1.50 and 2.50. Gammanpila *et al*. (2019) suggested that even within a trophic guild, fish species sometimes occupy different trophic levels, relaxing competition for food resources. Quirino *et al*. (2017) mentioned that diet breadth is normally high during the high-water season, when food resources are more abundant. Macpherson and Roel (1987) also pointed out that fish species with high abundance commonly showed wider diet breadth than those with lower abundance. Moreover, within a species, ontogenetic niche shift significantly affects the variation in trophic level and diet breadth; larger individuals generally have a higher trophic level and wider trophic niche because they can effectively consume larger prey and more varied diets (Nakazawa *et al*., 2010).

## CONCLUSION

In this study, cyprinid fishes were the most dominant group, with the largest number of species found in all habitats surveyed. Macroalgae was the most common food group, followed by oligochaetes and aquatic insect larvae. Trophic index and diet breadth of common fish species showed the ability for wide feeding plasticity and spatio-temporal fluctuation. Laboratory work in food preferences, incorporated with advanced techniques such as stable isotope study, would provide deeper understanding of feeding behavior of these fishes. Knowledge of food preferences and feeding behavior is beneficial for fisheries resource management, as these are important elements of ecosystem balance. This knowledge can also be applied to aquaculture, particularly in integrated multi-trophic systems.

## ACKNOWLEDGEMENTS

## LITERATURE CITED

Agostinho, A.A., A.E.A.M. Vazzoler and S.M. Thomaz. 1995. **The High River Paraná basin: limnological and ichthyological aspects.** In: Limnology in Brazil (eds. J.G. Tundisi, C.E.M. Bicudo and T. Matsumura-Tundisi), pp. 59-103. ABC/SBL, Rio de Janeiro, Brazil.

Amarasinghe, U.S., J. Vijverberg, W.S. Weliange and M. Vos. 2014. Food-web patterns and diversity in tropical fish communities. **Lakes and Reservoirs: Research and Management** 19(1): 56-69. DOI: 10.1111/lre.12056.

Braga, R.R., H. Bornatowski and J.R.S. Vitule. 2012. Feeding ecology of fishes: An overview of worldwide publications. **Reviews in Fish Biology and Fisheries** 22(4): 915-929. DOI: 10.1007/s11160-012-9273-7.

Buckland, A., R. Baker, N. Loneragan and M. Sheaves. 2017. Standardising fish stomach content analysis: The importance of prey condition. **Fisheries Research** 196: 126-140. DOI: 10.1016/j.fishres.2017.08.003.

Bureau of Project Management. 2017. **Environmental Impact Mitigation Plan: EIMP Khlong Luang Rachalothorn Reservoir 2017.** Bureau of project management, Royal irrigation department, Bangkok, Thailand. 392 pp.

Cachera, M., B. Ernande, M.C. Villanueva and S. Lefebvre. 2017. Individual diet variation in a marine fish assemblage: Optimal foraging theory, niche variation hypothesis and functional identity. **Journal of Sea Research** 120: 60-71. DOI: 10.1016/j.seares.2016.08.004.

Cerdier, R.G.P., M.L. Ruffino and V. Isaac. 2000. Fish catches among riverside communities around Lago Grande de Monte Alegre, lower Amazon, Brazil. **Fisheries Management and Ecology** 7: 355-374. DOI: 10.1046/j.1365-2400.2000.007004355.x.

Chittapalapong, T., A. Rungrangsri and M. Lempan. 2014. **Fish Feeding Analysis.** Central Administrative Office, Department of Fisheries, Bangkok, Thailand. 29 pp.

Dabrowski, K. and M.C. Portella. 2005. **Feeding plasticity and nutritional physiology in tropical fishes.** In: The Physiology of Tropical Fishes 21 (eds. A.L. Val, V.M.F De Almeida-Val and D.J. Randall), pp. 155-224. Elsevier Science Publishing Co Inc, San Diego, USA.

De Mérona, B., R. Vigourouxand and V. Horeau. 2003. Changes in food resources and their utilization by fish assemblages in a large tropical reservoir in South America (Petit-Saut Dam, French Guiana). **Acta Oecologica** 24(3): 147-156. DOI: 10.1016/S1146-609X(03)00065-1.

De Oliveira, J.C.D., J.F. de Oliveira, A.D.O. Marques, D. Peretti, R.S. da Costa and J.L.C. Novaes. 2020. Trophic ecology of detritivorous fish along a reservoir cascade in a tropical semi-arid region. **Ecology of Freshwater Fish** 30(2): 234-243. DOI: 10.1111/eff.12579.

Dugan, P.J., C. Barlow, A.A. Agostinho, E. Baran, G.F. Cada, D. Chen, I.G. Cowx, J.W. Ferguson, T. Jutagate, M. Mallen-Cooper and G. Marmulla. 2010. Fish migration, dams, and loss of ecosystem services in the Mekong basin. **Ambio: A Journal of Environment and Society** 39(4): 344-348. DOI: 10.1007/s13280-010-0036-1.

Edwards, C.A. 2004. **Earthworm Ecology.** CRC Press, Boca Raton, Florida, USA. 456 pp.

Elliott, M., A.K. Whitfield, I.C. Potter, S.J. Blaber, D.P. Cyrus, F.G. Nordlie and T.D. Harrison. 2007. The guild approach to categorizing estuarine fish assemblages: a global review. **Fish and Fisheries** 8(3): 241-268. DOI: 10.1111/j.1467-2679.2007.00253.x.

Fonseca, A.L.S., I. Bianchini, C.M.M. Pimenta, C.B.P. Soares and N. Mangiavacchi. 2016. The effect of hydrostatic pressure on the decomposition of inundated terrestrial plant detritus of different quality in simulated reservoir formation. **Lakes and Reservoirs** 21: 216-223. DOI: 10.1111/j.1467-2679.2007.00253.x.

Froese, R. and D. Pauly. 2021. **FishBase.** http://www.fishbase.org. Cited 14 Jul 2022.

Gammanpila, M., U.S. Amarasinghe and M.J.S. Wijeyaratne. 2019. Dietary guild structure in fish assemblages and trophic position of constituent species in brush parks of a tropical estuary. **Asian Fisheries Science** 32(1): 8-18. DOI: 10.33997/j.afs.2019.32.01.002.

Hynes, H.B.N. 1950. The food of fresh water stickleback (*Gasterosteus aculeatus* and *Pygosteus pongitius*) with a review of methods used in studies of the food of fishes. **Journal of Animal Ecology** 19: 36-58. DOI: 10.2307/1570.

Inland Fisheries Research and Development Division. 2012. **Fisheries Resources Monitoring and Evaluating Operation Plan: Khlong Luang Rachalothorn Reservoir 2012.** Department of Fisheries, Bangkok, Thailand. 29 pp.

Johnson, B.L., W.B. Richardson and T.J. Naimo. 1995. Past, present, and future concepts in large river ecology: how rivers function and how human activities influence river processes. **Bioscience** 45: 134-141. DOI: 10.2307/1312552.

Jutagate, T., B. Srichareondham, S. Lek, U.S. Amarasinghe and S.S. De Silva. 2012. Variations, trends and patterns of fish landings in large tropical reservoirs. **Lakes and Reservoirs: Research and Management** 17: 35-53. DOI: 10.1111/j.1440-1770.2012.00494.x.

Kadye, W.T. and A.J. Booth. 2020. Environmental niche patterns of native and non-native fishes within an invaded African river system. **Journal of Fish Biology** 96(5): 1269-1277. DOI: 10.1111/jfb.13988.

Levins, R. 1968. **Evolution in Changing Environments.** Princeton University Press, Princeton, USA. 121 pp.

Macpherson, E. and B.A. Roel. 1987. Trophic relationships in the demersal fish community off Namibia. **South African Journal of Marine Science** 5(1): 585-596. DOI: 10. 2989/025776187784522432.

Marmulla, G. 2001. **Dams, Fish and Fisheries: Opportunities, Challenges and Conflict Resolution.** Food and Agriculture Organization of the United Nations, Rome, Italy. 172 pp.

McCartney, M. 2009. Living with dams: Managing the environmental impacts. **Water Policy** 11(S1): 121-139. DOI: 10.2166/wp.2009. 108.

Meksumpun, C. 2020. **Reservoir Hydro-Ecology for Conservative Management.** Faculty of Fisheries, Kasetsart University, Bangkok, Thailand. 302 pp.

Miranda, L.E., R.V. Granzotti and D.J. Dembkowski. 2019. Gradients in fish feeding guilds along a reservoir cascade. **Aquatic Sciences** 81: 15. DOI: 10.1007/s00027-018-0615-y.

Nakazawa, T., Y. Sakai, C. Hsieh, T. Koitabashi, I. Tayasu, N. Yamamura and N. Okuda. 2010. Is the relationship between body size and trophic niche position time-invariant in a predatory fish? First stable isotope evidence. **PLoS ONE** 5(2): e9120. DOI: 10.1371/journal.pone.0009120.

Nelson, J.S. 2006. **Fishes of the World,** 4th ed. John Wiley and Sons, Inc., New Jersey, USA. 601 pp.

Novakowski, G.C., N.S. Hahn and R. Fugi. 2008. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. **Neotropical Ichthyology** 6(4): 567-576. DOI: 10.1590/S1679-62252008000400004.

Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs and H. Wagner. 2020. **Vegan: Community ecology package. R package version 2.5-7.** https://CRAN.R-project.org/package= vegan. Cited 10 Jan 2021.

Pettit-Wade, H., K.W. Wellband, D.D. Heath and A.T. Fisk. 2015. Niche plasticity in invasive fishes in the Great Lakes. **Biological Invasions** 17: 2565-2580. DOI: 10.1007/ s10530-015-0894-3.

Pianka, E.R. 1973. The structure of lizard communities. **Annual Review of Ecology and Systematics** 4: 53-77. DOI: 10.1146/ annurev.es.04.110173.000413.

Quirino, B.A., N. Carniatto, R. Guglielmetti and R. Fugi. 2017. Changes in diet and niche breadth of a small fish species in response to the flood pulse in a Neotropical floodplain lake. **Limnologica** 62: 126-131. DOI: 10.1016/j.limno.2016.10.005.

R Core Team. 2021. **R: A language and environment for statistical computing.** R Foundation for Statistical Computing [Computer software] Vienna, Austria. https://www.R-project.org. Cited 10 Dec 2021.

Saowakoon, S., K. Saowakoon, A. Jutagate, M. Hiroki, M. Fukushima and T. Jutagate, 2021. Growth and feeding behavior of fishes in organic rice-fish systems with various species combinations. **Aquaculture Reports** 20: 100663. DOI: 10.1016/j.aqrep. 2021.100663.

Sá-Oliveira, J.C., R. Angelini and V.J. Isaac-Nahum. 2014. Diet and niche breadth and overlap in fish communities within the area affected by an Amazonian reservoir (Amapa, Brazil). **Anais da Academia Brasileira de Ciências** 86: 383-405.

Seanghong, S., P. Phomikong, C. Grudpan and T. Jutagate. 2021. Fish diversity, habitat preference and assemblage patterns during the dry season in the upper Petchaburi River, Thailand. **Journal of Fisheries and Environment** 45(3): 100-111.

Suriani-Affonso, A.L., R.S. França, M. Marchese and O. Rocha. 2011. Environmental factors and benthic Oligochaeta (Annelida, Clitellata) assemblages in a stretch of the Upper São Francisco River (Minas Gerais State, Brazil). **Brazilian Journal of Biology** 71(2): 437-446. DOI: 10.1590/s1519-69842011000300013.

Vehanen, T., J. Jurvelius and M. Lahti. 2005. Habitat utilisation by fish community in a short-term regulated river reservoir. **Hydrobiologia** 545(1): 257-270. DOI: 10.1007/s10750-005-3318-z.

Welcomme, R.L., K.O. Winemiller and I.G. Cowx. 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. **River Research and Applications** 22(3): 377-396. DOI: 10.1002/rra.914.

Winemiller, K.O. and D.B. Jepsen. 1998. Effects of seasonality and fish movement on tropical river food webs. **Journal of Fish Biology** 53: 267-296. DOI: 10.1111/j.1095-8649.1998.tb01032.x.

Wolff, L.L., N. Carniatto and N.S. Hahn. 2013. Longitudinal use of feeding resources and distribution of fish trophic guilds in a coastal Atlantic stream, southern Brazil. **Neotropical Ichthyology** 11(2): 375-386. DOI: 10.1590/S1679-62252013005000005.