Original Article

Morphology-based prediction of migratory degrees in cyprinids (Cyprinidae) in the Mekong Delta, Vietnam

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Abstract

Requiring relatively large space for migration makes cyprinids vulnerable to habitat alteration, hydropower dam construction, and climate change. Knowledge of migratory degrees of each species could help to assess potential impacts of regional development, especially dyke system construction in the Mekong Delta. In the present study, we tried to classify thirteen cyprinids into different migratory distance patterns using their morphological features. The morphological parameters, principal component analysis (PCA) and a dispersal model were employed for categorizing. Results show that the PCA and the dispersal model could group the cyprinid fishes into short-, moderate-, and long-distance migratory classes but the PCA could only explain 77.8% of variation in the data. The dispersal model could be a very helpful tool in migratory classification but in order to use its outputs (distances), further investigation is needed. From the analyses and reviewed data, the proposed list of migratory distance patterns was suggested. Our findings could be used in fisheries management and regional development planning, especially in the contexts of climate change and increasing construction of dyke systems in the Mekong Delta.

Keywords: migration distance, morphometrics, prediction, the Mekong Delta

1. Introduction

Located in the lowermost Mekong River, the Vietnamese Mekong Delta is known as one of the most biodiverse hotspots in the world, ranking twelfth in the world and second in the Mekong countries in terms of fish diversity (Baran *et al.*, 2012). Its aquatic resources play important roles in the regional economy and provide livelihoods for local people living under poverty line (Baran, Jantunen, & Kieok, 2007). However, recent years have witnessed drastic habitat alteration and fisheries resources degradation due to both anthropogenic and natural factors. For instance, expansion of rice fields and construction of dyke systems in the last 20

years have caused shrinking of remnant wetlands, which are important as breeding and feeding grounds of many fish species (Chea, Brosse, Lek, & Grenouillet, 2016; Huynh *et al.*, 2019; Nguyen, Dargusch, Moss, & Tran, 2016). The development of hydropower dams upstream has altered water regime (Ziv, Baran, Nam, Rodriguez-Iturbe, & Levin, 2012), reduced sediments flowing downstream (Baran, Guerin, & Nasielski, 2015), and blocked migration routes of many fishes (Baran, 2010), which could cause annual losses of 27,847 tons of white fish (long migratory species), 19,491 tons of grey fish (moderate migratory species) and 11,478 tons of black fish (non-migratory species) (Yoshida *et al.*, 2020). In addition, destructive fishing gears (small mesh size net, electric and chemical fishing), overfishing, and fishing in spawning grounds have put already over-fished resources under huge pressure (Baran *et al.*, 2007). In the recent years, the Mekong Delta has been experiencing strong impacts from climate change related issues such as saline intrusions, droughts, and

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other abnormal weather patterns (Research Program on Climate Change, Agriculture and Food Security – Southeast Asia [CGIAR-SEA], 2016; Apel, Khiem, Quan, & Toan, 2020), causing responses of the government in construction of dyke systems to prevent future impacts. These dyke systems fragment wetlands into many patches and cause corridor loss. Therefore, sustainable use together with good planning and management of fisheries resources are needed.

Among fish families, Cyprinidae is the most abundant family with approximately 2,420 species accounting for 8.9% of all living fish species and inhabiting mainly freshwater (Nelson, 2006). In the Mekong Basin, of 540 fish species collected, 216 were cyprinid fishes accounting for 40%. They are diverse in forms (carp-like, herring-like, or eel-like forms) and sizes (300 cm TL of *Catlocarpio siamensis*, 150 cm TL of *Ctenopharyngodon idella*, 1.3 cm TL of *Boraras micros*, or 4.0 cm TL of *Boraras urophthalmoides*) (Nagao Natural Environmental Foundation [NEF], 2021; Froese & Pauly, 2022). In the Mekong Delta, 46 species of this family have been recorded accounting for 13.5% of the total number of species. Most of them are seasonal migrators at different distance migration patterns. Typically, they migrate from the upstream to the Mekong Delta for feeding and/or breeding in flooding season, and return back to the upstream as water recedes (Poulsen & Valbo-Jørgensen, 2000; Tran *et al.*, 2013). As other fishes, cyprinids face risks of ecosystem degradation, especially for long-distance migration species. Determination of migration degrees of each species is an important step in building their life history traits and in fisheries management and conservation planning (Loury *et al.*, 2021).

The relationship between external morphology and swimming performance of fishes has long been studied and the swimming can be classified into several types including body and caudal fin (BCF) periodic, BCF transient, and appendage-based swimming modes (Webb, 1984; Blake, 2004). Examinations of these relationships have been investigated in many fish species, both in juvenile (Fisher, Bellwood, & Job, 2000; Fisher & Hogan, 2007; Nanami, 2007) and adult stages (Assumpção *et al.*, 2012a; Radinger & Wolter, 2014; Sambilay, 1990; Walker, Alfaro, Noble, & Fulton, 2013). These studies used typical morphological characteristics, e.g., body length, aspect ratio of the caudal fin, body fineness ratio, caudal peduncle depth factor, propulsion ratio, caudal fin length ratio, etc., in order to reveal swimming capability and/or predict the migratory traits (Assumpção *et al.*, 2012a; Radinger & Wolter, 2014). Among the morphological traits, body length, fineness ratio, and aspect ratio give an accurate prediction of the swimming performance. A recent study of Chea, Brosse, Lek, & Grenouillet (2021) predicted the ecological guilds (non-migratory, short-migratory, and long-migratory species) of the Mekong River fishes based on their external morphologies. However, the authors used only one individual for each species, which could fail to distinguish species with similar morphology and not be statistically sound. In the present study, we aimed to predict the migratory distance patterns of cyprinid fishes distributed in the Mekong Delta based on their external morphologies, which could be useful for fisheries management and planning, and impact assessments of dyke system construction on the region.

2. Materials and Methods

2.1 Data collection

Fish photos were retrieved from the project of "Basic study on the aquatic fauna and flora and conservation activities participated by local residents in the Mekong-Chao Phraya region", which was partly implemented by our team (College of Aquaculture and Fisheries, Can Tho University) (NEF, 2021; Tran *et al.*, 2013). The project aimed to i) investigate current status of fish diversity and distribution based on voucher specimens, ii) gain specimens and photos for scientific and educational purposes, and iii) develop human resources in ichthyological taxonomy. Therefore, fishes were carefully photographed with fins extended, and the photos were used for pictorial identification books. Thirteen cyprid fishes displaying well preserved morphological features and sufficient number of replicates were chosen for analyzing including: *Barbonymus gonionotus* (Bleeker, 1849) (N=22), *Crossocheilus reticulatus* (Fowler, 1934) (N=21), *Cyclocheilichthys enoplos* (Bleeker, 1849) (N=17), *Cyprinus rubrofuscus* Lacepède, 1803 (N=14), *Hampala macrolepidota* Kuhl & Van Hasselt, 1823 (N=15), *Henicorhynchus lobatus* (Fowler, 1934) (N=17), *Henicorhynchus siamensis* (Sauvage, 1881) (N=17), *Labiobarbus leptocheila* (Valenciennes, 1842) (N=17), *Labiobarbus siamensis* (Sauvage, 1881) (N=15), *Osteochilus vittatus* (Valenciennes, 1842) (N=16), *Puntioplites proctozystron* (Bleeker, 1865) (N=22), *Puntius brevis* (N=23), and *Puntius orphoides* (Bleeker, 1849) (N=20). Data on standard length (SL), total length (TL), body depth (BD), caudal peduncle depth (CPD), caudal fin height (CFH), caudal fin length (CFL), and caudal fin area (CFA) were measured using software ImageJ 1.51j8 (National Institutes of Health, USA). Specific measurements are given in Figure 1. Although many external variables have been employed for classification of the migratory guilds, the four most useful variables are fitness ratio (FR), aspect ratio of the caudal fin (AR), caudal fin length ratio (CFR), and caudal peduncle depth ratio (CPR). They are good indicators for migratory performance, especially when examination of species with similar morphology (Assumpção *et al.*, 2012a; Assumpção, Makrakis, Makrakis, & Piana, 2012b; Chea *et al.*, 2021; Walker *et al.*, 2013). Therefore, the four morphological ratios including FR (Blake, 2004, 2006; Webb, 1989), AR (Pauly, 1989; Sambilay, 1990), CFR (Nanami, 2007; Rouleau, Gle´met, & Magnan, 2010), and CPR (Webb & Weihs, 1986) were employed in this study. Details of calculation are given in Table 1.
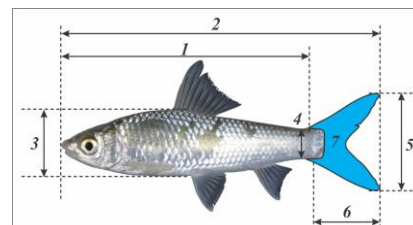
Symbols: 1 standard length; 2 total length; 3 body depth; 4 caudal peduncle depth; 5 caudal fin height; 6 caudal fin length; 7 caudal fin area. Photo(Henicorhynchus lobatus) was modified from Tran *et al.*, (2013) with permission.

Figure 1. Morphometric measurements related to swimming capability

2.2 Statistical analysis

In order to determine the differences in the morphometric ratios, FR, AR, CFR, and CPR were tested for normality and homogeneity of variance using Shapiro-Wilk and Levene's tests, respectively. Then, one-way ANOVA followed by post-hoc Tukey (normality and homogeneity of variance of data) or post-hoc Welch (normality and heterogeneous variance of data) tests or Kruskal-Wallis ANOVA followed by Wilcoxon-Mann-Whitney post-hoc tests (non-normal distribution of the data) were applied (Morgan, 2017). Principal component analysis (PCA) was applied for FR, AR, CFR, and CPR. Besides, in order to predict migration distance of each species, the dispersal model developed by Radinger (2015), synthesized from 71 studies covering 62 fish species, was applied. The input data for the model include the standard length, AR, stream order, time of migration, and cumulative probability (area under kernel) in which, standard lengths were retrieved from NEF (2021) and ARs were calculated in the present study. The stream order was set to 5 for all species based on geomorphology of the main rivers in the Mekong Delta (Google Maps, 2022; Strahler, 1975). The time of migration was set to be 150 days due to the flooding season in the Mekong Delta being from May or June to November (Hung *et al.*, 2012). The cumulative probability was set to default of 0.06, which means 6% of population moving to a certain distance as guided by Radinger (2015).

All statistical analyses were performed in Rstudio version 0.99.903 (Rstudio, Inc). The package "FactoMineR" (Lê, Josse, & Husson, 2008) and "factoextra" (Kassambara & Mundt, 2020) were employed to performed the PCA. The package "fishmove" was used for prediction of dispersal distance (Radinger, 2015) and the package "Rcmdr" (Fox, 2005; Fox & Boutchet-Valat, 2020) was used for the remaining analyses.

3. Results

Thirteen cyprinid fishes share similarities and differences in their morphometric characters. They all possess forked caudal fins with AR varying between 2.48 and 3.98. ARs in *Puntioplites proctozystron*, *Barbonymus gonionotus*, *Cyclocheilichthys enoplos*, and *Labiobarbus leptocheila* are significantly larger than those of the remaining species. The lowest AR value was found in *Cyprinus rubrofuscus* (Table 2). Regarding the body fineness ratio, *Puntius brevis*, *Cyprinus rubrofuscus*, *Barbonymus gonionotus*, and *Puntioplites proctozystron* have relative deep body with their FR values being lowest among the species, whereas the body form of *Crossmocheilus reticulatus* and *Henichorhynchus lobatus* is more elongated with large FR values (Table 2). The caudal fin length ratio slightly fluctuated among the species, increasing from *Cyprinus rubrofuscus* (0.20) and *Labiobarbus siamensis* (0.22) to *Henicorhynchus siamensis* (0.24) and *Puntioplites proctozystron* (0.25). The caudal peduncle depth ratio is significantly smallest in *Labiobarbus leptocheila*, *Barbonymus gonionotus*, and *Puntioplites proctozystron*, but largest in *Henicorhunchus lobatus* and *Crossocheilus reticulatus* (Table 2).

Figure 2 shows the principal component analysis of the four morphological variables. The first two components explain 77.8% of total variance. Among the variables, FR,

Table 1.   Morphometric ratios related to swimming performance

Morphometric ratio	Calculation	Description
Body fineness ratio (FR)	BD/SL	Body depth divided by standard length
Aspect ratio of the caudal fin (AR)	$(CFH)^2/CFA$	Squared caudal fin height divided by caudal fin area
Caudal fin length ratio (CFR)	CFL/TL	Caudal fin length divided by total length
Caudal peduncle depth ratio (CPR)	CPD/BD	Caudal peduncle depth divided by body depth

Table 2.   Morphometric ratios (mean ± SD) of the studied species

Species	N	AR	FR	CFR	CPR
Hampala macrolepidota	15	2.96 ± 0.44[bd]	3.21 ± 0.17[e]	0.22 ± 0.01[ab]	0.42 ± 0.02[e]
Cyclocheilichthys enoplos	17	3.24 ± 0.46[ab]	3.48 ± 0.28[b]	0.23 ± 0.03[bc]	0.40 ± 0.03[c]
Barbonymus gonionotus	22	3.54 ± 0.29[a]	2.34 ± 0.17[a]	0.23 ± 0.02[bc]	0.34 ± 0.02[a]
Osteochilus vittatus	16	2.94 ± 0.34[d]	2.81 ± 0.23[f]	0.23 ± 0.02[bc]	0.39 ± 0.02[bd]
Labiobarbus leptocheila	17	3.23 ± 0.33[ac]	3.38 ± 0.25[b]	0.22 ± 0.01[bc]	0.35 ± 0.03[a]
Cyprinus rubrofuscus	14	2.48 ± 0.27[cd]	2.61 ± 0.19[c]	0.20 ± 0.01[a]	0.37 ± 0.02[d]
Puntioplites proctozystron	22	3.98 ± 0.50[a]	2.08 ± 0.14[g]	0.25 ± 0.02[d]	0.31 ± 0.02[b]
Puntius orphoides	20	2.98 ± 0.40[b]	2.87 ± 0.17[f]	0.22 ± 0.01[b]	0.41 ± 0.02[g]
Labiobarbus siamensis	15	2.94 ± 0.37[b]	3.63 ± 0.22[bd]	0.22 ± 0.01[ab]	0.39 ± 0.03[bd]
Henicorhynchus siamensis	17	3.07 ± 0.41[bd]	3.46 ± 0.17[b]	0.24 ± 0.01[cd]	0.44 ± 0.02[e]
Crossocheilus reticulatus	21	2.81 ± 0.41[bc]	3.85 ± 0.30[h]	0.23 ± 0.02[bc]	0.48 ± 0.03[b]
Henicorhynchus lobatus	17	2.90 ± 0.33[b]	3.70 ± 0.23[d]	0.23 ± 0.01[bc]	0.45 ± 0.02[f]
Puntius brevis	23	2.81 ± 0.34[bd]	2.66 ± 0.12[c]	0.24 ± 0.02[cd]	0.40 ± 0.02[b]
One-way ANOVA or Kruskal-Wallis		$\chi^2 = 103.71$ $p < 0.001$	$\chi^2 = 208.86$ $p < 0.001$	F = 11.25 $p < 0.001$	F = 89.08 $P < 0.001$

One-way ANOVA followed by post-hoc Tukey test and Wilcoxon-Mann-Whitney were performed for CFR and CPR, respectively. Kruskal-Wallis followed by Wilcoxon-Mann-Whitney test were performed for the remaining morphometric ratios. All pairwise comparisons were applied Bonferroni-adjusted *p*-values. Data with different letters in respective columns are significant different ($p < 0.05$).
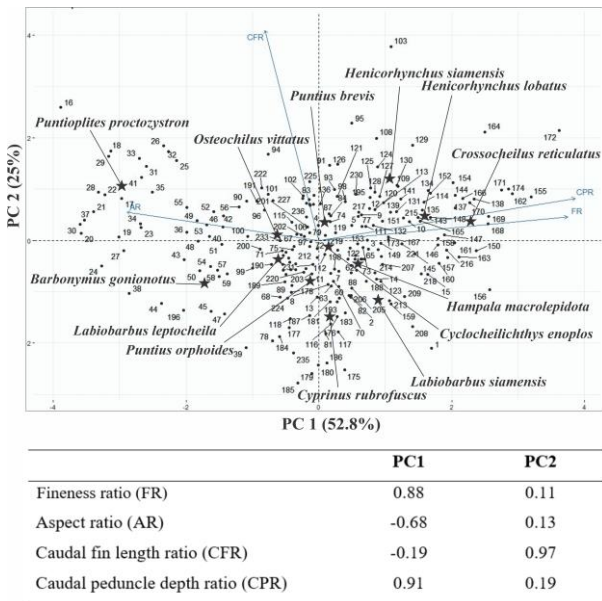
PCA bi-plot of the 1st and 2nd components showing the multivariate morphometric ordination (upper box). The external morphometrics are represented by vectors with correlated variables having similar orientation. Contribution of each variables along PC1 and PC2 is shown in the lower table. Symbols: 1-15 *Hampala macrolepidota*, 16-37 *Puntioplites proctozystron*, 38-59 *Barbonymus gonionotus*, 60-79 *Puntius orphoides*, 80-102 *Puntius brevis*, 103-119 *Cyclocheilichthys enoplos*, 120-136 *Henicorhynchus siamensis*, 137-153 *Henicorhynchus lobatus*, 154-174 *Crossocheilus reticulatus*, 175-188 *Cyprinus rubrofuscus*, 189-205 *Labiobarbus leptocheila*, 206-220 *Labiobarbus siamensis*, 221-236 *Osteochilus vittatus*.

Figure 2. PCA bi-plot of the 1st and 2nd components

	PC1	PC2
Fineness ratio (FR)	0.88	0.11
Aspect ratio (AR)	-0.68	0.13
Caudal fin length ratio (CFR)	-0.19	0.97
Caudal peduncle depth ratio (CPR)	0.91	0.19

CPR, and AR mainly contribute to the PC1 axis (lower table of Figure 2), along which *Puntioplites proctozystron* and *Barbonymus gonionotus* (high AR, low CPR and FR) are in one extremity of the axis, *Crossocheilus reticulatus*, *Henicorhynchus lobatus* and *Henicorhynchus lobatus* (low AR, high CPR and FR) are in the other extremity, and the remaining species are in between of these two groups. On the PC2 axis, among the morphometrics, CFR mainly contributes to the species distribution. *Cyprinus rubrofuscus* and *Labiobarbus siamensis* are separated along the PC2 by possession of low CFR, whereas *Henicorhunchus lobatus* is on the other side with high CFR.

Results from dispersal model classified thirteen species into migratory distance groups. Among the species, *Cyclocheilichthys enoplos* and *Hampala macrolepidota* were predicted to possess longest migratory distance (14,469 m and 13,875 m, respectively), followed by *Barbonymus gonionotus* (7,213 m) and *Puntioplites proctozystron* (5,565 m). *Puntius brevis*, *Crossocheilus reticulatus*, *Henicorhynchus lobatus*, and *Henicorhynchus siamensis* were classified as short- or non-migratory species. The remaining species fell into the middle-range migratory species with predicted distance ranging from 2,120 m to 4,829 m (Table 3).

4. Discussion

4.1 Form-function relationship in swimming performance

In general, fish external morphology is correlated to the swimming modes with body design following the rule of producing maximum thrust while minimizing drag (Webb,

1984), and therefore, some critical swimming morphometrics, i.e., the body fineness ratio (FR), the aspect ratio of the caudal fin (AR), and the caudal peduncle depth ratio (CPR), have been widely used in investigation of swimming performance (Blake, 2004; Sambilay, 1990; Videler & Wardle, 1991). Besides, other morphometrics, e.g., muscle ratio, propulsion ratio, caudal fin length ratio, caudal peduncle depth factor, pectoral fin length ratio, length from snout to pectoral fin base ratio, etc., have been also employed in recent studies (Assumpção *et al.*, 2012a; Assumpção, Makrakis, Makrakis, & Piana, 2012b; Chea *et al.*, 2021; Radinger & Wolter, 2014; Walker *et al.*, 2013). Although these morphological features have been proven very useful in prediction of swimming performance in various groups of fishes, some failed to predict swimming performance. For instance, body fineness ratio failed to predict swimming performance in reef fishes (Walker *et al.*, 2013), or the aspect ratio, caudal fin length ratio, propulsion ratio, and muscle ratio failed to distinguish similar morphology species (Assumpção *et al.*, 2012a). In the present study, employing the four morphometrics (FR, AR, CFR, and CPR) in the PCA could classify cyprinid fishes into different migration distance patterns. Short-distance migratory species have high FR, high CPR, and low AR (top right quantile of the biplot, Figure 2). The classification agrees with the model (Table 3) and the current knowledge of the migration capability (Table 4). Moderate-distance migratory group possesses high-to-moderate AR, and low-to-moderate CPR and FR (the two right quantiles of the biplot). The findings agree with many studies which have concluded the fitness ratio, caudal peduncle depth ratio, and caudal fin aspect ratio being the most important (Assumpção *et al.*, 2012a, 2012b; Chea *et al.*, 2021; Radinger & Wolter, 2014; Sambilay, 1990). The PCA failed to distinguish long-distance migratory species (*Hampala macrolepidota* and *Cyclocheilichthys enoplos*) from the moderate-distance group. This could be because their external morphology is similar, except for the body length. The longer-distance migratory species have longer body which provides more energy for swimming (Cano-Barbacil *et al.*, 2020; Videler & Wardle, 1991; Walker *et al.*, 2013). Therefore, besides the AR, FR, and CPR, as regards the prediction of migratory capability, the body length should be considered. In addition, the morphometrics not only serve swimming performance but also assist the feeding and predator-prey interaction. In fact, locomotion during foraging is influenced by spatiotemporal distribution and evasive degrees of prey. For instance, BCF swimmers hunting for food that are widely dispersed in space and/or time have body form enabling long-lasting swimming (Webb, 1984). In contrast, BCF transient species (consuming locally abundant evasive prey) and median and paired fin swimmers (hunting non-evasive food in complex habits) possess body forms of short- or non-migratory fish (Blake, 2004; Keast & Webb, 1966). In the present study, most of the assessed cyprinid fishes utilize small non-evasive food items (Table 4), except for *Hampala macrolepidota* hunting for large fish, and therefore, their body form may both serve for foraging food and migration.

Similarly, results from the dispersal model (Table 3) are in line with findings from the PCA and these data are summarized in Table 4. *Cyclocheilichthys enoplos* and *Hampala macrolepidota* were predicted as long-distance migratory species while *Henicorhynchus siamensis*,

Table 3.   Dispersal distance prediction of the studied species

Species	SL (mm)	AR	Dispersal distance (m)
Cyclocheilichthys enoplos	550	3.24	14,469
Hampala macrolepidota	600	2.96	13,875
Barbonymus gonionotus	300	3.54	7,213
Puntioplites proctozystron	210	3.98	5,565
Labiobarbus leptocheila	260	3.23	4,829
Osteochilus vittatus	270	2.94	4,302
Cyprinus rubrofuscus	280	2.48	3,505
Puntius orphoides	200	2.98	2,857
Labiobarbus siamensis	165	2.94	2,120
Henicorhynchus siamensis	120	3.07	1,443
Henicorhynchus lobatus	107	2.90	1,094
Crossocheilus reticulatus	109	2.81	1,085
Puntius brevis	80	2.81	698

Parameters used in the model include 150-day time of dispersal, 5 of the river levels, and probability of 6% population migrates to certain distance.

Table 4.   Migratory degrees and feeding habits of studied species

N	Species	Migratory characteristics	Feeding habits
1	*Hampala macrolepidota*	A migratory species (1); migrate into floodplain (2) or longitudinal migration into upstream (9) in the rainy season.	Piscivorous with large prey (1).
2	*Cyclocheilichthys enoplos*	One of long migration species of the Mekong River (4, 5, 6, 8); reported to migrate into floodplains for breeding (1).	Omnivorous with primary animal matter: bivalves, zooplankton, plant roots (1).
3	*Barbonymus gonionotus*	Lateral/middle-distance migratory species; usually migrate into floodplains in rainy season (1, 5, 6).	Omnivorous with primary plant matter: leaves, weeds, invertebrates (1).
4	*Osteochilus vittatus*	Lateral migration species; usually migrate into floodplains in rainy season (1, 2, 3).	Herbivorous: small plant matter (1).
5	*Labiobarbus leptocheila*	Lateral migration species; usually migrate into floodplains in rainy season (1, 3).	Omnivorous: phytoplankton, benthic algae, zooplankton (1).
6	*Cyprinus rubrofuscus*	Usually migrate into floodplains in the rainy season (1).	Detritivorous (10).
7	*Puntioplites proctozystron*	Lateral migration species; usually migrate into floodplains in the rainy season (1, 3).	Carnivorous: insects, zooplankton (1).
8	*Puntius orphoides*	Lateral migration species; migrate into floodplains for breeding in the rainy season (7).	Omnivorous: zooplankton, phytoplankton, detritus (11).
9	*Labiobarbus siamensis*	Migrate into floodplains for feeding in the rainy season (1).	Herbivorous: phytoplankton, benthic algae (1).
10	*Henicorhynchus siamensis*	Lateral migration species; usually migrate into floodplains in the rainy season (1, 5, 6).	Herbivorous: small plant matter (1).
11	*Crossocheilus reticulatus*	Lateral migration species; usually migrate into floodplains for feeding in the rainy season (1, 6).	Herbivorous: small plant matter (1).
12	*Henicorhynchus lobatus*	Lateral migration species (5, 6).	-
13	*Puntius brevis*	Lateral migration species; migrate into floodplains for breeding in the rainy season (1, 3).	Carnivorous: crustaceans, worms, zooplankton (1).

The table gives suggested order of migratory degrees from long-distance (*Hampala macrolepidota*) to short-distance (*Puntius brevis*) migration. (1) Froese & Pauly (2022); (2) Wongyai, Jutagate, Grudpan, & Jutagat, (2020); (3) Parr *et al*., (2014); (4) Phallavan & Bun (2000); (5) MRC (2005); (6) Poulsen & Valbo- Jørgensen (2000); (7) Termvidchakorn & Hortle (2013); (8) Baird & Flaherty (2004); (9) Makmur *et al*., (2021); (10) Collins *et al*., (2022); (11) Kakkaeo, Chittapalapong, & Villanueva, (2004).

Henicorhynchus lobatus, *Crossocheilus reticulatus*, and *Puntius brevis* were classified into the short-migratory group (Table 3). The two most important morphological features in the model are the standard length and aspect ratio of the caudal fin, which have been proven to strongly correlate with swimming speeds (Pauly, 1989; Radinger & Wolter, 2014; Sambilay, 1990). In this context, standard length is much more important because a larger body size (possession of higher energy) endows longer migratory distance compared to a smaller one with same morphometric ratios (Cano-Barbacil *et al.*, 2020). The dispersal model could be useful in classification of migratory degrees but may cause misleading migration distances. This could be because the migration distance is also largely dependent on the Mekong River flow (Binh *et al.*, 2020), and the distribution and intrinsic configurations of specific species (Radinger & Wolter, 2014; Videler, 1993; Webb, 1984). In addition, the model outputs are strongly influenced by input data such as river level, time of migration, fish morphology, and the cumulative probability (Radinger, 2015). Overall, from PCA, the dispersal model, and reviewed data in Table 4, we tentatively presume that *Hampala macrolepidota* and *Cyclocheilichthys enoplos* are

long-migratory species, *Barbonymus gonionotus*, *Osteochilus vittatus*, *Labiobarbus leptocheila*, *Cyprinus rubrofuscus*, *Puntioplites proctozystron*, *Puntius orphoides*, and *Labiobarbus siamensis* are middle-migratory species, and *Henicorhynchus siamensis*, *Crossocheilus reticulatus*, *Henicorhynchus lobatus*, and *Puntius brevis* are short-migratory species (Table 4).

4.2 Implications for fisheries management

Migration enables fish to use more than one habitat during their life cycle. In this context, each habitat is suitable for spawning, nursing, feeding, and/or over-dry season (Smith, 1991). In the Mekong River, cyprinids show two main migratory types including longitudinal (up- and down-stream migrations) and lateral (between streams and flooded riparian forest) migrations (Rainboth, 1991). Their migration is primarily triggered by water level, precipitation, water turbidity, and lunar phase (Mekong River Commission [MRC], 2007), and serves for spawning, feeding, and/or refuge (Smith, 1991). These migratory features make cyprinids vulnerable to habitat and hydrologic regime alterations (especially dam constriction and dyke system development), which blocks migration routes and depletes their critical habitats (Baird, Flaherty, & Phylavand, 2003; MRC, 2007). Therefore, one of the top priorities in migratory fish management is to determine migration distances and routes which ensure the protection of corridors and vital habitats in river basin development (Loury *et al.*, 2021). In the Mekong Delta, agriculture development in the last 20 years has dramatically altered wetland ecosystems through turning wetlands into rice fields (leaving only 1.7% of wetland area under protected) and building dyke systems (Nguyen *et al.*, 2016; Huynh *et al.*, 2019). Recent severe droughts and saline intrusions have caused development of dyke systems between main river and tributaries, which blocks remnant corridors and alters habitats (Apel *et al.*, 2020; CGIAR, 2016). Our findings could be useful in planning and operation of a dyke system in the region. Distinguishing migratory degrees could be used in impact assessment of certain dyke systems on this group of fish. In fact, the longer migration and the wider habitat required for a species, the more vulnerable that species is as it faces these conditions depleted (Kang & Huang, 2021; MRC, 2007). Additional data on environmental parameters triggering migration could be helpful in operation of the dyke gates. For instance, the dyke gates could be opened in certain times of the year providing vital corridors for cyprinids. Therefore, species listed as having long- and moderate-distance migratory degrees should have priority during planning, development, and operation of dyke systems in the region.

5. Conclusions

Employing morphological parameters and the dispersal model could classify cyprinids into different migratory distance patterns. However, the output of the models underestimated the migration distance of many species in the Mekong River. The proposed list of migratory distance guilds could be helpful in fisheries management and regional development planning.

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