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DATA ARTICLE

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FISHMORPH: A global database on morphological traits of freshwater fishes

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Abstract

Motivation: Global freshwater fish biodiversity and the responses of fishes to global changes have been explored intensively using taxonomic data, whereas functional aspects remain understudied owing to the lack of knowledge for most species. To fill this gap, we compiled morphological traits related to locomotion and feeding for the world freshwater fish fauna based on pictures and scientific drawings available from the literature.

Main types of variables contained: The database includes 10 morphological traits measured on 8,342 freshwater fish species, covering 48.69% of the world freshwater fish fauna.

Spatial location and grain: Global.

Major taxa and level of measurement: The database considers ray-finned fishes (class Actinopterygii). Measurements were made at the species level.

Software format: .csv.

Main conclusion: The FISHMORPH database provides the most comprehensive database on fish morphological traits to date. It represents an essential source of information for ecologists and environmental managers seeking to consider morphological patterns of fish faunas throughout the globe, and for those interested in current and future impacts of human activities on the morphological structure of fish assemblages. Given the high threat status of freshwater environments and the biodiversity they host, we believe this database will be of great interest for future studies on freshwater ecology research and conservation.

KEYWORDS

Actinopterygii, biodiversity, body shape, conservation, eye size, feeding, fin size, functional traits, locomotion, mouth size

1 | INTRODUCTION

Freshwater ecosystems are being considered increasingly in biodiversity and conservation studies (Reid et al., 2019; Tickner et al., 2020) because they host a substantial fraction of the world diversity and provide irreplaceable goods and services to humanity (Albert et al., 2021). Yet, freshwaters are among the most anthropized and at-risk ecosystems of the globe (Su et al., 2021; WWF, 2020) and host numerous endemic and endangered species (Tedesco et al., 2012; Toussaint et al., 2016). Among freshwater organisms, freshwater fishes are of particular interest because they make up one-quarter of all vertebrate species, provide food to millions of people and contribute to the world economy (McIntyre et al., 2016). Such awareness has motivated the development of global- and regional-scale initiatives to inventory the freshwater fish fauna across the globe (e.g., Jézéquel et al., 2020; Tedesco, Beauchard et al., 2017) to determine the spatial patterns and drivers of freshwater fish richness and endemism (Dias et al., 2014; Tedesco et al., 2012; Oberdorff et al., 2011; Guégan et al., 1998) and to reveal the intensity of anthropic disturbances of fish faunas. Those studies showed that introductions of non-native species, river fragmentation and climate change blurred the historical composition of fish species assemblages (Comte & Olden, 2017; Dias et al., 2017; Leprieur et al., 2008) and the faunistic dissimilarity between rivers (Baiser et al., 2012; Villéger et al., 2011). Future biodiversity trends under various scenarios of anthropic activity were also proposed, and all predicted a reinforcement of these biodiversity changes in the near future (Herrera-R et al., 2020; Villéger et al., 2014).

All those previous studies focused on the taxonomic dimension of biodiversity (i.e., where all species are equivalent), not properly representing the specific roles of fish species in aquatic ecosystems (Villéger et al., 2017). Fish account for a wide range of functions, including food-web control, bioturbation or nutrient cycling (Estes et al., 2011; McIntyre et al., 2007); nonetheless, the individual role of most species in such processes remains unknown, a knowledge gap that would require decades of research to be filled. Fortunately, another way to approach the roles played by fish species is to consider the ecological, behavioural, physiological or morphological characteristics of the species (Villéger et al., 2017). Ecological, physiological and behavioural traits such as maturity, fecundity, diet, habitat or dispersal capacities are well informed at the species level for some Northern Hemisphere regions, such as the USA (Frimpong & Angermeier, 2009) or Western Europe (Kuczynski et al., 2018), but are still lacking for a large part of the world fish fauna. Overall, FishBase (https://www.fishbase.org; Froese & Pauly, 2020), the most up-to-date database on fish biology, provides complete ecological information for <2,000 out of the *c*. 17,134 described freshwater species.

In contrast, morphological traits can be measured easily from fish pictures or scientific drawings available in the literature for most species. Based on fish lateral views, several morphological traits related to locomotion (e.g., body shape, fin size and position) and feeding (e.g., mouth and eye size and position; Villéger et al., 2017) can be measured. The FISHMORPH database provides such morphological traits for freshwater fish species from collected pictures and scientific drawings. This database aims to cover all continental realms and ecosystems, and the whole morphological range of freshwater fishes, from tiny loricariid algae browsers (e.g., dwarf suckers, *Otocinclus* sp.) to large esocid predators (e.g., pikes, *Esox* sp.) and from elongated anguliliforms (e.g., eels, *Anguilla* sp.) to laterally compressed cichlids (e.g., discus, *Symphysodon* sp.). These morphological data will provide a unique opportunity to investigate morphological characteristics for most of the freshwater fish species and assemblages of the globe, and to go beyond taxonomic approaches for local- to global-scale studies.

2 | METHODS

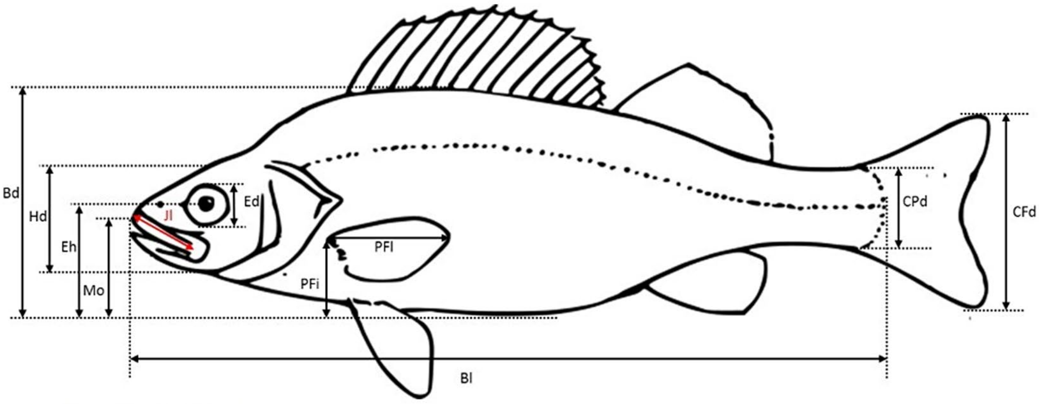
2.1 | Data acquisition

2.1.1 | Collection of fish pictures

To measure morphological characteristics, we carried out an extensive literature review to collect at least one lateral view picture of each described species of freshwater fish. More than 590 scientific literature sources, including peer-reviewed articles, books and scientific websites, were considered. Pictures were taken primarily from regional fish atlases either as printed books or as scientific websites. We then complemented the database using monographs and peer-reviewed articles on fish taxonomy. Fish hobbyist websites, grey literature and unpublished illustrations of fresh and museum specimens were also considered after checking for accurate taxonomy of the illustrated species. We collected at least one picture (validated photograph or scientific drawing) of fish lateral view per species. Only pictures and scientific lateral view drawings of entire adult animals were kept. We searched primarily for photographs of fresh or preserved specimens, and drawings were used only when no picture was found. Drawings were taken from the fish taxonomy literature (references are provided in the database), thereby limiting artistic interpretations. Juveniles were not considered because morphological changes can occur during ontogeny. In cases of sexual dimorphism, we considered only male morphology, because pictures of females are scarce for most species (especially for perciforms and cyprinodontiforms). Although working on lateral view pictures provides less external morphological information than working with fresh animals (e.g., oral gape surface and body transversal shape are not measurable from lateral views), it is the most efficient way to collect morphological measures when targeting the world freshwater fish fauna, compared with the highly demanding collection of fresh or museum specimens.

2.1.2 | Functional trait measures

For each specimen, 11 morphological measurements were recorded (Figure 1a) using ImageJ software (http://rsb.info.nih.gov/ij/index.html). Each measurement was expressed as a number of pixels because pictures rarely contained a metric scale. Measurements were expressed as biologically meaningful ratios between measurements taken from the same picture, allowing for comparisons between pictures (Toussaint et al., 2016; Villéger et al., 2017). We computed nine unitless ratios (hereafter called morphological traits; Figure 1b). In addition, we also considered an estimate of maximum body length (MBl) as a measure of body size, taken from FishBase (https://www.fishbase.org; Froese & Pauly, 2020). The resulting 10 morphological traits (nine unitless ratios and body size) are commonly used in assessments of morphological diversity of freshwater (e.g., Pease et al., 2015; Su et al., 2019; Toussaint et al., 2016) and marine fishes (e.g., Bellwood et al., 2014; Villéger et al., 2010). Complementary



(a) Morphological measures

Code	Name	Protocol for measurement
MBl	Maximum Body length	Maximum adult length in centimetres
Bl	Body length	Standard length (snout to caudal fin basis)
Bd	Body depth	Maximum body depth
Hd	Head depth	Head depth at the vertical of eye
CPd	Caudal peduncle depth	Minimum depth of the caudal peduncle
CFd	Caudal fin depth	Maximum depth of the caudal fin
Ed	Eye diameter	Vertical diameter of the eye
Eh	Eye position	Vertical distance between the centre of the eye to the bottom of the body
Mo	Mouth height	Vertical distance from the top of the mouth to the bottom of the body
Jl	Maxillary jaw length	Length from snout to the corner of the mouth
PFl	Pectoral fin length	Length of the longest ray of the pectoral fin
PFi	Pectoral fin position	Vertical distance between the upper insertion of the pectoral fin to the bottom of the body

(b) Morphological traits

Morphological traits	Formula	Potential link with fish functions
Maximum body length (**MBl**)	MBl	Metabolism, trophic impacts, locomotion ability, nutrient cycling
Body elongation (**BEl**)	$\frac{Bl}{Bd}$	Hydrodynamism
Vertical eye position (**VEp**)	$\frac{Eh}{Bd}$	Position of fish and/or of its prey in the water column
Relative eye size (**REs**)	$\frac{Ed}{Hd}$	Visual acuity
Oral gape position (**OGp**)	$\frac{Mo}{Bd}$	Feeding position in the water column
Relative maxillary length (**RMl**)	$\frac{Jl}{Hd}$	Size of mouth and strength of jaw
Body lateral shape (**BLs**)	$\frac{Hd}{Bd}$	Hydrodynamism and head size
Pectoral fin vertical position (**PFv**)	$\frac{PFi}{Bd}$	Pectoral fin use for swimming
Pectoral fin size (**PFs**)	$\frac{PFl}{Bl}$	Pectoral fin use for swimming
Caudal peduncle throttling (**CPt**)	$\frac{CFd}{CPd}$	Caudal propulsion efficiency through reduction of drag

FIGURE 1 (a) Morphological measures and (b) morphological traits measured on each fish species morphological traits, such as oral gape area and shape, or body thickness, were not included because they need front and dorsal views of the fish, which were available for only a few species.

Some species have unusual morphologies (e.g., species without a tail, flatfishes) that prevent some morphological traits from being measured. For these few exceptions, we followed the rules defined by Villéger et al. (2010): (1) for species with no visible caudal fin (e.g., Sternopygidae, Anguilidae, Plotosidae), caudal peduncle throttling (CPt) was set to one, assuming that caudal fin depth is equal to caudal peduncle depth (Figure 1); (2) for the algae browser species with the mouth positioned under the body (e.g., Loricaridae, or some Balitoridae, such as *Gastromyzon*) oral gape position (OGp) and relative maxillary length (RMl) were set to zero; (3) for the species without pectoral fins (e.g., Synbranchiforms and some Anguiliforms) pectoral fin vertical position (PFv) was set to zero; and (4) for flatfishes, the body depth measure was the body width because the fish lies on one side of its body. We therefore assumed that Pleuronectiforms are functionally closer to dorsoventrally flattened fishes (e.g., *Gastromyzon*) than to laterally compressed fishes (e.g., *Symphysodon*). This rule is relevant to flatfish species ecology and makes the meaning of traits consistent for all the fishes, as underlined by Villéger et al. (2017).

2.2 | Quality control

2.2.1 | Taxonomy

We validated species scientific names following FishBase (Froese & Pauly, 2020) through the R package *rfishbase* (as of December 2020; Boettiger et al., 2012) and confirmed names with no match manually using the Catalog of Fishes (Fricke et al., 2018). We then selected only records involving ray-finned fishes (class Actinopterygii), excluding sharks, rays, lampreys and unidentified species. Only freshwater species are considered in our database. Freshwater species were selected from all the species listed in FishBase as inhabiting the freshwater environment, therefore including the species with a marine or brackish life stage listed as "Freshwater-Brackish or "Freshwater-Brackish-Marine" in FishBase. We also considered some species (14 species) not listed as freshwater species in FishBase but retrieved in the literature as occasionally entering freshwaters (Tedesco, Beauchard, et al., 2017).

2.2.2 | Pictures

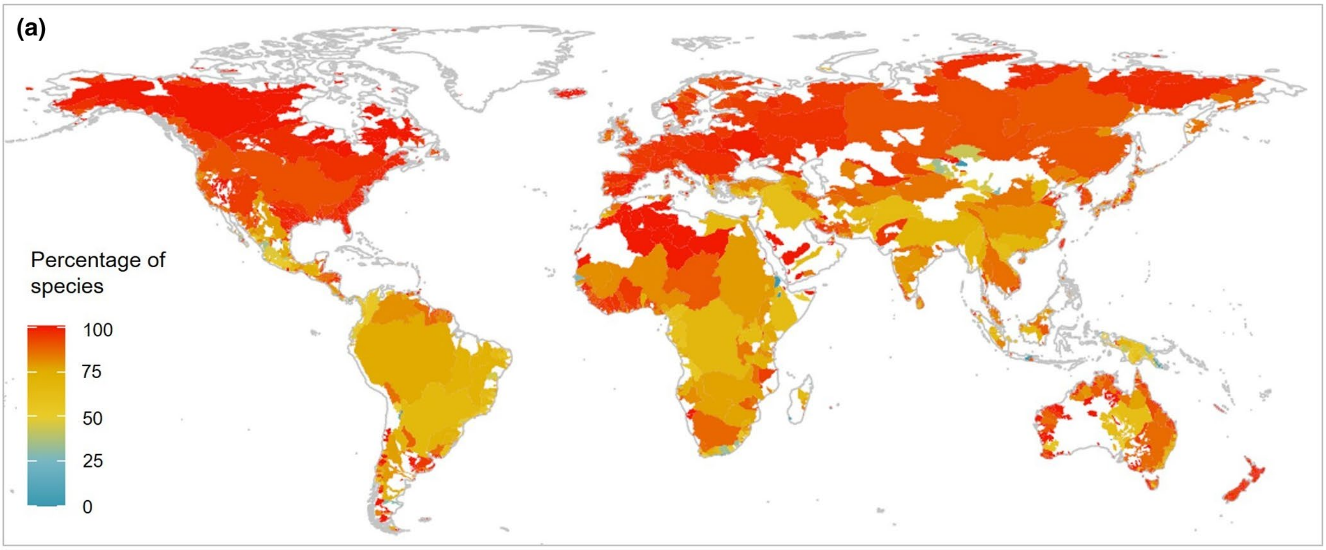
When several pictures were available for a species, measures were taken on the one allowing for a maximum of morphological measures. All pictures with no lateral view and pictures not representing the entire fish body were discarded systematically. Pictures of ancient museum specimens, with dried bodies and fins, were also discarded to conserve only live, fresh or well-conserved specimens. Drawings were conserved only if they provided a precise representation of the fish species and only in the event that no adequate picture was found. Despite those restrictions, the quality of the pictures did not allow the measurement of all morphological traits in all species, owing to inappropriate positioning of body parts or to damage (this was particularly true for fins, which are sometimes truncated). All those doubtful measures were discarded.

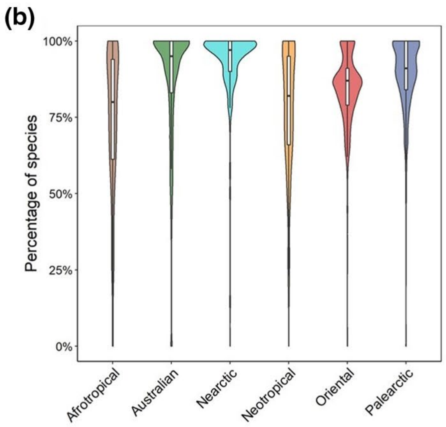
2.3 | Database formatting

The database is organized in a single table (.csv format), with the taxonomy of the species in the five first columns accounting for superorder, order, family and binomial species name (genus and species). Given that the nomenclature of species can change, we also added the FishBase identification number of each species, ensuring a real-time follow-up of taxonomic changes. The next 10 columns account for each one of the morphological traits as listed in Figure 1b. Each row of the table corresponds to one species. A static version of FISHMORPH is available through figshare (https://doi.org/10.6084/m9.figshare.14891412), although future updates will continue, complementing the database (see *Data Availability Statement*), adding information from new pictures or measures for additional species that become available or that any interested reader would like to provide. Traits not measured are coded as "NA" to ease analysis with R software. Finally, the last two columns indicate the type of illustration (photograph or drawing) and the source of the illustration.

3 | RESULTS AND DISCUSSION

We provide the most comprehensive fish morphological trait database existing to date. It is based on the collection of 8,342 fish pictures (7,057 photographs and 1,285 drawings). Among the 8,342 considered species, all 10 morphological traits were measured for 6,391 species (76.61% of the species). Unmeasured traits account for 3.06% of all traits and range between 0.96% and 10.33% of the traits according to fish orders (Figure 2). The entire database encompasses 8,342 freshwater fish species out of the 17,134 valid freshwater fish species listed in FishBase (accessed on 15 March 2021) and accounts for 48.69% of the global freshwater fish fauna. The species included in the FISHMORPH database belong to 32 of the 34 fish orders inhabiting freshwaters and contain species from >90% of all the freshwater fish families (199 of the 220 fish families with freshwater species) and >80% of all the freshwater fish genera (1,881 of the 2,315 freshwater fish genera; Figure 2). The FISHMORPH database accounts for the fish fauna inhabiting the six biogeographical realms of the globe, with morphological data covering on average 85.44% of the fish species per river basin for the 3,119 basins considered by Tedesco, Beauchard, et al. (2017) in their global fish species distribution database. The percentage of species considered in the FISMORPH data per river basin varies among realms, with completeness levels >80% in the Australian (87.61%), Nearctic (92.71%), Oriental (83.55%) and Palaearctic (88.40%) rivers,





(c)

Taxonomic Order	Number of families	Number of genera	Number of species	Percentage of missing traits	Percentage of described species
Cypriniformes	11	393	1933	2.52	42.95
Perciformes	47	439	1826	1.89	54.04
Siluriformes	36	405	1800	5.45	48.15
Characiformes	19	256	1281	1.62	59.06
Cyprinodontiformes	10	107	554	1.75	42.10
Osteoglossiformes	7	29	156	1.54	61.42
Clupeiformes	5	47	104	0.96	61.90
Gymnotiformes	5	29	101	3.66	42.26
Salmoniformes	1	12	92	1.30	40.71
Atheriniformes	6	21	71	3.80	25.45
Scorpaeniformes	6	19	70	2.43	60.34
Synbranchiformes	3	6	48	4.58	39.67
Beloniformes	3	11	33	1.82	25.58
Others (19 orders)	40	107	273	10.33	54.93

FIGURE 2 FISHMORPH database completeness. (a) Percentage of species morphologically informed in each of the 3,119 river basins from Tedesco, Beauchard, et al. (2017). (b) Violin plots showing differences in FISHMORPH database completeness among river basins belonging to the six biogeographical realms. (c) Number of families, genera, species, percentage of missing trait values and percentage of known freshwater fish species for the main taxonomic orders (orders with >100 freshwater species in FishBase) included in the FISHMORPH database

whereas it is lower in the other two realms (74.76% and 77.48% in Afrotropical and Neotropical rivers, respectively; Figure 2).

Used in recent studies, the FISHMORPH database revealed strong differences between taxonomic and morphological richness among biogeographical realms (Toussaint et al., 2016), which were driven, in part, by a few species with extreme morphologies (Su et al., 2019). The FISHMORPH data were also used to investigate human impacts on the freshwater fish fauna, showing that morphological diversity in the world rivers has changed vastly after introductions of exotic species (Toussaint et al., 2018), because humans have preferentially introduced species with particular morphologies (Su et al., 2020). We believe the FISHMORPH data are of great interest for further investigation of the impacts of global change on the freshwater fish biodiversity throughout the globe. Understanding how observed and predicted changes in fish taxonomic diversity translate into morphological changes would be of particular interest, for instance, to understand the functional and evolutionary consequences of global changes, as shown by Carmona et al. (2021) for plants and vertebrates. In addition, morphological data can be combined with other descriptors of biodiversity, such as taxonomic and phylogenetic diversity, to develop comprehensive indicators of changes in biodiversity throughout the world, as proposed by Su et al. (2021), or at regional scales, as in the studies by Dézerald et al. (2020) and Herrera-R et al. (2020).

4 | CONCLUSIONS

The FISHMORPH database provides the most comprehensive global-scale database on freshwater fish morphology to date. It accounts for almost 50% of the described freshwater fish fauna, and therefore contains taxonomic gaps that should be filled progressively in the future. In addition, the FISHMORPH database currently considers only a single individual per species and does not account for intraspecific trait variability. Future developments could therefore consider morphological measures for several individuals per species from different life stages and/or rivers. It would also be useful to consider more traits, including not only morphology but also ecological, physiological and behavioural traits. Although information on these traits is lacking for most species, previous initiatives offer such data for U.S. and European faunas (Frimpong & Angermeier, 2009; Kuczynski et al., 2018). Given that ecological and morphological traits provide complementary information on the functional structure of fish assemblages (Kuczynski et al., 2018), merging those databases would be a useful endeavour to gain a better understanding of how natural and human determinants shape the functional diversity of freshwater fish faunas over the globe.

Another limitation of the database is the lack of information on marine fishes, and we therefore encourage the extension of our database to marine fauna. This would provide useful information to explore the differences in diversification rates observed for marine and freshwater faunas (Tedesco, Paradis, et al., 2017) or to gain a better understanding of the processes explaining fish distribution across the globe (Carvajal-Quintero et al., 2019). Such future developments, although desirable, do not hinder the use of the FISHMORPH database for both macroecological and local-scale studies. We are confident that the morphological measures provided here will be helpful in the assessment of anthropogenic impacts on freshwater faunas and for the development of local to global indicators of river health.

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DATA AVAILABILITY STATEMENT

FISHMORPH is publicly available through figshare (https://doi.org/10.6084/m9.figshare.14891412). We kindly ask users to cite the present paper in any published material produced using these data. Users are free to use the FISHMORPH data and to contact the authors for details or collaborations. We also encourage any potential data contributor to contact S.B. with potential datasets to expand the database.

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BIOSKETCH

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