


Communication

# Do Morphological Traits Predict Ecological Guilds of the Mekong Fish Fauna?

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**Abstract:** Southeast Asian riverine fishes are classified into three guilds ('black', 'white' and 'grey' species) based on their reproductive and migration strategies. In this study, we aimed to investigate whether fish morphology could be used to predict the Mekong fish guilds. Nine dimensionless ratios of fish morphological traits were used to describe the locomotion and food acquisition strategies of 121 fish species. The links between morphological traits and fish guilds were assessed using a principal component analysis (PCA) and a variance partitioning analysis, which revealed a strong morphological overlap between the guilds. Despite the high contribution of intra-guild variability to overall morphological variability (~90%), black and white fish significantly differed in terms of locomotion-related traits. Mekong fish guilds were satisfactorily predicted by using a random forest (RF) model, which produced a percentage of successful classification of ca 50% for each of the three guilds. Caudal propulsion efficiency, pectoral fin vertical position and body elongation were the most significant traits in the RF predictive model. Although the present study provides initial insight into the links between Mekong fish morphology and ecological guilds, further research is needed in order to clarify the relationship between species morphology, migratory status and responses to environmental variation.

**Keywords:** ecological guilds; fish migration; Mekong River; morphological traits; Tonle Sap Lake



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## 1. Introduction

The Mekong River Basin (MRB) is a biologically diverse and highly productive ecosystem, ranked third in the world in terms of fish diversity, just after the Amazon and Congo River Basins, with more than 850 freshwater fish species [1]. These species are classically clustered into three guilds according to their migratory habits called 'black', 'white' and 'grey' guilds [2,3]. White fishes are long-distance migrators, migrating along the Mekong mainstream or between the Mekong mainstream and Tonle Sap Lake in Cambodia, the largest flood pulse lake system in Southeast Asia [4]. Grey fishes are short-distance migrators, often migrating between the Tonle Sap Lake or the Mekong River and their floodplains or tributaries. Black fishes do not migrate and stay permanently in the same water body, such as lakes, ponds, rivers or paddy fields. A similar classification has been applied to the Amazonian fish fauna, in which Winemiller (1989) distinguished between sedentary, short-migratory and long-migratory species. Each of these three fish categories have different life history strategies sustained by distinct reproductive and morphological traits [5,6]. There is, however, no equivalent classification for the Mekong fish fauna, and the pronounced taxonomic, functional and ecological differences between Neotropical and Oriental faunas make the Amazonian migratory classification of Winemiller (1989) not applicable to the context of the Mekong fish fauna [7]. Currently, in the Mekong River, the white, black or

grey status of fish species is known for only 24% of fish fauna (165 species), and determining if such a classification is supported by morphological characteristics might help to extend this classification to the 76% of the species for which migratory status remains unknown [2,3,8]. Such findings would be of particular interest because the Mekong River currently faces major anthropogenic threats, such as overharvesting and fragmentation by dams, that might affect fish species differently according to their migration status [1].

Previous studies based on other river systems revealed significant links between fish morphology and their migration status, life history and functional groups [9]. In research conducted on the Pearl River in Southern China, the authors described changes in fish morphological traits along environmental gradients, while a remarkable association between morphometric variables and the migratory status of fish species was reported from Parana River Basin in Amazonia [10,11]. Reciprocally, in studies on Scandinavian lakes, the migratory behavior of freshwater fish was used as a predictor for fish morphological traits [12]. Consequently, our study aimed (1) to investigate the links between morphological traits and the migration status for the Mekong fish species already classified into black, white and grey fishes, and (2) to test whether fish morphology can predict the Mekong fish guilds. Identifying black, white and grey fish through their morphology while their migration status and life history are unknown would prove to be an important step for building ecological knowledge on Mekong fish migration and the life histories of the species.

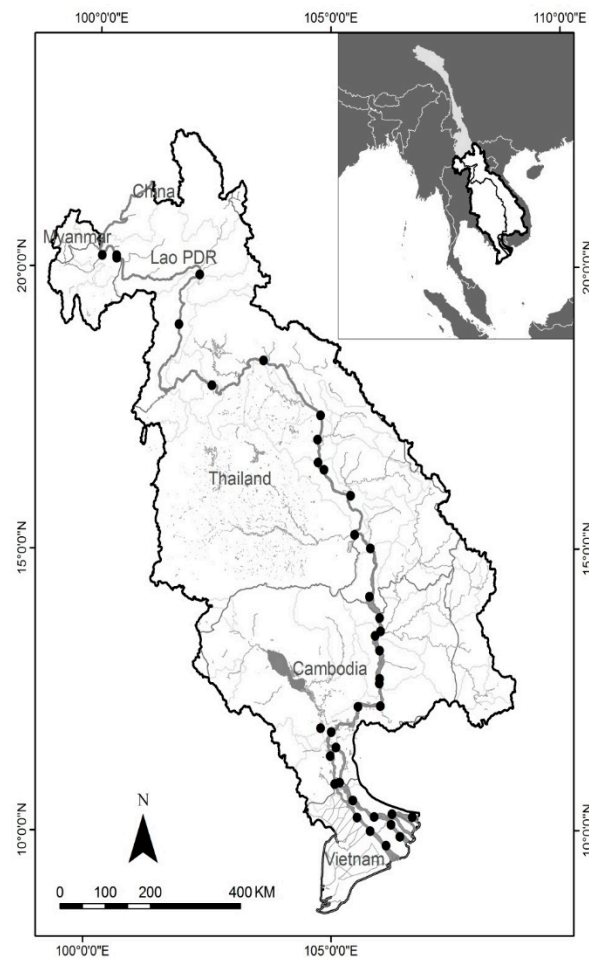
## 2. Materials and Methods

### 2.1. Fish Guilds and Morphological Trait Data

The fish data used in this study were derived from the Mekong River Commission (MRC), under the Assessment of Mekong Fisheries Component of the MRC Fisheries Program. The daily fish catches were monitored at 38 sites along the Lower Mekong mainstream (Figure 1) and are detailed in Chea et al. [13]. The ecological guild data were derived from the regional bio-ecological studies of the Mekong fisheries program conducted by the MRC in collaboration with Inland Fisheries Research and Development Institute (IFREDI) in Cambodia since 2006 [2,8,14–16]. To investigate the links between morphological traits and fish guilds, 11 morphological measurements were recorded based on a lateral view of the fish. These morphological measurements were then computed into 9 dimensionless ratios describing fish species strategies for locomotion and food acquisition by quantifying the size, shape of mouth, body and fins of the fish (Table 1, Figure S1) [7,17]. All the measurements were undertaken on adults, and only a single fish per species was measured, because only one good quality picture was available for most of the species. Nevertheless, intraspecific variability in morphological traits was low between adults [18,19]. Some species with unusual morphologies (e.g., species without a tail, or flatfish) were removed from the list in order to avoid bias. In total, 121 freshwater fish species belonging to 9 orders and 27 families, representing more than 40% of fish family diversity in the Mekong's system, were used in this study. These studied species consisted of 16%, 47% and 37% of black, grey and white fish, respectively (Table S1) [2,3,20].

**Table 1.** List of external morphological traits and their potential links to fish functions. Traits were dimensionless ratios (Toussaint et al. [7]).

Traits	Code	Description	Potential Links to Fish Functions
Bl/Bd	BlBd	Body elongation	Hydrodynamism
Eh/Bd	EhBd	Eye vertical position	Position of fish and/or of its prey in the water column
Ed/Hd	EdHd	Relative eye size	Visual acuity
Mo/Bd	MoBd	Oral gape position	Feeding position in the water column
Jl/Hd	JlHd	Relative maxillary length	Size of mouth and strength of jaw
Hd/Bd	HdBd	Body lateral shape	Hydrodynamism and head size
Pfi/Bd	PfiBd	Pectoral fin vertical position	Pectoral fin use for swimming
Pfl/Bd	PflBd	Pectoral fin size	Pectoral fin use for swimming
Cfd/CPd	CfdCPd	Caudal peduncle throttling	Caudal propulsion efficiency through reduction of drag



**Figure 1.** Lower Mekong Basin. Black dots represent the fish monitoring sites along the mainstem Lower Mekong River.

## 2.2. Statistical Analyses

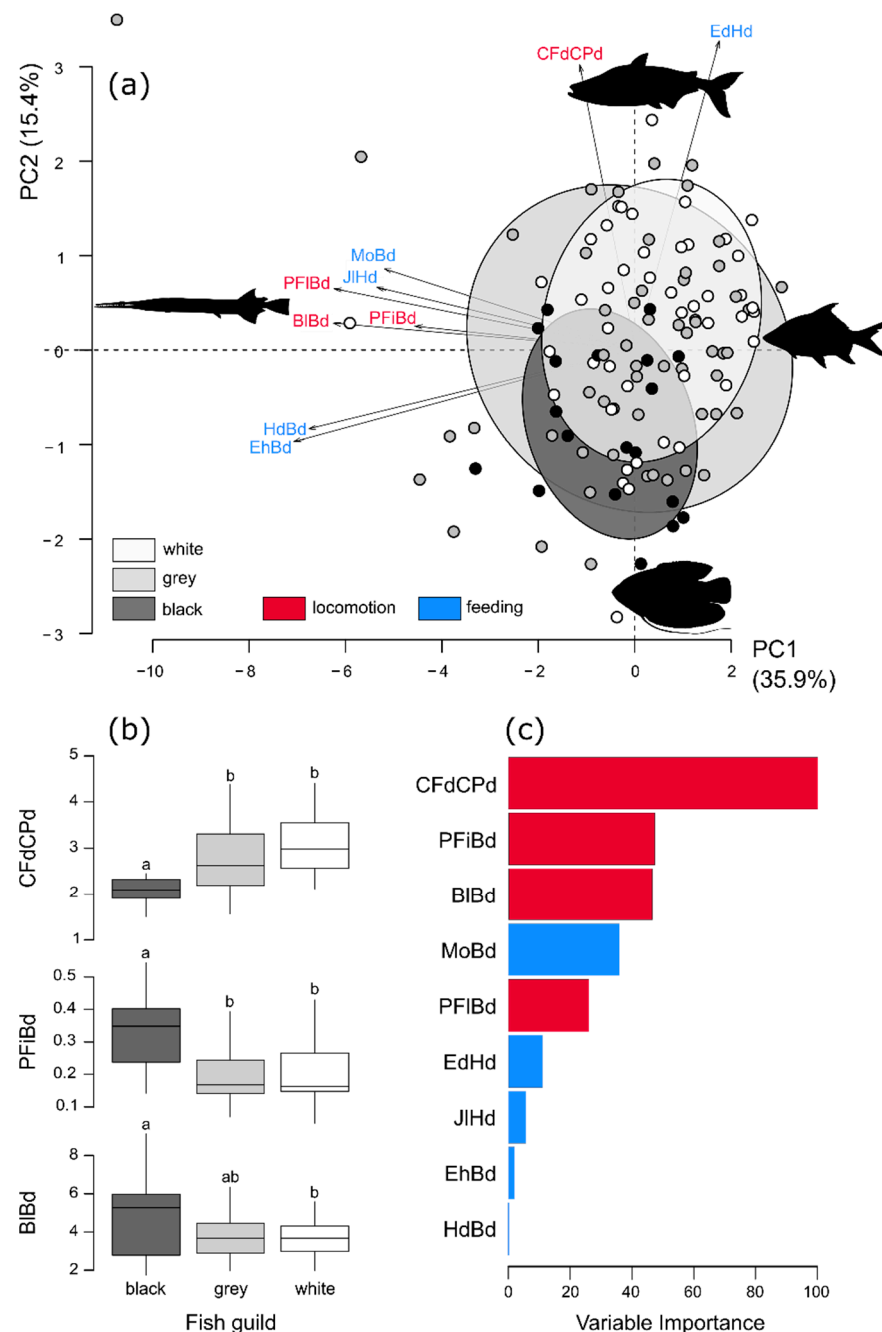
Initially, a principal component analysis (PCA) was applied on the fish morphological trait table in order to examine the distribution of fish species in a multidimensional trait space and to assess the links between morphological traits and fish guilds [21]. All morphological traits were tested between the guilds, using analyses of variance (ANOVA), and compared between groups (post hoc test) with an alpha level of 0.05.

To decompose the part of the total variance due to the differences between guilds, we used between-PCA on the nine traits [22]. As the number of species differed among fish guilds, we used a re-sampling procedure to balance the datasets (i.e., equal numbers of species) and then sub-sampled the original dataset by drawing randomly from 1000 balanced data subsets containing the smallest number of species per guild [23]. Following this, a random forest model was used in order to predict the Mekong fish guilds (black, white and grey) based on morphological trait descriptors [24]. A leave-one-out cross-validation (LOOCV) technique was used to evaluate the model performance and the process was repeated 3 times in order to improve the model accuracy [25]. The accuracy of model predictions was estimated from these simulated models, and variable importance in the model was measured in order to determine the contribution of each morphological trait in fish guild prediction. All statistical analyses were conducted using R program [26].

## 3. Results

The first two axes of the PCA explained 51.3% of the total variance and showed a marked overlap between the three fish guilds (black, white and grey) (Figure 2a). Overall, the re-sampling procedure used to partition the total variability with between-PCAs did

not affect the variance decomposition and confirmed this morphological overlap between the three guilds, identifying a strong and consistent component of intraguild variability (mean = 0.894, SD = 0.017).



**Figure 2.** Association between fish morphological traits and the Mekong fish guilds (black, white and grey). (a) Bi-plot on the 1st and 2nd axes of PCA showing the relationship between fish guilds and their morphological traits; (b) boxplots of significantly (ANOVA,  $p < 0.05$ ) different morphological traits between fish guilds, with different letters showing the significant differences between groups (Tukey post hoc tests,  $p < 0.05$ ); (c) importance of guild predictors from random forest model. Red and blue indicate the traits (codes as in Table 1) related to locomotion and feeding functions, respectively.

In regard to the traits that significantly ( $p < 0.05$ ) differed between the guilds, black and white fish were mainly distinguished by three locomotion-related traits (Figure 2b), while grey fish appeared to be an intermediate group encompassing a wide range of morphologies (Figure 2b). From a morphological point of view, the white fish group was distinguished by

its high caudal peduncle throttling (CFdCPd) and low body elongation (BlBd) compared to the black fish group, indicating that white fish species have a high swimming capacity and a fusiform and/or compressiform body shape (Figure 2b). In contrast, the black fish group was characterized by its low caudal peduncle throttling (CFdCPd), high pectoral fin vertical position (PFiBd) and body elongation (BlBd), indicating a sedentary behavior and an elongated or anguilliform body shape (Figure 2b). The grey fish group morphology was similar to the white fish group, despite a lower swimming capacity (i.e., lower value of CFdCPd) and a higher body elongation (BlBd) (Figure 2b).

Despite the strong morphological overlap between the three guilds, the predictive performance of the random forest algorithm showed an overall accuracy of 50.4% (61/121 species), with correct assignments of 52.6% for black and grey fish guilds and 46.7% for the white fish guild. Caudal peduncle throttling (CFdCPd) and pectoral fin vertical position (PFiBd) were the most important predictors of fish guilds, followed by body elongation (BlBd) and oral gape position (MoBd) (Figure 2c).

#### 4. Discussion

Morphologically, the black fish guild was well distinguished from the white fish guild, although some overlaps exist between the groups. Such differences underline distinct locomotion capacities between fish groups. The white fishes were characterized by high swimming endurance indicated by their high caudal peduncle throttling [27,28]. Those white fishes also exhibited important maneuverability at high swimming speeds due to the ventral position of their pectoral fins [29]. Such morphological features indicate highly mobile species adapted to long travels in riverine environments [17]. It is thus suitable for long-distance migratory species, which move along the Mekong mainstream and in large tributaries, such as *Cyclocheilichthys enoplos*, *Gymnostomus siamensis*, and *Pangasius hypophthalmus*. In contrast, the black fish group was characterized by a higher, although more energy-consuming, propulsion efficiency by the caudal fin due to a low caudal peduncle throttling [27,28]. This trait is associated with hydrodynamic body shapes (elongated bodies) and indicates that the black species are able to achieve fast accelerations to pass obstacles (such as rapids and waterfalls), avoid predation and capture mobile prey [27,30]. These species also use their pectoral fins for locomotion and are able to make precise movements in complex environments (e.g., flooded vegetation) owing to the lateral position of their pectoral fins [17,27,29]. These fish are therefore adapted to short-distance movements in complex environments, such as shallow waters, flooded forests or littoral zones. Such habitats are suitable for black species such as *Clarias macrocephalus*, *Trichogaster* sp., *Channa striata* or *Macrognathus siamensis*. Finally, although the traits related to feeding have a secondary role, white fishes tend to have bigger eyes and a smaller mouth than those of black fishes, indicating that vision plays a more significant role for migratory fish that prey on smaller food items than it does for black fishes. This tendency is reflected in the higher proportion of pelagic plankton feeders in the white fish guild, whereas black fishes are more often benthic (e.g., *Macrognathus* sp.) or ichthyophagous (e.g., *Channa* sp.), with a vision being less important for prey detection in the dusky bottom of rivers.

Such morphological differences between guilds have allowed for the development of a random forest model predicting guild membership based on morphology, with those traits related to fish swimming, such as caudal propulsion efficiency (CFdCPd), pectoral fin vertical position (PFiBd) and body elongation (BlBd), making a major contribution. Nevertheless, the quality of guild membership prediction, although fair, with 50% of correct prediction for the three guilds, remains reliable.

The limited predictive efficiency of the random forest model may first be due to the high diversity of fish species in the Mekong (>850 species), combined with the marked morphological similarity of Mekong fish fauna when compared with the Neotropical mega-diverse rivers, such as the Amazon, the Paraguay–Parana or the Orinoco Rivers [7]. This morphological similarity was at least in part supported by the dominance of a single fish



family (Cyprinidae), which includes more than 200 species with similar body forms but distinct reproductive and migratory guild status [31].

Secondly, the definition of the grey fish guild was not sufficiently clear, as the term short-distance migration is vague, thus requiring further detail on the definition of the migration range (e.g., a quantification of migration distance). In tropical regions, many fish species undertake seasonal migration in order to reach their essential habitats (feeding, spawning and dry season refugee grounds) [5]. Thus, the migration range for the grey and white fish guilds (i.e., semi-migrant vs. long-distance migrant) must be defined clearly in order to ensure a relevant guild classification [32,33].

Thirdly, the complexity of the Mekong system (i.e., connectivity between the Mekong and the Tonle Sap Lake, or with other important tributaries) makes it difficult to distinguish between longitudinal (upstream–downstream) migrations in the main stream (characterizing white fishes) and lateral migrations between lakes and tributaries attributed to grey fishes. Nevertheless, white fish have also been observed to conduct these lateral migrations, not only grey fish as previously believed [34,35], which might explain some confusion between the white and grey fish guilds.

To tackle these uncertainties, complementary biological traits, such as dispersal capacity, feeding and spawning information associated with environmental factors, would be complementary to morphological traits and enhance the prediction accuracy of the Mekong fish guilds [33]. This is particularly true for the speciose fish families with similar morphologies among species (e.g., for Cyprinidae, Siluridae, Pangasiidae, Bagridae, Osphronemidae, Clupeidae) or even with similar morphologies between families (e.g., Cyprinidae vs. Osphronemidae; Siluridae vs. Bagridae) [8,34]. In addition, the quality of the guild prediction could also be improved by increasing the number of species considered. In this study we used 121 species, representing less than 20% of the fish fauna, while the migration status is still unknown for almost all the remaining fish fauna of the Mekong [3]. Among the species considered, many of them belonged to the Cyprinidae family (56 species), which potentially limited the model's predictive accuracy.

Given these potential biases in the black–grey–white guild classification, in this study, we demonstrated the morphological differences between guilds that are consistent with the migratory status of the species. We therefore appeal for more research that can extend the basic ecological knowledge on the Mekong fish fauna, and particularly on the significant proportion of the fauna for which the ecology remains unknown. These current findings provide insight into predicting unknown fish guilds based on available external morphological traits, which could enrich the available dataset on the Mekong fish migration status for the remaining species once the data on fish morphology are available. This technique could be very beneficial in understanding a biological system as diverse as the Mekong River. More importantly, this migration information is essential for biodiversity conservation and sustainable river basin development (e.g., a hydropower development plan). Accurate information on fish migration patterns would help to minimize or mitigate impacts induced by human activities—for instance, the delimitation of dam location by avoiding the destruction of critical habitats for migratory fish (e.g., spawning, feeding and nursing grounds). Additionally, the white fish group is often vulnerable to fragmentation of their critical habitats. Maintaining migration routes would help to maintain the white fish biomass in order to compensate for consumption, as white fish accounted for 36% of the total fish catch obtained for human consumption [13].

These current studies would permit the development of a more detailed guild typology, according to fish migration ranges and other associated bioecological information about the species (e.g., dispersal capacity, feeding and life history strategies) [33]. This would represent a step forward for further bio-ecological studies in the hyperdiverse Mekong system and could represent an opportunity to not only generalize such classifications to other similar systems in Asian rivers but also to extend it to other large and megadiverse rivers around the world. Therefore, the morphological trait database of the Mekong fish fauna needs to be expanded in order to build a specific multidimensional functional

space for the Mekong River Basin. This would be especially significant for the remaining species. Thus, more efforts to sample more fish species with examples of individuals from different size classes should be made to improve the quality of the functional dataset, particularly in regard to economically important and endangered species. In addition to fish morphology, biological characteristics (such as reproduction and feeding strategies) should be considered key information to be integrated in order to produce a comprehensive functional dataset for the Mekong River Basin that could improve the accuracy of guild prediction for the Mekong fish fauna. Finally, this comprehensive functional dataset could be used to tackle the migration status or ecological guild prediction of Mekong fishes, and it could also be used to assess long-term changes in the Mekong ecosystem stability and functional responses to multiple pressures from climatic factors and human activities.

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/article/10.3390/su13158401/s1>, Figure S1. Position of the 16 fish morphological trait measurements describing fish functions for locomotion and food acquisition (adapted from Villéger et al. [36]). Table S1. List of 121 Mekong fish species used in the study with ecological guild information.

**Author Contributions:** Conceptualization, R.C., G.G., S.B. and S.L.; methodology, R.C. and G.G.; software, R.C.; validation, R.C., G.G. and S.B.; formal analysis, R.C. and G.G.; investigation, R.C.; resources, R.C. and S.B.; data curation, R.C.; writing—original draft preparation, R.C.; writing—review and editing, R.C., G.G., S.B. and S.L.; visualization, R.C. and G.G.; supervision, G.G.; project administration, R.C.; funding acquisition, R.C. and G.G. All authors have read and agreed to the published version of the manuscript.

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**Conflicts of Interest:** The authors declare no conflict of interest.

## References

1. Ziv, G.; Baran, E.; Nam, S.; Rodríguez-Iturbe, I.; Levin, S.A. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 5609–5614. [[CrossRef](#)]
2. Baran, E.; So, N.; Degen, P.; Chen, X.-Y.; Starr, P. Updated information on fish and fisheries in the Mekong Basin. *Catch Cult.* **2013**, *19*, 24–25.
3. Baran, E. *Fish Migration Triggers in the Lower Mekong Basin and Other Tropical Freshwater Systems*; MRC Technical Paper No. 14; MRC: Vientiane, Laos, 2006.
4. Kumm, M.; Sarkkula, J. Impact of the Mekong River Flow Alteration on the Tonle Sap Flood Pulse. *Ambio* **2008**, *37*, 185–192. [[CrossRef](#)]
5. Winemiller, K.O. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* **1989**, *81*, 225–241. [[CrossRef](#)]
6. Winemiller, K.O. Life history strategies, population regulation, and implications for fisheries management. *Can. J. Fish. Aquat. Sci.* **2005**, *62*, 872–885. [[CrossRef](#)]
7. Toussaint, A.; Charpin, N.; Brosse, S.; Villéger, S. Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread. *Sci. Rep.* **2016**, *6*, 22125. [[CrossRef](#)]
8. Valbo-Jørgensen, J.; Coates, D.; Hortle, K. Fish Diversity in the Mekong River Basin. In *The Mekong Biophysical Environment of An International River Basin*; Campbell, I.C., Ed.; Elsevier Academic Press: New York, NY, USA, 2009; pp. 161–196. ISBN 9780123740267.

9. Frimpong, E.A.; Angermeier, P.L. Trait-based approaches in the analysis of stream fish communities. *Am. Fish. Soc. Symp.* **2010**, *73*, 109–136.
10. Assumpção, L.D.; Makrakis, M.C.; Makrakis, S.; Piana, P.A.; Silva, P.S.D.; Lima, A.F.D.; Fernandez, D.R. Morphological differentiation among migratory fish species from the Paraná River basin. *Biota Neotrop.* **2012**, *12*, 41–49. [[CrossRef](#)]
11. Shuai, F.; Yu, S.; Lek, S.; Li, X. Habitat effects on intra-species variation in functional morphology: Evidence from freshwater fish. *Ecol. Evol.* **2018**, *8*, 10902–10913. [[CrossRef](#)]
12. Chapman, B.B.; Hulthén, K.; Brönmark, C.; Nilsson, P.A.; Skov, C.; Hansson, L.A.; Brodersen, J. Shape up or ship out: Migratory behaviour predicts morphology across spatial scale in a freshwater fish. *J. Anim. Ecol.* **2015**, *84*, 1187–1193. [[CrossRef](#)]
13. *Mekong River Commission Study on Sustainable Management and Development of the Mekong River including Impacts of Mainstream Hydropower Projects*; MRC: Vientiane, Laos, 2018; Volume 4, pp. 1–129.
14. So, N.; Leng, S.V.; Baran, E.; Arthur, R. An Evaluation of Fish Species and Genetic Diversity of the Tonle Sap Great Lake, Cambodia. In Proceedings of the International Workshop and Training on Fish Diversity of the Mekong River, Sendai, Japan, 17–20 November 2006.
15. Phomikong, P.; Fukushima, M.; Sricharoendham, B.; Nohara, S.; Jutagate, T. Diversity and Community Structure of Fishes in the Regulated Versus Unregulated Tributaries of the Mekong River. *River Res. Appl.* **2015**, *31*, 1262–1275. [[CrossRef](#)]
16. Baran, E.; Guerin, E.; Nasielski, J. *Fish, Sediments, and Dams in the Mekong*; WorldFish and CGIAR Research Program on Water, Land and Ecosystem (WLE): Vientiane, Laos, 2015; Volume 53, ISBN 9788578110796.
17. Villéger, S.; Brosse, S.; Mouchet, M.; Mouillot, D.; Vanni, M.J. Functional ecology of fish: Current approaches and future challenges. *Aquat. Sci.* **2017**, *79*, 783–801. [[CrossRef](#)]
18. Cilleros, K.; Allard, L.; Grenouillet, G.; Brosse, S. Taxonomic and functional diversity patterns reveal different processes shaping European and Amazonian stream fish assemblages. *J. Biogeogr.* **2016**, *43*, 1832–1843. [[CrossRef](#)]
19. Manna, L.R.; Villéger, S.; Rezende, C.F.; Mazzoni, R. High intraspecific variability in morphology and diet in tropical stream fish communities. *Ecol. Freshw. Fish* **2018**, *28*, 41–52. [[CrossRef](#)]
20. Froese, R.; Pauly, D. FishBase. World Wide Web Electronic Publication. Available online: [www.fishbase.org](http://www.fishbase.org) (accessed on 10 June 2018).
21. Dray, S.; Dufour, A.B. The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* **2007**, *22*, 1–20. [[CrossRef](#)]
22. Dodédec, S.; Chessel, D. Recent developments in linear ordination methods in environmental sciences. *Adv. Ecol.* **1991**, *1*, 133–155.
23. Albert, C.H.; Thuiller, W.; Yoccoz, N.G.; Douzet, R.; Aubert, S.; Lavorel, S. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. *Funct. Ecol.* **2010**, *24*, 1192–1201. [[CrossRef](#)]
24. Liaw, A.; Wiener, M. Classification and Regression by random Forest. *R News* **2002**, *2*, 18–22.
25. Kuhn, M. Caret: Classification and Regression Training 2020. R Package Version 6.0-86. Available online: <https://CRAN.R-project.org/package=caret> (accessed on 10 June 2018).
26. *R Core Team R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2018.
27. Blake, R.W. Fish functional design and swimming performance. *J. Fish Biol.* **2004**, *65*, 970–983. [[CrossRef](#)]
28. Sfakiotakis, M.; Lane, D.M.; Davies, J.B.C. Review of fish swimming modes for aquatic locomotion. *IEEE J. Ocean Eng.* **1999**, *24*, 237–252. [[CrossRef](#)]
29. Dumay, O.; Tari, P.S.; Tomasini, J.A.; Mouillot, D. Functional groups of lagoon fish species in Languedoc Roussillon, Southern France. *J. Fish Biol.* **2004**, *64*, 970–983. [[CrossRef](#)]
30. Gatz, A.J. Community Organization in Fishes as Indicated by Morphological Features. *Ecology* **1979**, *60*, 711–718. [[CrossRef](#)]
31. Rainboth, W. The Family Cyprinidae (Carps). *Mekong Fish. Netw. Newsl.* **1998**, *3*, 1–2.
32. Lucas, M.C.; Baras, E.; Thom, T.J.; Duncan, A.; Slavik, O. *Migration of Freshwater Fishes*; Blackwell Science Ltd.: Oxford, UK, 2001; ISBN 0632057548. [[CrossRef](#)]
33. Tamario, C.; Sunde, J.; Petersson, E.; Tibblin, P.; Forsman, A. Ecological and Evolutionary Consequences of Environmental Change and Management Actions for Migrating Fish. *Front. Ecol. Evol.* **2019**, *7*, 1–24. [[CrossRef](#)]
34. Ngor, P.B.; Grenouillet, G.; Phem, S.; So, N.; Lek, S. Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of South-East Asia. *Ecol. Freshw. Fish* **2018**, *27*, 1087–1100. [[CrossRef](#)]
35. Chea, R.; Lek, S.; Ngor, P.; Grenouillet, G. Large-scale patterns of fish diversity and assemblage structure in the longest tropical river in Asia. *Ecol. Freshw. Fish* **2017**, *26*, 575–585. [[CrossRef](#)]
36. Villéger, S.; Miranda, J.R.; Hernández, D.F.; Mouillot, D. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* **2010**, *20*, 1512–1522. [[CrossRef](#)]