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Morphology and Niche Partitioning of Fish Assemblage in the Tonle Sap Biosphere Reserve - a Case Study of the Prek Toal Core Area

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Abbreviations

PCA:	Principal component analysis
TSBR:	Tonle Sap Biosphere Reserve
FP:	Floodplains or stagnant waters
RC:	River channels or flowing waters

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Declaration

I, ____, acknowledge that the research embodied in this paper is entirely my own work, that where the ideas of others have been used the sources have been duly acknowledged, and that no portion of this research has been submitted for grading at The School for Field Studies or Hollins University.

Signed:

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Lan Thi Ngoc Nguyen Date

Abstract

A morphological approach provides vital information on community structure and ecological adjustments among different species that occupy in the same habitat. The coexistence of competing species in a diverse community results in niche partitioning in order to increase stabilization. Tonle Sap Biosphere Reserve, one of the world's most productive inland wetlands is a tropical river ecosystem so dynamic that supports high biodiversity, especially fish population. This study tests the relationship between morphology and niche partitioning to understand the coexistence of diverse fish assemblages in the Tonle Sap Biosphere Reserve. By measuring 31 morphological variables and gathering ecological data of the collected 27 fish species, this study applies principal component analysis and cluster analysis to examine the influence of morphology on the ecological niches of the fish assemblage. The results of the study demonstrate that the diversifications in morphological characters directly determine niche partitioning of the fish assemblage in the Prek Toal core area of the Tonle Sap Biosphere Reserve.

Key words: ecomorphology, morphometrics, multivariate analysis, niche partitioning, Tonle Sap Biosphere Reserve, Prek Toal.

Introduction

Ecological morphology or ecomorphology involves the study of the link between form and function of an organism and serves as a tool to examine the ecological correlates of morphological variations in the organization of communities (Norton et al 1995). A morphological approach is an effective indicator to infer ecological roles based on theories in functional morphology and evolutionary adaptions to natural selective pressures (Losos and Miles 1974; Wainwright 1996). Wainwright (1996) emphasized the importance of morphology in shaping performance of an organism, which can influence its survival. As morphology can determine the behavior or capability of taxa to function with simple procedures and straightforward applications, ecomorphology has been commonly utilized to infer ecological relationships of biological communities. Preceding studies that used ecomorphological approach provided crucial understanding of many phylogenetic groups, such as bats (Aguirre et al 2002), fossil mice and rats (Kimura et al 2013), lizards (Losos 1990), birds (MacArthur 1958; Hutchinson 1959; Ricklefs 1977; Ricklefs and Travis 1980), and fishes (Gatz 1979; Wikramanayake 1990; Winemiller 1991; Norton and Brainerd 1993; Wainwright 1996). Many ecological aspects can be interpreted based on analysis of different morphological features. For example, analysis in tooth enamel of fossil rodents can reveal the dietary composition and habitat inhabitation (Kimura et al 2013). Mouth size and jaw of fish can limit prey capture and consumption capacity (Carlson 2009). Findings of fish assemblage from Oliveira et al (2010) demonstrated that piscivores and insectivores in lentic habitats have compressed bodies and well developed anal fins. Diversity in morphology, hence, correlates to the adaptations of species as a result saturated habitats to utilize different resources.

The concept of niche partitioning illustrates the adjustments of competing species in seeking different food and habitat use to coexist within a habitat. Classical theories behind this concept explain niche segregation as a result of limiting similarity among competing species in order to stabilize diverse communities (MacArthur 1958; Hutchinson 1959; MacArthur and Levins 1967; Schoener 1974; Gatz 1979). The evidence of niche differentiation in birds and mammals that hold high diversity after examining the length of the culmen in birds and the skull length in mammals was found in Hutchinson (1959). A conclusion was made that niche partitioning resulted from competition pressures that made closely-related warbler species to divide up a niche to coexist (MacArthur 1958).

The relationship between ecomorphology and niche partitioning is conspicuous, since previous analysis in segregation of niches by Hutchinson (1959) and Gatz (1979) involved the use of morphological patterns. On the other hand, the ecomorphological studies mentioned above have been used to infer ecological niches, either feeding ecology or habitat use. A study on niche partitioning of tropical lizard species articulated that species within the same group of feeding behavior had correlates of morphological adaptations (Vitt and Carvalho 1995). An attempt to relate differences in morphology to niche partitioning among fruit-eating birds was made (Ricklefs 1977). Due to a high variety of morphological structures, fish are critical to studying this relationship and exploring community patterns (Helfman et al 2009, as cited in Pessanha et al 2015). In particular, tropical fish assemblages have high diversity in size and shape that allow different species to utilize various niches; therefore, it is essential to examine species interactions through morphological features in the tropical regions (Winemiller 1992). A strong relationship between the chosen morphological features and microhabitat use was proved by the research on tropical stream fish assemblage in Sri Lanka (Wikramanayake 1990). A study on certain geophagine genera claimed that piscivores prefer to occupy a distinct group of morphospace that is characterized by elongated and shallow heads with only marginally protrusible mouths (Lopez-Fernandez et al 2012). Niche partitioning in relation to species distributions within morphological, habitat, and feeding ecology space was consistently affirmed through recent studies (Cochran-Biederman and Winemiller 2010; Oliveira et al 2010; Correa and Winemiller 2014; Pessanha et al 2015).

Tropical river floodplain ecosystems are ideal study sites to test niche partitioning by examining diverse fish assemblages because of regular changes in water levels and food resource (Correa and Winemiller 2014). The flood pulse system and seasonal hydrology of the Tonle Sap Biosphere Reserve (TSBR), one of the world's most productive inland waters, enables this extensive wetland to hold large freshwater biodiversity (Campbell et al 2006, and Cooperman et al 2012). As mentioned in Lamberts (2001), the seasonal variation in the Tonle Sap creates a dynamic exchange in nutrients, minerals, sediments, and biotic interactions between aquatic and terrestrial ecosystems, which can support a wide range of niches among fish populations (Lamberts 2001). The lake plays an important role as a major spawning ground for migratory fish populations in the Mekong River system (Hortle 2007, as cited by Cooperman et al 2012). Essentiality of the Tonle Sap fishery to the economies and livelihoods of people is emphasized in Lamberts (2001), Campbell et al (2006), Enomoto and Ishikawa (2011), and Berdik (2014). Despite its vital roles, the ecosystems and livelihoods of people on the Tonle Sap Lake are facing tremendous challenges, including harmful fishing practices, increasing population, increasing migration to the lake, deforestation, construction of hydroelectric dams upstream, and climate change (Berdik 2014; Campbell et al 2006; Cooperman et al 2012). The knowledge of fish ecology in the lake is still lacking and poorly understood (Lamberts 2001; Davidson 2006; Campbell 2006; Cooperman et al 2012). Although some research initiatives have included bird monitoring and economical assessment of this fishery, there is a research gap in fish ecology, particularly fish morphology, in relation to ecological niches within the inundated forest, a rich spawning and feeding ground for many species (Lieng and van Zalinge 2001, as cited in Davidson 2006).

To better understand the mechanisms that support coexistence of diverse fish assemblage in the tropical floodplain ecosystem, this study tests the hypothesis of the correlation between morphological patterns and niche partitioning of fish assemblage in the Prek Toal core area of TSBR. Specifically, two main hypotheses are tested: whether morphology determines niche partitioning among fish assemblage in Prek Toal and what morphological features strongly influence niche differentiation. Measures of morphological features of the fish collected and identified along with descriptions of feeding ecology and habitat type of each species were analyzed to test their relationship. The result of this study can be used as an implication for fishery management and biodiversity conservation.

Methods

Study Site. The data collection process took place in Prek Toal, one of the core areas of the Tonle Sap Biosphere Reserve. The Prek Toal core area is the forth Ramsar Site in Cambodia (Sun 2015; Sunleang 2011). Prek Toal is the largest remaining colony of globally-endangered and near threatened waterbird species and contains one of the most primitive floodplain habitats in the TSBR (Sunleang 2011). Prek Toal's fishery is the most productive site on the lake (Davidson 2006).

Located at the north-western edge of the Tonle Sap, Prek Toal was about 40km southwest of Siem Reap town, including parts of Ek Phnom and Sangkab Districts in Battambang Province. The study site was designated at the edge of a flooded forest in the Prek Da stream, which meanders through the flooded forest of the core area of Prek Toal (Figure 1). The vegetation on both sides of the stream was comprised of three different layers: dense mats of water hyacinths and other herbaceous floating vegetation, stands of shrubs, and medium-sized trees. Because Prek Toal lies within the floodplain of the Tonle Sap Lake, its hydrological regime is influenced directly by the climate of the wet-dry tropics and fluctuations of the lake as well as the Mekong River flow. The mean temperatures range from 20°C to 36°C; the amount of the rainfall is mainly concentrated between April and November (Campbell 2006). Hence, there are two main seasons, the wet and the dry season, primarily characterized by the precipitation patterns. During the dry season, forest covers the majority of the area; only the major streams, ponds, and creek systems contain water permanently. The area during this period is notable for its seasonally inundated swamp forest, grasslands, and mosaic shrubland. On the contrary, the rainy season creates complete coverage of water throughout the whole area, with the existence of floating vegetation and flooded forests (Davidson 2006, Sunleang 2011).

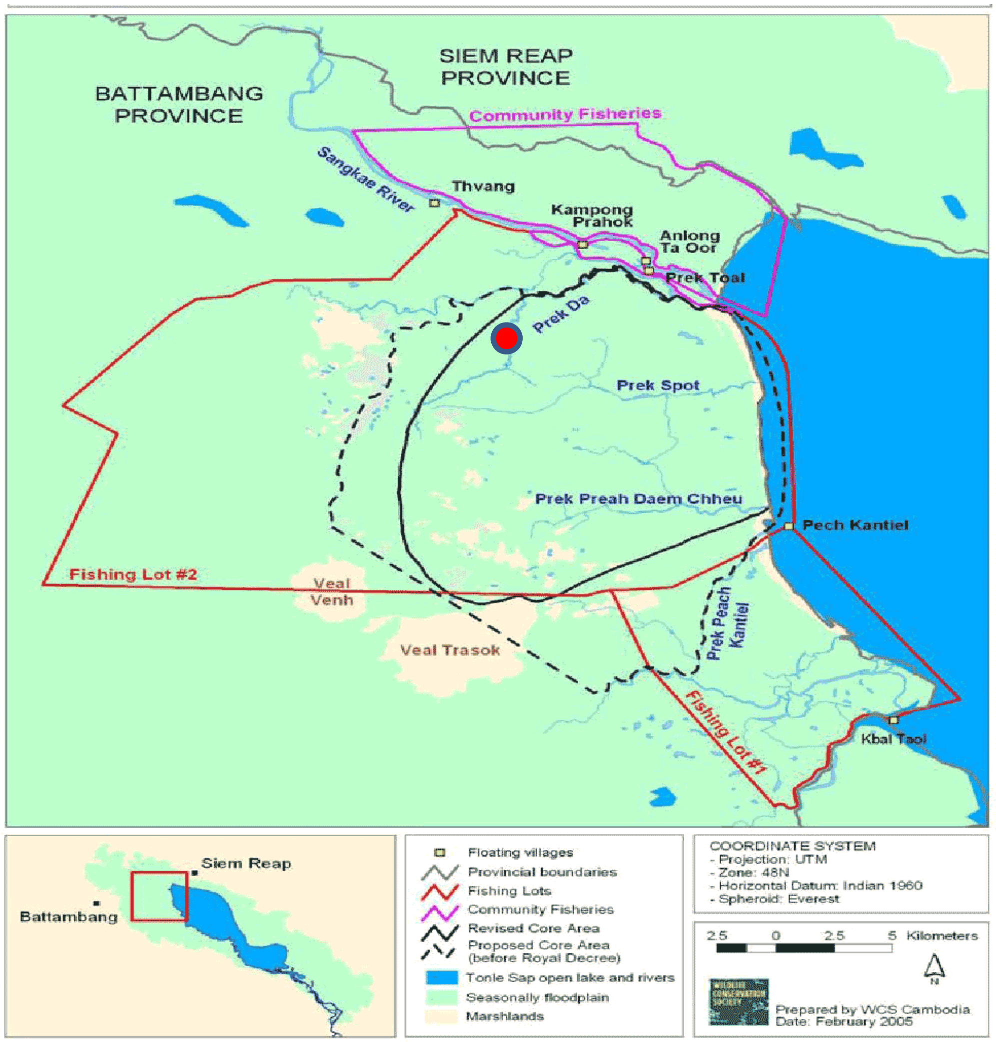

Figure 1: A map of the location of the study site (red dot) in the Prek Toal core area (adapted from Osmose 2006).

Sampling Methods. Fish were surveyed during the beginning of the dry season, from November 18 to November 28. The climate condition of this year is not usual: having a little rain during the wet season with an extension of rainfall to the beginning of the dry season. The water level of the lake this year is very low compared to the last ten years. At the edge of a flooded forest in the Prek Da stream, four to six 70-m-long gill nets of 1m width with mesh sizes of 2cm and 2.5cm were put out every day, and were left in the water overnight. The fish assemblage was sorted by hand and identified to species level. For each species identified, the three largest individuals were chosen as adult representatives to be measured and recorded with 31 morphological characters. A caliper, measuring tape, scalpel, and scissors were used to dissect stomach contents and measure specimens to the nearest 1.0 mm.

Morphometrics. Thirty-one morphological features of the fish sorted by hand and identified were measured and recorded based on the findings in Case (2015) and morphometrics in Winemiller's paper (1991). Distance measurements are recorded as the straight-line space between points, as presented in Winemiller's study (1991). Following are the codes of all 31 morphological features used in this study:

1. Maximum standard length (MSL) – the distance from the tip of the snout to the tip of the caudal fin;
2. Maximum body depth (BODD) – maximum vertical distance from dorsum to ventrum;
3. Maximum body width (BODW) – maximum horizontal distance from side to side;
4. Caudal peduncle length (PEDL) – distance from the posterior proximal margin of anal fin to the caudal margin of the ultimate vertebra;
5. Caudal peduncle depth (PEDD) – minimum vertical distance from dorsum to ventrum of the caudal peduncle;
6. Caudal peduncle width (PEDW) – width of the caudal peduncle in horizontal plane at mid-length;
7. Body depth below midline (BDBM) – vertical distance from midline to ventrum, midline defined as the imaginary line passing from the pupil of the eye through to the center of the ultimate vertebra;
8. Head length (HEAL) – distance from tip of the upper jaw to the most-caudal extension of the operculum;
9. Head depth (HEAD) – vertical distance from dorsal to ventral passing through the pupil;
10. Eye position (EYEP) – vertical distance from the center of pupil to ventrum;
11. Eye diameter (EYED) – horizontal distance from eye margin to eye margin;
12. Mouth position (MOUP) – coded as 1 for superior (imaginary vertical plane tangent to both upper and lower jaws with mouth closed between 10-80 degrees), coded as 2 for terminal (tangent plane at approximately 90 degrees), and coded as 3 for inferior (tangent plane between 100-180 degrees);

13. Mouth width (MOUW) – horizontal distance measured inside of fully open mouth at widest point;
14. Mouth height (MOUH) – vertical distance measured inside of fully open mouth at tallest point;
15. Snout length shut (SNTL) – distance from the pupil of the eye to tip of the upper jaw with mouth shut;
16. Snout length open (SNTO) – distance from the pupil of the eye to tip of the upper jaw with mouth fully open and extended;
17. Dorsal fin height (DORH) – maximum distance from proximal to distal margin of the dorsal fin;
18. Dorsal fin length (DORL) – distance from anterior proximal margin to posterior proximal margin of the dorsal fin
19. Pectoral fin height (PECH) – maximum vertical distance across the fully spread pectoral fin;
20. Pectoral fin length (PECL) – maximum distance from proximal to distal margin of the pectoral fin;
21. Caudal fin height (CAUH) – maximum vertical distance across the fully spread caudal fin;
22. Caudal fin length (CAUL) – maximum distance from proximal to distal margin of the caudal fin (excluding filaments);
23. Pelvic fin height (PELVH) – maximum vertical distance across the fully spread pelvic fin;
24. Pelvic fin length (PELVL) – maximum distance from proximal to distal margin of the pelvic fin;
25. Anal fin height (ANAH) – maximum distance from proximal to distal margin of the anal fin;
26. Anal fin length (ANAL) – distance from anterior proximal margin to posterior margin of the anal fin;
27. Pigment code (PIGM) – coded as 0 for transparent, 1 for silvery/reflective, 2 for silvery with dark lateral stripe or spots, 3 for uniform light coloration with

countershading, 4 for lateral or vertical bars with background countershading, 5 for mottled, densely spotted, or uniform dark with countershading, and 6 for black;

28. Tooth shape (TSHA) – coded as 0 for absent, 1 for unicuspid (rasping), 2 for multicuspid (crushing), 3 for short conical (grasping), 4 for long conical (piercing), 5 for triangular serrated (shearing), 6 for tooth combination of 3 and 4 (2 types of teeth), and 7 for beak-like;
29. Gill raker (GRAK) – coded as 0 for absent, 1 for short, blunt, or tooth-like (*help food digestion → mostly predators)*, 2 for intermediate or long and sparse, 3 for long and comb-like, and 4 for short and tiny;
30. Gut length (GRAK) – measured from the beginning of the esophagus to anus (fully extended without stretching);
31. Swim bladder length (SWBL) – maximum straight line distance from anterior to posterior margins.

Classifications of trophic groups, habitat types, and migration patterns. Based on FishBase (www.fishbase.org), the Encyclopedia of Life, and FAO species identification field guide for the Cambodian Mekong (Rainboth 1996), feeding ecology, habitat, and migration patterns of each species were recorded into various categories to analyze the relationships between morphology, resource use, and habitat use of fish assemblages at Prek Toal. Because some information of certain species were not available on those resources above, previous research of those fish species was used to complete the data analysis (Hamid et al 2014). Due to the fact that some individuals of certain species collected did not reach their maturation stage (adult size), some classifications were made based on their juvenile stages.

For resource use, fish were divided into five trophic groups including algaevore, herbivore, insectivore, omnivore, and piscivore (Lanoue 2014). Algaevores are fish species consuming mostly algae and phytoplankton. Herbivores are fish that mostly consume plant matter, plant roots, and fruits. Insectivores are fish that eat insects, crustaceans, mollusks, invertebrates, worms, and zooplankton. Omnivores are defined as fish feeding on insects, invertebrates, plants, and other fish. Piscivore are fish that consume other fish.

Regarding habitat use, the main habitat that each fish species spends most of their life time in was categorized into two main groups: floodplains or stagnant waters (FP) and river channels or flowing waters (RC). Fish that seasonally migrate into flooded forests and floodplains during the rainy season, for spawning purposes, or live in a standing or slow moving environment belong to the habitat type of FP. Fish species found in fast-flowing large rivers, streams, and channels were grouped into RC.

Migration patterns of each species were grouped into one of three categories: lateral, longitudinal, and residential (Brill 2015). Fish classified into the lateral group migrate laterally in and out of the floodplains that are next to the lake based on the water level. Longitudinal fish migrate upstream or downstream in rivers or streams. Fish that stay in the same general area and do not utilize any migration behavior are put into the residential group.

Data analysis. Morphological measurements of all the individuals within each species were averaged. All the linear distance measures for each species were then converted to ratios to serve as components of body, head, and fin shape, based on the methods in Winemiller's paper (1991). Calculated ratios as morphological features indices was chosen to analyze the data from size-independent dimensions of shape and ensure equal variances prior to use in comparisons among all the species collected (Winemiller 1991). Thus, this method can also reduce the dominance of a single variable like body size. Regarding components of the body, body length was entered as SL; body depth (BODD) was used as the denominator for PEDD, BDBM, HEAD, and MOUTH; body width (BODW) was the denominator for PEDW and MOUW. In terms of head components, head length (HEAL) was the denominator for EYED and SNTL, and head depth (HEAD) was the denominator for EYEP. Relative mouth protrusibility (MOUPO) was the outcome of the division of SNTO by SNTL. All other distance measures including BODD, BODW, PEDL, HEAL, DORH, DORL, PECL, PECH, CAUL, CAUH, PELVL, PELVH, ANAH, ANAL, GUTL, and SWBL were divided by SL. MSL, MOUP, PIGM, TSHA, and GRAK were the remaining features that were kept as their original data. For the variables containing ratios equal to zero, all the ratios under those variables were added one to be qualified for logarithm transformations. This study applied logarithm transformations before running the statistical test to normalize the measures.

The relationships between morphological features and feeding ecology and habitat type were tested by conducting principal component analysis (PCA). A code name given for each species was recorded. Each feeding ecology group was given a symbol: square for algaevore, triangle for herbivore, dot for insectivore, plus for omnivore, and diamond for piscivore. For habitat categories, red was given for the FP group and blue for the RC group. Eigenvalues and variance percentages of the first two components of the PCA test were recorded, along with the eigenvalues of 31 morphological variables. A classical cluster analysis was run on the same software to examine the similarity among the fish assemblage in terms of ecological niche. Past 3.10 statistic software was used to conduct all the statistical analysis (Hammer et al 2001).

Results

The fish assemblage collected in the Prek Toal core area was comprised of 27 species, 13 families, and 7 orders (Table 1). Cypriniformes order consisted of only Cyprinidae family, but contained the highest number of species. The order that held the second highest number of species belonged to Perciformes, in which six families were recorded. In contrast, Osteoglossiformes, Beloniformes, Synbranchiformes, and Tetraodontiformes had only one family with one species that were collected in this fish assemblage. At the family level, Notopteridae, Chandidae, and Tetraodontidae were the families in which one species was found. Cyprinidae was the largest group with 11 species collected. Both Siluridae and Belontiidae were comprised of three species. Within the fish assemblage collected, both adult and juvenile individuals were chosen to represent their species.

Morphological relationships. The first two principal components (PC1 and PC2) conveyed 60.72% of the total variation in morphological space within the data set of 27 species. The first component explained the highest proportion of the variation (39.73%), which almost doubled the variation explained by the second component (20.99%). The eigenvalue of PC1 was highest 0.38, which is higher than PC2’s eigenvalue at 0.20. Eigenvectors of the log-transformed morphological variables on the PC axis showed that gut length (GUTL) and caudal peduncle width (PEDW) had the highest positive values on PC1, while the highest negative scores on PC1 were associated with tooth shape (TSHA) and pigmentation pattern (PIGM) (Table 2, Figure 2). High scores on PC2 were positively associated with anal fin length (ANAL) and body depth (BODD) while mouth height (MOUH) and swim bladder length (SWBL) had the highest negative scores (Table 2, Figure 2).

Table 1: The taxonomic information of the fish assemblage along with given code names of the abbreviated versions of each species.

	Order	Family	Species	Code
1	**Osteoglossiformes**	**Notopteridae**	Notopterus notopterus	N.n
2	**Cypriniformes**	**Cyprinidae**	Paralaubuca typus	P.t
3	Cypriniformes	Cyprinidae	Rasbora aurotaenia	R.a
4	Cypriniformes	Cyprinidae	Cyclocheilichthys apogon	C.a
5	Cypriniformes	Cyprinidae	Hypsibarbus lagleri	H.l
6	Cypriniformes	Cyprinidae	Hampala macrolepidota	H.m
7	Cypriniformes	Cyprinidae	Puntius brevis	P.b
8	Cypriniformes	Cyprinidae	Puntius leiacanthus	P.l
9	Cypriniformes	Cyprinidae	Thynnichthys Thynnoides	Th.t
10	Cypriniformes	Cyprinidae	Dangila spilopleura	D.s
11	Cypriniformes	Cyprinidae	Henicorhynchus siamensis	H.s
12	Cypriniformes	Cyprinidae	Osteochilus hasselti	O.h
13	**Siluriformes**	**Bagridae**	Mystus multiradiatus	M.m
14	Siluriformes	**Siluridae**	Micronema apogon	M.a
15	Siluriformes	Siluridae	Ompok bimaculatus	O.b
16	Siluriformes	Siluridae	Ompok eugeneiatus	O.e
17	**Beloniformes**	**Belonidae**	Xenentodon cancila	X.c
18	**Synbranchiformes**	**Mastacembelidae**	Macrognathus siamensis	M.s
19	**Perciformes**	**Chandidae**	Ambassis kopsi	A.k
20	Perciformes	**Toxotidae**	Toxotes microlepis	To.m
21	Perciformes	**Nandidae**	Pristolepis fasciata	P.f
22	Perciformes	**Anabantidae**	Anabas testudineus	A.t
23	Perciformes	**Belontiidae**	Trichogaster microlepis	Tr.m
24	Perciformes	Belontiidae	Trichogaster pectoralis	Tr.p
25	Perciformes	Belontiidae	Trichogaster trichopterus	Tr.t
26	Perciformes	**Channidae**	Channa striata	C.s
27	**Tetraodontiformes**	**Tetraodontidae**	Monotreta fangi	M.f

Table 2: Variable loadings of 31 morphological features from principal component analysis of 27 fish species in the fish assemblage. Eigenvectors between -0.20 and 0.20 are listed only as positive and negative signs.

	PC 1	PC 2
MSL	-	-
BODD	0.2003	0.2681
BODW	+	+
PEDL	+	-
PEDD	+	-
PEDW	0.22205	-0.2569
BDBM	-	-
HEAL	+	-
HEAD	-	-
EYEP	+	-
EYED	+	+
MOUPO	-	-
MOUW	-	-
MOUH	-0.2814	-0.40431
SNTL	-	-
SNTO	+	+
DORH	+	+
DORL	+	+
PECL	+	+
PECH	+	+
CAUL	+	+
CAUH	+	+
PELVL	+	+
PELVH	+	+
ANAH	+	+
ANAL	-0.36999	0.51757
PIGM	-0.32432	+
TSHA	-0.46009	+
GRAK	+	+
GUTL	0.40701	0.32995
SWBL	+	-0.31799

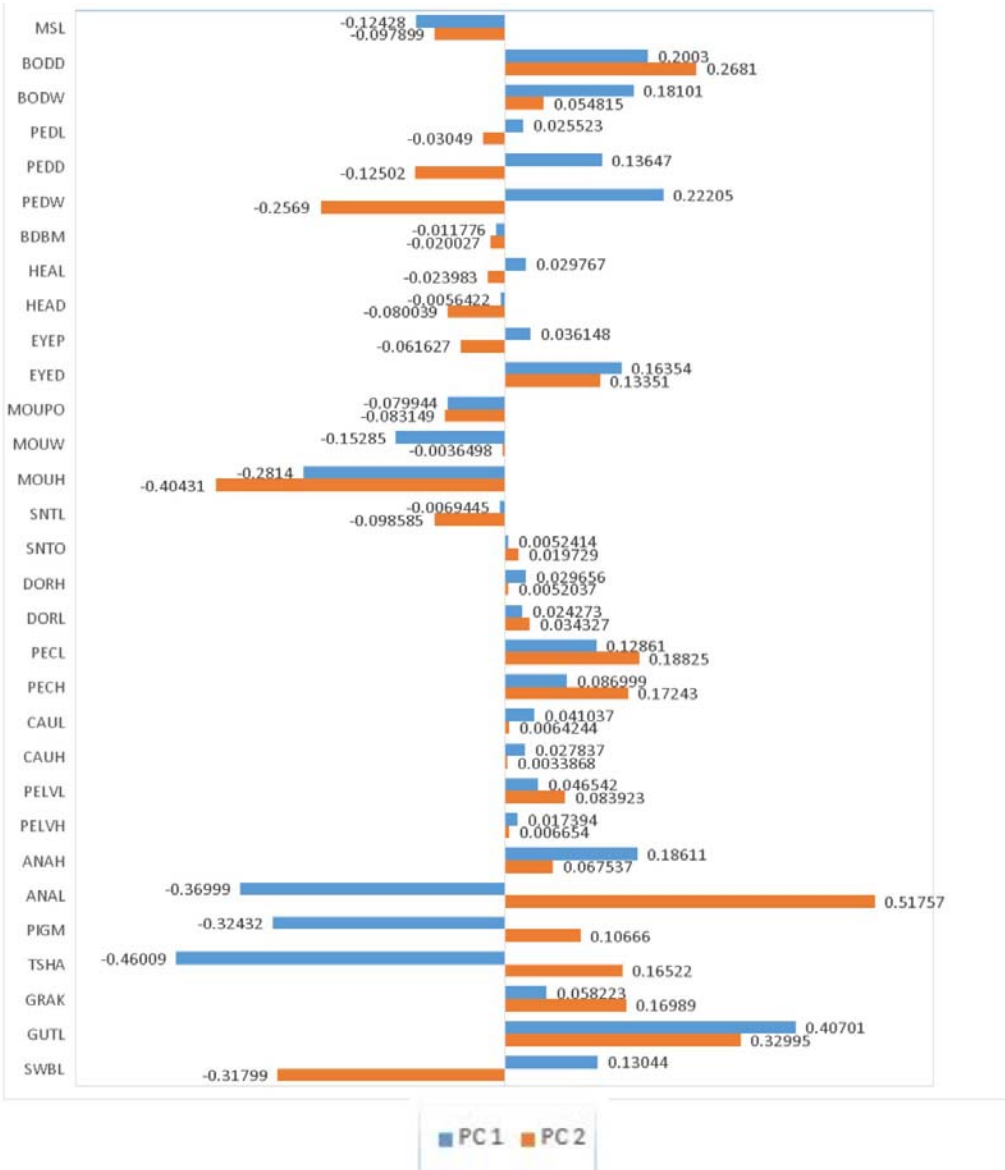

Figure 2: Factor loads from principal component analysis on 31 morphological attributes.

Species scoring positively high on the PC1 axis have long guts, wide caudal peduncles, unicuspid or absent teeth, and light pigmentation patterns, as represented by *Osteochilus hasselti*, *Dangila spilopleura, and Henicorhynchus siamensis* (Figure 3). The negative direction on the PC1 axis contained species with short guts, narrow caudal peduncles, predatory tooth shapes, and dark pigment, such as *Micronema apogon, Channa striata, Ompok bimaculatus, and Ompok eugeneiatus* (Figure 3). The group of fish with positive scores on the PC2 axis included species characterized by long anal fins, deep bodies, small mouth opening, and short swim bladders, for example, three species in genus *Trigchogaster* (Figure 3). The species that situated lowest on the

PC2 axis was *Xenentodon cancila* possess a short anal fins, a thin body, large mouth opening, and long swim bladders (Figure 3).

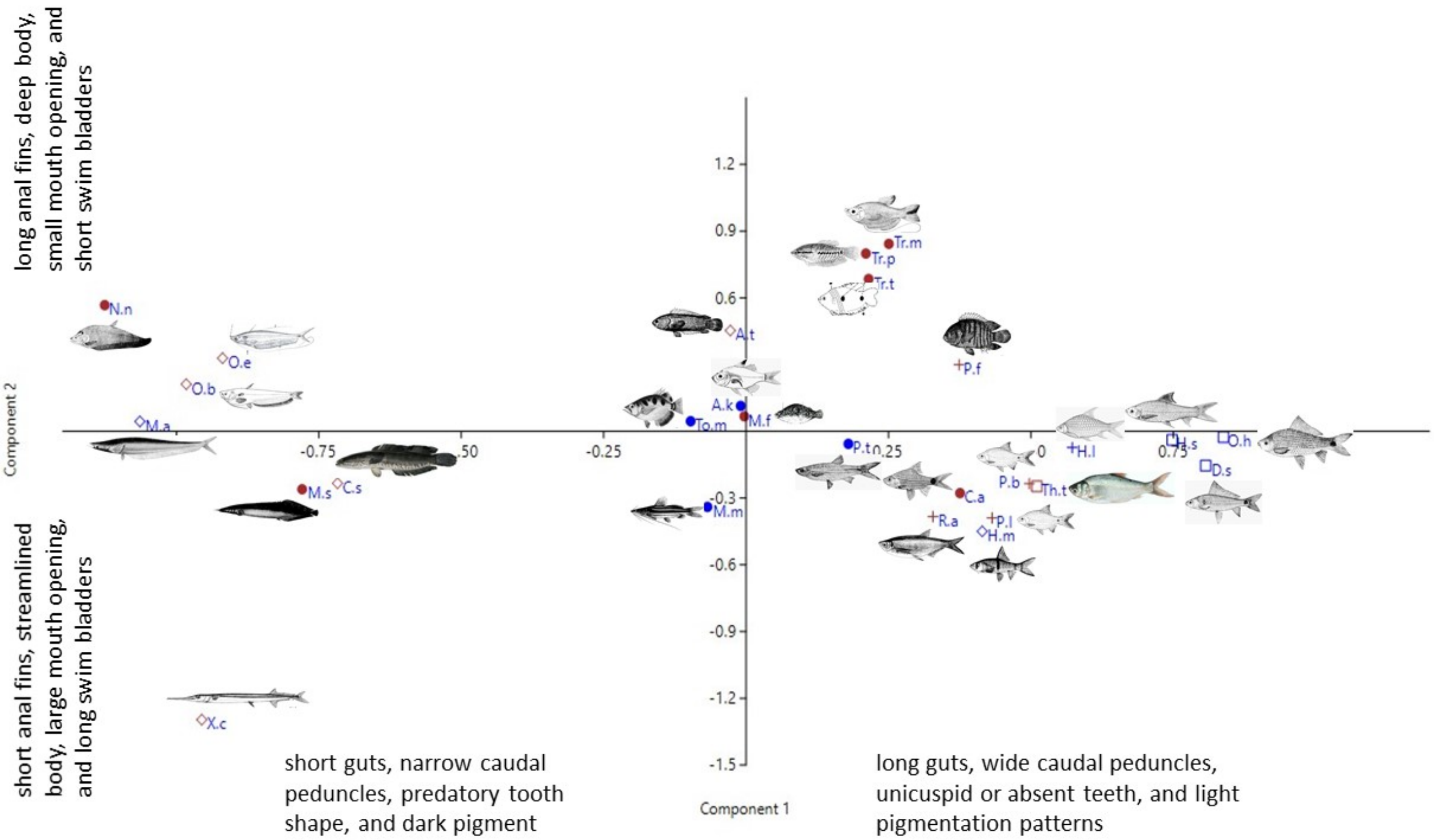

Figure 3: Ordination diagram from the first two components for the ecomorphological variables of 27 studied species. Squares are used to represent algaevores, dots for insectivores, plus for omnivores, and diamonds for piscivores. Brown color are fish in the FP.

The cluster analysis divided the fish assemblage into five main groups based on their morphological scores (Figure 4). The first group contained the fish species that have compressiform body shape: laterally flattened and deep bodied, long anal fins, unicuspid teeth, and a superior mouth position (Figure 4). All the species in this group belong to the order Perciformes. Species in the second group possess streamlined body shape or fusiform type, absent or unicuspid teeth, a superior mouth, light pigment, long and wide caudal peduncles, forked caudal fins, and long swim bladders (Figure 4). Except for *Mystus multiradiatus*, the other fish species of the second group are *Cyprinidae*. The third group belonged to one species

Monotreta fangi, which has a globiform body shape and beak-like tooth shape that make it stand out from the rest of the studied fish assemblage (Figure 3). The forth group consisted of mostly compressiform fish and one anguilliform fish, *Channa striata* (Figure 4). They have a predatory tooth shape, superior and terminal mouth position, long anal fins, short guts, and dark pigment. The fifth group included two species *Macrognathuus siamensis* and *Xenentodon cancila*, which have anguilliform and sagittiform respectively (Figure 4). These two species have predatory teeth, long snouts, short guts, long anal fins, short dorsal and pectoral fins, long swim bladder, and dark pigmentation patterns. *Macrognathus siamensis* has an inferior mouth position while *Xenentodon cancila*'s mouth position is terminal.

Ecological characteristics. Data gathered from other sources about feeding ecology, habitat type, and migration patterns were recorded for 27 studied species (Figure 2, Table 3). There were no herbivores recorded in this fish assemblage. Species in the same group of feeding ecology were close together on the PC axes (Figure 2). The three species scoring highest on PC1 were all algaevores (Figure 2). In the positive direction of PC1, all four species of omnivores were grouped together, while insectivores were mainly distributed close to the origin or middle of the PC1 axis except two species *Notopterus notopterus* and *Macrognathus siamensis* (Figure 2). All the piscivores except *Hampala macrolepidota* had negative scores on PC1. Most of the species with positive scores on PC2 are categorized into the habitat group of floodplain or standing waters (FP). All species that have longitudinal migration patterns had positive scores on PC1 while species in the residential group were on the other extreme of the PC1 axis.

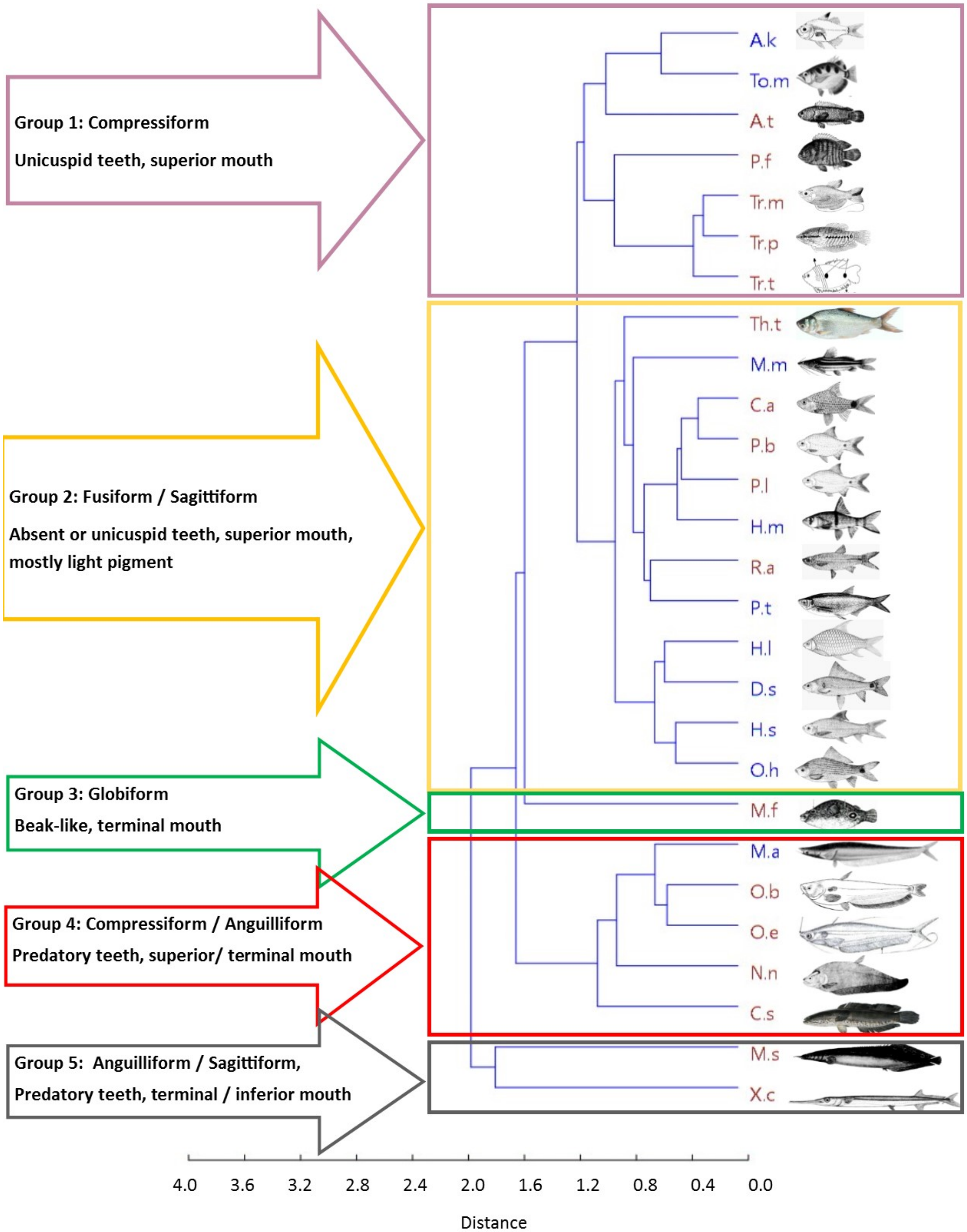

Figure 4: Dendrogram from cluster analysis for ecomorphological features of 27 fish species

Table 3: Feeding ecology, habitat type, and migration patterns of the fish assemblage.

Species	Code	Feeding ecology	Habitat type	Migration pattern
Notopterus notopterus	N.n	insectivore	FP	lateral
Paralaubuca typus	P.t	insectivore	RC	lateral
Rasbora aurotaenia	R.a	omnivore	FP	lateral
Cyclocheilichthys apogon	C.a	insectivore	FP	lateral
Hypsibarbus lagleri	H.l	omnivore	RC	longitudinal
Hampala macrolepidota	H.m	piscivore	RC	longitudinal
Puntius brevis	P.b	omnivore	FP	lateral
Puntius leiacanthus	P.l	omnivore	FP	lateral
Thynnichthys Thynnoides	Th.t	algaevore	FP	lateral
Dangila spilopleura	D.s	algaevore	RC	lateral
Henicorhynchus siamensis	H.s	algaevore	RC	longitudinal
Osteochilus hasselti	O.h	algaevore	RC	lateral
Mystus multiradiatus	M.m	insectivore	RC	lateral
Micronema apogon	M.a	Piscivore	RC	lateral
Ompok bimaculatus	O.b	piscivore	FP	lateral
Ompok eugeneiatus	O.e	piscivore	FP	lateral
Xenentodon cancila	X.c	piscivore	FP	residential
Macrognathus siamensis	M.s	insectivore	FP	lateral
Ambassis kopsi	A.k	insectivore	RC	longitudinal
Toxotes microlepis	To.m	insectivore	RC	lateral
Pristolepis fasciata	P.f	Omnivore	FP	lateral
Anabas testudineus	A.t	Piscivore	FP	residential
Trichogaster microlepis	Tr.m	insectivore	FP	lateral
Trichogaster pectoralis	Tr.p	insectivore	FP	lateral
Trichogaster trichopterus	Tr.t	insectivore	FP	lateral
Channa striata	C.s	piscivore	FP	residential
Monotreta fangi	M.f	insectivore	FP	lateral

Discussion

The hypothesis of the relationship between morphology and niche partitioning was accepted in this case study in the Prek Toal core area. Species within the studied fish assemblage were grouped together by their similarities in morphology and niche segregation, including trophic groups, habitat types, and migratory behaviors. The PCA analysis validated the theory suggested by ecomorphological studies that morphological characters are correlated to feeding ecology and habitat use (Losos and Miles 1974; Ricklefs 1977; Gatz 1979; Webb 1984). The cluster analysis exhibited evidence of niche partitioning within a structurally diverse community of fish assemblage to therefore support stable coexistence of competing species (MacArthur 1958; Hutchinson 1959).

The result of the PCA test illustrated that gut length, tooth shape, and mouth height strongly determine the distribution of species according to their trophic groups. Meanwhile, anal fin length, body depth, caudal peduncle width, pigmentation pattern, and swim bladder length are predictors of different habitat occupations and migration patterns. As trophic groups and habitat occupation are niche components, niche partitioning was examined based on the abovementioned morphological features.

The principal component results split the fish assemblage into different groups with comparable morphological characters mostly attributed to feeding ecology. All four algaevores were grouped together since characters with long guts and absent teeth all belong to this tropic group, while six piscivorous species congregated together into a distinct guild with short guts for digestive efficiency and predatory tooth shape (conical or triangular serrated) for prey capture. These findings were mentioned in other studies on fish of tropical systems (Wikramayake 1990; Winemiller 1991; Cochran-Bieder & Winemiller 2010). Omnivorous species were also grouped together, separate from insectivores. *Notopterus notopterus* and *Macrognathus siamensis* are two exceptional cases of insectivores that evolve to have predatory tooth shape, and were therefore grouped closer to the piscivorous species. *Hampala macrolepidota* is classified into the piscivore group; however, there is a case in West Java that has a diet of aquatic insects (FishBase 2015). Thus, this species was closer to the algaevore group with long guts. Additionally, the division by the first principal component implied the differentiation among the fish assemblage in habitat preference, migratory characters, and foraging behavior. Light pigmentation and wide, developed caudal peduncles are associated with species that prefer lotic or semi-lotic environments like river channels and often migrate for medium to long distances (Oliveira et al 2010; Welcomme 1985). In contrast, dark pigmentation and narrow caudal peduncles characterized species that inhabit stagnant waters or residual pools of floodplains (Welcomme 1985).

The findings of PCA analysis indicated the distribution of species, mainly according to habitat difference reflected from anal fin length, body depth, and swim bladder. Long anal fins and deep bodies facilitate maneuverability and agility of species, as seen in the genus *Trichogaster*, and inhabit low-velocity, structurally complex habitats like floodplains (Gatz 1979; Webb 1984; Winemiller 1991; Norton & Brainerd 1993; Oliveira et al 2010). Species with short swim bladders do not require long movements that necessitate of buoyancy and oxygen (Hall 1924). On the other hand, the distributions of carps and peacock eels together were associated with short anal fins, streamlined bodies, and long swim bladders, which imply their preference for flowing waters, like streams and river channels, and their migratory patterns (Webb 1984; Pessanha et al 2015). One morphological feature that strongly determined the separation of this fish assemblage was mouth height. Possession of a large mouth gape relates to piscivorous species' ability to capture large prey, as represented by *Xenentodon cancila* with the largest mouth height ratio in this study (Wikramanayake 1990; Norton & Brainerd 1993; Cochran-Bieder & Winemiller 2010).

The dendrogram generated by the cluster analysis conveyed niche partitioning through the coexistence of different fish species with five different body shapes. The morphological distribution also illustrated the diversifications of the collected fish species in tooth shape and mouth orientation, to exhibit where they feed at various relative water-column depth. The morphological features of the first group with compressiform body shape, laterally flattened and deep bodied, long anal fins, and superior mouth indicate their precise turning, lateral maneuverability, and foraging behavior at the water surface in slow flowing water (Webb 1984; Wikramanayake 1990; Winemiller 1991; Norton & Brainerd 1993). Most of species in the first group are insectivores and have unicuspid teeth for rasping. An exceptional case in the first group is the appearance of the piscivore *Anabas testudineus*, which actually shares a similar habitat in stagnant waters. The fusiform group was categorized by its streamlined body shape that enables them to increase thrust in order to sustain swimming for migration or predation (Webb 1984; Wikramanayke 1990; Pease et al 2015). This group contains mostly fish with silvery pigment, which is an indicator of long migration (Welcomme 1985). A superior mouth with absent or unicuspid teeth indicates surface foraging behavior. Although *Mystus multiradius* was included in this group because its morphology and ecology overlap with the first and the second group, at a shorter Euclidian distance this species actually fit in the middle of these two groups. The group that contained only one puffer fish *Monotreta fangi* is a specialized group with its globiform body shape and beak-like tooth shape. The puffer fish group of *Tetraodontidae* family is distinctive from the other groups by its inflatability as a natural defense to make up for its slow swimming and its fused teeth for crushing the shells of mollusks and crustaceans (FishBase 2015). The major characteristics of the forth group, compressiform as well as one anguilliform body shape, along with predatory teeth and dark pigment, can support piscivores and insectivores, like *Notopterus Notopterus*, that prefer lentic habitat (Oliveira et al 2010). Most of the species in the fourth group are black fish, with an overall dark pigmentation pattern, and possess residential or lateral migration patterns. The five species in this group feed from the middle to the surface level of the water column because of their mix of terminal and superior mouth positions. The fifth group consists of two predators that have sagittiform, elongated bodies (freshwater garfish) and anguilliform bodies (peacock eel), and common predatory characteristics with long snouts and large gape size (Cochran-Bieder & Winemiller 2010). These two predators with their terminal and inferior mouth positions seek food resource from the middle to the bottom of the water.

Besides the relationship between morphology and ecological niches, the distribution of this fish assemblage on the dendrogram also reflects the influence of phylogeny on morphological space. All the species in the first group belonged to the Perciformes order. Apart from *Mystus multiradius*, all species from the fusiform group were Cypriniformes. The forth group was represented mostly by Siluriformes order. Even though two species from the fifth group did not belong to the same order, they were still closest together in terms of morphology. It is crucial to acknowledge that this finding is not a part of this study's conclusion, as phylogeny might influence morphological traits. Instead, this study emphasizes the vital roles of ecological processes in shaping the community structure without disregarding the phylogenetic factor, as illustrated in Winemiller (1991), Lopez Fernandez et al (2012), and Oliveira et al (2010).

The strong correlation between morphology and niche partitioning found in this case study is consistent with preceding studies in fish communities. The hypothesis of adaptive divergence in key functional morphological traits was articulated in recent morphological studies, including an examination of neotropical cichlidae by Cochran-Bieder & Winemiller (2010) and a study on associations between functional traits and environmental factors in Central Texas by Pease et al (2015). Particularly, this study in Prek Toal ascertains the vital role of morphological approaches in studying fish assemblage in tropical ecosystems, like the Amazonian floodplain forests in Correa &Winemiller (2014) and the tropical estuarine in Brazil studies in Pessanha et al (2015). The notion that specializations in feeding behavior and microhabitat utilization can be observed through morphological diversification was embraced by an intercontinental comparison among lowland freshwater fish assemblages (Winemiller 1991; Norton and Brainerd 1993). In a study on the fish assemblage in a Sri Lankan stream, morphological features were found to diversify as adaptations to support resource partitioning and minimize interspecific competition (Wikramanayake 1990). The evidence of niche partitioning within the morphologically diverse community in this study has contributed to the correlation between morphological traits and ecological niches, which has been accepted not only in fish, but also to other taxa of vertebrates (Vitt and Carvalho 1995; Losos 1990; Travis & Ricklefs 1983).

Conclusion

The evidence of the association between the morphological and ecological distribution of the fish assemblage as well as the coexistence of different fish species proved the hypothesis of the relationship between morphology and niche partitioning. In a diverse community in a tropical freshwater ecosystem like the Tonle Sap Biosphere Reserve, morphological features can reflect niche partitioning within the community. The results of this study can be used in discussing distributions of fish populations, which can support better decision on fishing practice and management. The study also conveys the efficiency of morphological approaches in studying biodiversity through its direct implications and simple methods. It is possible to further apply this method to gather ecological data in the TSBR, one of the most productive inland fisheries in the world, to advocate a growing body of ecological research in biodiversity on the lake. Scientific research can serve as an essential tool to save a hotspot like the Tonle Sap Biosphere Reserve from current threats including overfishing, increasing population, and hydropower construction.

Some of the limitations of this study involved that fact that some species had only one individual that was collected due to a short time period of this study. Some individuals are still at the juvenile stages, not fully developed to their maturity. Their morphological features may influence the result. There is a possibility of data error or lack of adult representatives. The low water level of the lake this year along with the unusual scattered rain at the beginning of the dry season is an important factor that can affect the results of this study.

Seasonal hydrology plays an important role in altering the availability of resources and biological and ecological interactions. This case study was conducted during a short time period of the low-water season, when food is least available for fish populations in TSBR. Examining niche partitioning and morphological diversification throughout a full annual cycle would be ideally more conclusive.

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Appendix

List of 27 species with their common names and the average 31 original morphological measurements for each species.

Species	Notopterus notopterus	Paralaubuca typus	Rasbora aurotaenia	Cyclocheilichthys apogon	Hypsibarbus lagleri	Hampala macrolepidota
Code	N.n	P.t	R.a	C.a	H.l	H.m
Common name	Bronze featherback	Paralaubuca	Pale rasbora	Beardless barb	Yellow Eyed Silver Barb	Hampala barb
Khmer name	Trey slat	Trey slak russey	Trey changwa mool	Trey srakardam	Trey chhpin	Trey Khman
# Individual	#1	#3	#3	#1	#1	#1
MSL (mm)	96	83.66666667	75.33333333	67	74	81
BODD	25	24.33333333	16.16666667	22	26	25
BODW	7	9.333333333	11	10	11	12
PEDL	0	7	12.66666667	9	9	12
PEDD	4	8.333333333	9.333333333	8	10	10
PEDW	0.5	3.333333333	3.5	3	3	4
BDBM	12.5	12.33333333	8.166666667	11	13	13
HEAL	21	17	19	19	19	25
HEAD	14	12.66666667	10	13	15	16
EYEP	7	6.333333333	4.666666667	7	7	11
EYED	5	5.166666667	5.166666667	5	6	6
MOUPO	2	1	1	1	1	1
MOUW	5	4.666666667	5.5	5	5	7
MOUH	10	9	8.333333333	7	7	13
SNTL	5	6	6.5	7	5	9
SNTO	6	9	9.333333333	8	7	12
DORH	12	11.66666667	8.333333333	16	19	18
DORL	2.5	5	6.833333333	10	10	13
PECL	14	20.66666667	13	14	14	14
PECH	3	5	3.666666667	3	3	5
CAUL	0	18.66666667	17.66666667	16	20	21
CAUH	0	13	8.833333333	11	13	18
PELVL	0	9.666666667	10	14	13	14
PELVH	0	2.333333333	3	4	4	6
ANAH	7	8.333333333	8	10	10	12
ANAL	79	19.66666667	6.333333333	9	10	8
PIGM	5	1	2	2	2	2
TSHA	6	0	0	0	0	0
GRAK	2	1	2	1	1	1
GUTL	80	103.3333333	107	80	250	130
SWBL	5	10.33333333	8.833333333	20	22	28

Species	Puntius brevis	Puntius leiacanthus	Thynnichthys Thynnoides	Dangila spilopleura	Henicorhynchus siamensis	Osteochilus hasselti
Code	P.b	P.l	Th.t	D.p	H.s	O.h
Common name	Swamp barb	Swamp barb	Tiny scale barb	Long-finned barb	Siamese mud carp	silver sharkminnow
Khmer name	Trey angkat prak	Trey angkat prak	Trey linh	Trey ach kok	Trey riel	Trey kros
# Individual	#3	#1	#2	#3	#3	#3
MSL (mm)	69	62	71.5	71.66666667	81.66666667	79.66666667
BODD	24.66666667	22	18.5	18.66666667	22.33333333	25.33333333
BODW	10.33333333	8	10.5	9.666666667	12.66666667	12.66666667
PEDL	10.33333333	11	11.5	10	12.33333333	11
PEDD	10	8	8.25	7.333333333	9	10
PEDW	3.333333333	3	3.5	3	4	3.666666667
BDBM	12.33333333	9	9.5	9.333333333	11	12.66666667
HEAL	18	17	16.5	17	18.5	19.66666667
HEAD	15	15	11.5	11.33333333	14	15.33333333
EYEP	6.666666667	8	7	6.333333333	6.333333333	8.333333333
EYED	5.666666667	5	5	5	5	5.333333333
MOUPO	1	1	1	1	2	1
MOUW	5	6	4.5	5	4.5	5.5
MOUH	7	8	6	5.333333333	5.666666667	6.333333333
SNTL	7	7	7.25	5.666666667	7	8
SNTO	8	10	8.25	6.666666667	9	10.33333333
DORH	16	11	13.25	13.33333333	18.33333333	13.66666667
DORL	14.66666667	12	10.5	33	13.33333333	25.66666667
PECL	13.33333333	11	12	14	15	15.66666667
PECH	3.333333333	2	3.25	4	4	3.666666667
CAUL	19.66666667	17	14.75	19.33333333	20.66666667	24
CAUH	12	9	10.5	9	11.66666667	11.66666667
PELVL	12.33333333	12	10.5	13.66666667	12.66666667	15.66666667
PELVH	3.666666667	3	4.25	3.666666667	3.333333333	5
ANAH	9	9	8	11.66666667	12.66666667	13.66666667
ANAL	7.333333333	7	6	5.666666667	7	7.333333333
PIGM	2	2	1	2	1	2
TSHA	0	0	0	0	0	0
GRAK	2	2	0	1	4	4
GUTL	105.6666667	90	211.5	546	510	593.3333333
SWBL	19.66666667	27	7.5	26.33333333	16	29

Species	Mystus multiradiatus	Micronema apogon	Ompok bimaculatus	Ompok eugeneiatus	Xenentodon cancila	Macrognathus siamensis
Code	M.m	M.a	O.b	O.e	X.c	M.s
Common name	Bagrid catfish	Sheatfish	butter catfish	Malay glass catfish	Freshwater garfish	Peacock eel
Khmer name	Trey kanchos chhnoht	Trey kes	Trey krormorm	Trey ta aun	Trey phtoung	Trey chhlonh chhnoht
# Individual	#4	#1	#2	#1	#3	#2
MSL (mm)	85.25	110	126	75	136.6666667	157.5
BODD	20.625	17	28	15	9	18
BODW	12.25	7	12	6	8.666666667	10.5
PEDL	12.625	4	4.5	1	5	1
PEDD	9.25	4	6.5	4	3.666666667	2
PEDW	3.625	1	1.5	1	2.333333333	0.5
BDBM	11	8	14	7	5.333333333	9.5
HEAL	23.75	25	24.5	14	56.33333333	25.5
HEAD	12.75	10	15.5	8	8.666666667	8.5
EYEP	4.875	3	7.25	2.5	5	6
EYED	4.875	4	4.5	3	5	2.75
MOUPO	2	1	1	1	2	3
MOUW	9	11	13.5	6	4.333333333	3.5
MOUH	9.5	13	14.5	10	36.66666667	6
SNTL	8.25	9	9.5	5	39.66666667	13
SNTO	8.875	12	14	7	40.33333333	13
DORH	16.75	0	16	10	6.333333333	7.5
DORL	11.375	0	1.25	0.5	13.66666667	80
PECL	16.25	15	21	12	10.66666667	10.5
PECH	3.875	4	7.5	4	2.333333333	4
CAUL	21.25	12	16	11	14.33333333	5
CAUH	13.375	5	6.5	7	7.666666667	2
PELVL	13.5	7	8.5	3	6	0
PELVH	3.75	2	3.5	1	1.333333333	0
ANAH	9.5	8	10.5	9	11	6
ANAL	10.5	65.5	68.5	47	17.33333333	57
PIGM	4	3	5	4	3	6
TSHA	1	6	6	6	3	1
GRAK	3	2	2	2	0	0
GUTL	67.5	115	85.5	77	88	149
SWBL	15.75	25	18	6	44	45

Species	Ambassis kopsii	Toxotes microlepis	Pristolepis fasciata	Anabas testudineus	Trichogaster microlepis
Code	A.k	To.m	P.f	A.t	Tr.m
Common name	Singapore Glassy Perchlet	Smallscale archerfish	Malayan leaffish	Climbing perch	Moonlight gourami
Khmer name	N/a	Trey kancheak sla	Trey kantrob	Trey kranh srai	Trey kamphlaenh
# Individual	#2	#1	#1	#3	#2
MSL (mm)	46	63	70	69.66666667	65.5
BODD	20	27	37	26.66666667	28
BODW	7	11	14	14.66666667	8.5
PEDL	5	3	4	3.333333333	0.5
PEDD	5	7	12	10.5	7.5
PEDW	2	2	2	1.833333333	1.25
BDBM	10	13	19	13.66666667	13.5
HEAL	22	22	27	24	19
HEAD	13	18	22	17	14
EYEP	8	10	14	7.666666667	6.5
EYED	6	7	7	6.333333333	5.5
MOUPO	1	1	1	1	1
MOUW	7	7	8	7.666666667	3.5
MOUH	11	16	10	11.33333333	5
SNTL	7	8	8	6.333333333	7.5
SNTO	9	11	9	9	9
DORH	6	12	18	10.33333333	10.5
DORL	19	20	43	181	9
PECL	13	17	20	16.33333333	18
PECH	3	4	6	5.333333333	3.75
CAUL	15	15	20	17	18.5
CAUH	14	13	12	12	10
PELVL	11	11	17	12.66666667	85.5
PELVH	3	3	4	4	0.75
ANAH	12	12	14	9.333333333	9
ANAL	11	20	15	27.33333333	40.5
PIGM	0	4	5	5	1
TSHA	1	1	1	1	1
GRAK	3	2	1	1	2
GUTL	40	48	245	143.3333333	457.5
SWBL	5	15	24	5	8

Species	Trichogaster pectoralis	Trichogaster trichopterus	Channa striata	Monotreta fangi
Code	Tr.p	Tr.t	C.s	M.f
Common name	Shakeskin gourami	Three-spot gourami	Striped snakehead	Buffer fish
Khmer name	Trey kawnthor	Trey kawmphleanh samrai	Trey phtouk	Trey kampot
# Individual	#5	#1	#1	#1
MSL (mm)	70.4	63.25	120	51
BODD	29	23.75	18	21
BODW	8.8	8	15	17
PEDL	0	0	12	7
PEDD	9	7.75	9	6
PEDW	1.4	1	3.5	5
BDBM	14	13.125	11	12
HEAL	21.2	16.75	37	17
HEAD	16.4	14.25	14	13
EYEP	7.6	6.25	8	8
EYED	5.7	4.625	6	4
MOUPO	1	1	1	2
MOUW	3.8	2.75	12	7
MOUH	5	4	20	4
SNTL	8.5	6.125	9	6
SNTO	9.5	7.5	11	6
DORH	10.8	8.75	10	4.5
DORL	13.1	12	67	3.5
PECL	18.9	15.5	21	5
PECH	3.6	3.25	7	6
CAUL	18.6	15.875	22	11
CAUH	10.4	9	9	5
PELVL	32.2	36	14	0
PELVH	0.4	0.5	3	0
ANAH	10.2	7.25	9	3
ANAL	44.6	31.75	43	3.5
PIGM	2	2	6	5
TSHA	1	1	5	7
GRAK	2	2	1	1
GUTL	440.4	337.3333	140	128
SWBL	7.4	10	34	9