Regular paper

A simple framework for the exploration of functional biodiversity

by

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Submitted: 31 Mar. 2022
Accepted: 21 Nov. 2022
Editors: F. Teletchea, A. Tilley

Key words
Functional biodiversity
Productivity
Trophic level
form factor
Evolutionary age

Abstract. – Key traits of functional biodiversity are examined for 31,134 species of fishes. These traits are maximum body weight, productivity, and trophic level. A new, simple framework is presented that shows the combined usage of these traits, in ordinal categories, for close to 90% of extant species of fishes. Most species are clustered tightly along an evolutionary axis in size-productivity-trophic space (SPT-space) from few large, evolutionary old species with very low productivity to many medium-sized newly evolved species with high productivity, superseding Cope's rule of a within-lineages trend towards larger size and lower productivity. The across-lineages evolutionary axis is also found in the subsets of marine, freshwater, and Arctic species. Another notable prediction is the five-fold increase in top predators in Arctic waters in 2100, which could cause the extinction of endemic species. The main purpose of this study is to demonstrate the usefulness of the SPT-framework for comparing functional biodiversity patterns in ecosystems by salinity, geography or time. Also, the SPT-framework was used to explore correlations with other traits such as body shape, and to display the position of individual species, represented by pictograms of body shape and habitat, within SPT-space.

Résumé. – Un cadre pour l'exploration de la biodiversité fonctionnelle.

Les traits clés de la biodiversité fonctionnelle sont examinés pour 31 134 espèces de poissons. Ces traits sont : le poids corporel maximal, la productivité et le niveau trophique. Un nouveau cadre simple est présenté qui montre l'utilisation combinée de ces traits, dans des catégories ordinales, pour près de 90% des espèces de poissons existantes. La plupart des espèces sont étroitement regroupées le long d'un axe évolutif dans l'espace taille-productivité-trophique (espace SPT), allant de quelques espèces anciennes de grande taille ayant une productivité très faible à de nombreuses espèces de taille moyenne ayant une productivité élevée. Cet axe évolutif se retrouve chez les espèces marines et d'eau douce, ainsi que chez les espèces arctiques. L'objectif principal de cette étude est de démontrer l'utilité du nouveau cadre SPT pour comparer les modèles de biodiversité fonctionnelle dans les écosystèmes en fonction de la salinité, de la géographie ou du temps. En outre, le cadre SPT a été utilisé pour explorer les corrélations avec d'autres caractéristiques telles que la forme du corps, et pour afficher la position des espèces individuelles, représentées par des pictogrammes de la forme du corps et de l'habitat, dans l'espace SPT.

INTRODUCTION

As Matthews (1998) put it: "There are so many kinds of fishes, occupying such diverse habitats, evolving in such complex ways, and with such complicated ecological traits, that a total synthesis of 'understanding fishes' will always elude ichthyologists and ecologists." Faced with such diversity, all that we can hope to achieve is a partial understanding through exploring the obvious patterns in functional traits among extant species of fishes. Toward this end, this study presents a simple framework that facilitates such exploration for a high number of species, focusing on functional diversity as a key aspect of the many other measures of biodiversity (Magurran and McGill, 2011).

Evolution favours the traits of those individuals that, under given circumstances, produce the highest number of reproductively successful offspring. The new-born or newly hatched individuals have to survive, feed and grow to reach maturity, mate with matching partners, and maximize chances of survival for their offspring, including dying at a rate

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that reduces competition with their offspring for space, food, or mates. Life-history strategies thus balance various traits related to morphology, feeding, growth, predator avoidance, mating success, number of offspring, parental care, and longevity.

The number of conceivable life-history patterns is essentially infinite, if judged by possible combinations of the many known traits (Peters, 1983; Dawkins, 1986; Brown *et al*., 2004). This study focuses on fishes and on fitness-related traits that are highly correlated with many other traits and thus can serve as proxies for the elucidation of life-history strategy preferences. Such choice is consistent with the fact that a limited number of dimensions is usually sufficient to describe the position occupied by species in food webs or other types of ecological networks (Eklöf *et al*., 2013). As a practical consideration, these traits had to be available for a high number of species across all Classes of fishes. The three main traits considered in this study are body size, productivity, and trophic level, and their combination is referred to as SPT-space from here onward. Other traits considered within SPT-space are body shape, salinity preference, and preference for cold water, to provide first examples of the application of SPT-plots. The purpose of this study is to introduce the SPT-framework and plot, and to identify patterns in the frequency distribution of extant species of fishes in SPT-space, considering (1) all fishes, (2) typical body shapes of fishes, (3) freshwater versus marine fishes, and (4) current versus future species composition in Arctic waters, as examples. The results found are preliminary and by no means exhaustive. They are instead meant to provide examples of the usefulness of the SPT-framework and to encourage further research. This study is a contribution to a special edition of *Cybium* dedicated to the FishBase information system (http://www.fishbase.org) from which the underlying data were drawn.

MATERIAL AND METHODS

All data used in this study were extracted from FishBase version 2/2022 (Froese and Pauly, 2022), referred to as FishBase from here onward. The required information on body size, productivity and trophic level was available for 31,134 (89%) of altogether 34,836 species recorded in FishBase (or 86% of the valid species recorded in Eschmeyer's Catalog of Fishes at the time; Fricke *et al*., 2022).

Body size was either taken as the largest reported (wet or live) weight or as the weight derived by applying a length-weight relationship to the maximum reported body length. For the purpose of this study, body weights were then grouped into the ordinal categories small, medium, large, and very large. The numerical bounds of these categories were derived by taking the geometric mean of maximum body weights and subtracting one standard deviation in $\log_{10}$ space to obtain the upper size of small fishes, adding one standard deviation to the mean to get the upper range of medium sized fishes, adding three standard deviations to get the upper range of large fishes, and designating heavier fishes as very large (Fig. 1).

Productivity is provided in FishBase in ordinal categories of resilience (very low, low, medium, high) based on a variety of other life history traits. It serves as a substitute for the intrinsic rate of population increase (r), which is available only for some commercial fish species. The approach used by the FishBase team to assign productivity categories follows Musick (1999) as modified in Froese *et al*. (2000, 2017) and updated in Table I. Note that the trait with the lowest productivity match determines the chosen productivity level. For example, if a species has a medium growth performance, with the parameter of the von Bertalanffy growth function (VBGF) $K = 0.3$ year^{-1}, but produces less than 100 eggs or pups a year, then it is assigned to low productivity.

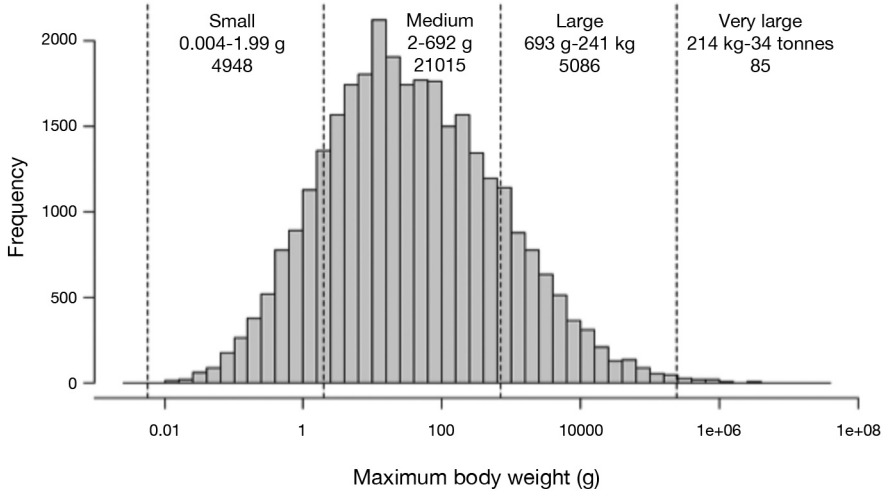

Figure 1. – Histogram of maximum body weights of 31,134 species of fishes. The dashed vertical lines indicate –3, –1, 1 and 3 standard deviations in log space and are used as borders between the displayed body size categories, with indicated weight ranges and number of species. Geometric mean body weight is 37.2 g.

Table I. – Associations between ordinal categories of productivity and other life-history traits, where *r* is the intrinsic rate of population increase, *K* is a parameter of the von Bertalanffy growth function, Fecundity is the annual number of eggs or offspring produced by a female, t_m is the age where 50% of females reach maturity, and t_{max} is the reported life span.

Productivity	High	Medium	Low	Very low
r (year^{-1})	> 0.6	0.2-0.8	0.05-0.5	< 0.1
K (year^{-1})	> 0.4	0.15-0.4	0.05-0.15	< 0.1
Fecundity (year^{-1})	> 1000	100-1000	10-100	< 10
t_m (years)	< 1	2-4	5-10	> 10
t_{max} (years)	< 3	3-15	16-30	> 30

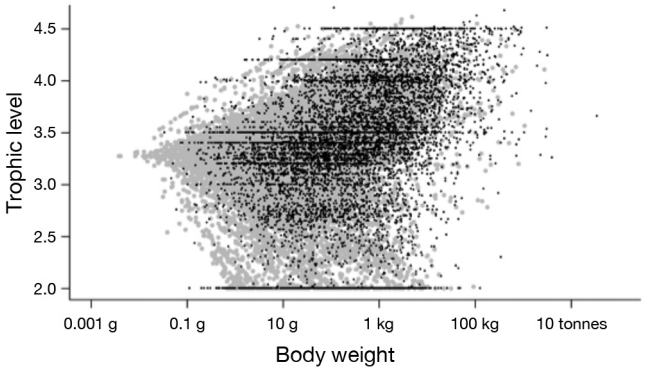

Figure 2. – Scatterplot of trophic level over body weight for 31,134 species of fishes with trophic level and body weight information in FishBase. The grey dots represent trophic levels predicted with Equation 1 whereas the black dots represent trophic levels based on observations. The horizontal lines are artefacts of the method used to assign trophic levels in data-poor situations.

Trophic levels are derived in FishBase preferably from published diet compositions or alternatively from individual food items, with certain assumptions on the relative importance of these items in the overall diet of the species (Pauly and Sa-a, 2000; Sa-a *et al*., 2000). If no diet or food information is available for a species, the trophic level of the closest relatives (same Genus, Subfamily, Family or Order) is used to predict a preliminary trophic level. All Orders in FishBase have at least one observed trophic level.

Pauly and Palomares (2000) and Pauly *et al*. (2001) pointed out two properties of trophic levels relative to body size: (1) small fish or fish larvae feed on zooplankton (not on phytoplankton, even if they later become herbivores) and (2) the trophic levels of closely related species show a correlation with body size such that trophic level increases with body size in carnivores and decreases in omnivores and herbivores (Fig. 2). Their approach is adopted in Equation 1.

$$troph = 3.27 + b \times log_{10}(L_{max}) \quad (1)$$

where *troph* is the estimated trophic level, 3.27 is the median observed trophic level of 26 species with maximum lengths less than 3 cm, L_{max} is the maximum reported length (in cm) for the species for which the trophic level is to be predicted, and *b* is the slope of a linear regression with the intercept forced to 3.27, fitted to trophic levels versus $log_{10}(L_{max})$ of the closest related species. In FishBase, these preliminary trophic levels are stored in the Estimate table, separate from the observed data in the Ecology, Food items and Diet tables. In https://www.fishbase.org, these preliminary trophic levels are shown near the bottom of a species summary page in the section 'Estimates based on models.' For the purpose of this study, trophic levels were grouped in 5 categories from herbivores to top predators as shown in Table II and Fig. 4.

Table II. – Assignment of trophic groups by trophic level for 31,134 species of fishes with observed or predicted trophic level information in FishBase. See Figure 5 for number of species by trophic group.

Trophic group	Trophic level
Herbivores/Detritivores	2.0-2.2
Omnivores	> 2.2-2.8
Low-level predators	> 2.8-3.8
Mid-level predators	> 3.8-4.2
Top predators	> 4.2

Evolutionary age of Orders was approximated from the TimeTree project (Kumar *et al*., 2017; Hedges and Kumar, 2022) for jawless fishes, hagfishes and lampreys (Agnatha, Myxiniformes and Petromyzontiformes). Recent work of Stein *et al*. (2018) on cartilaginous fishes (Chondrichthyes) was not yet integrated in the TimeTree project, resulting in several missing Orders (Echinorhiniformes, Pristiophoriformes, Squatiniformes). Hence the values from Preikshot *et al*. (2000) were used for the purpose of this study. Hughes *et al*. (2018) were followed for bony fishes (Actinopterygii) and lobe-finned fishes (Coelacantiformes and Ceratodontiformes), with a few adjustments to fit with the classification used in FishBase (Tab. III). Some other adjustments were adopted from The Fish Tree of Life project, www.fishtreeoflife.org (Rabosky *et al*., 2018).

Salinity tolerance is encoded in FishBase as Yes/No evidence of occurrence in saltwater, brackish water, or freshwater. For the purpose of this study, primary marine species were selected as saltwater = Yes and freshwater = No, and primary freshwater species as saltwater = No and freshwater = Yes, meaning that diadromous species and purely brackish water species were excluded from the analysis. For marine species in Arctic waters, brackish = No was applied in addition to exclude a few estuarine species in continental waters. Note that in the tropics, neritic species may enter freshwater bodies without the species being considered diadromous (see below).

Body shapes of fishes are encoded in FishBase in categories of 'eel-like', 'elongated', 'fusiform/normal', 'short and/or deep' and 'other', based on the judgement of the encoder when seeing an image of the species. In addition, published parameters of the length-weight relationship were available for 6,098 species and were extended to practically

Table III. – Phylogeny recognized in FishBase for 34,836 species of fishes, with indication of number and percentage of species included in this study, and the number and percentage of a total of 80 used life history strategies, defined as a combination of body size, productivity, and trophic group.

Class	Orders	Families	Genera	Species	Included	Size	Productivity	Trophic level	Strategies
Myxini	1	1	6	88	69 (78%)	Medium & Large	Low	Low-level – Top predators	5 (6%)
Petromyzonti	1	3	10	49	46 (94%)	Medium & Large	Low	Omnivores – Top predators	5 (6%)
Elasmobranchii	13	63	210	1,254	1,164 (93%)	Medium-Very large	Very low & Low	Low-level – Top predators	18 (23%)
Holocephali	1	3	6	55	55 (100%)	Medium & Large	Low	Low & Mid-level predators	4 (5%)
Cladistii	1	1	2	14	5 (36%)	Medium & Large	Low	Low-level predators	2 (3%)
Actinopteri	74	527	4,941	33,368	29,788 (89%)	Small-Very large	Very low-High	Herbivores – Top predators	52 (65%)
Coelacanthi	1	1	1	2	1 (50%)	Large	Very low	Top predators	1 (1%)
Dipneusti	1	3	3	6	6 (100%)	Medium & Large	Very low & Low	Low-level – Top predators	4 (5%)

all species based on available data for close relatives with the same body-shape (Froese *et al*., 2014). Parameter *a* of the Length-Weight function $W = a L^b$ can be interpreted as a form factor if parameter *b* is close to 3.0 (Froese, 2006). For species in which *b* is different from 3, a form factor $a_{3.0}$ can be approximated from Equation 2.

$$a_{3.0} = 10^{\log_{10}(a) + 1.358(b-3)} \quad (2)$$

where $a_{3.0}$ is the approximated form factor, *a* and *b* are the parameters of the length-weight function, and 1.358 is an empirical factor (Froese, 2006). The form factor is used to explore differences in body shape in species with different combinations of body size, productivity and trophic level.

Recent **Arctic** species composition, labelled as year 2000 for convenience, was derived from AquaMaps (www.aquamaps.org) by selecting marine fish species (saltwater = Yes, brackish = No, freshwater = No) that were predicted with a probability > 0.6 to find suitable environmental conditions north of 75° latitude. AquaMaps offers a similar prediction of species occurrences for the year 2100, assuming environmental conditions according to the high-greenhouse-gas-emissions 'business-as-usual' scenario RCP8.5 (Kaschner *et al*., 2019). That scenario was used for comparing Arctic taxonomic diversity and functional biodiversity in the years 2000 and 2100.

A function in the programming language R was developed to facilitate use of SPT-plots by interested colleagues. The input to the SPT function is a comma-separated file (CSV) containing species data in each row. A row includes information on the species' (i) taxonomy (from Class to specific epithet), (ii) trophic level, (iii) maximum recorded length and weight, and (iv) estimated resilience (*i.e*. proxy for productivity). The function accepts user-provided labels for size, productivity and class acronyms, otherwise it uses the default labels of Fig. 7. The R-code employing this function is part of the online supplementary material.

Correct assignment of species to the traits considered in this study was checked randomly overall and completely for trait-combinations with few (n < 100) species. The encoding errors that were found were corrected in FishBase. All data and the R-code used to produce the graphs are available from https://oceanrep.geomar.de/id/eprint/55211/. FishBase data can also be accessed through the R-package 'rfishbase' https://cran.r-project.org/web/packages/rfishbase/rfishbase.pdf.

RESULTS

Maximum body size

FishBase had information on maximum body weight for 31,134 species. The smallest estimated weight was for Alor clingfish (*Aspasmichthys alorensis* Allen & Erdmann, 2012) with 0.8 cm standard length and a body weight of 0.004 g. The largest fish is the whale shark (*Rhincodon typus* Smith, 1828) for which a maximum length of 20 m and weight of 34 tonnes has been reported (Chen *et al*., 1999). The geometric mean weight across all fishes was 37.2 g ($\log_{10} = 1.57$, SD = 1.27). The ranges for the size classes used in this study are shown in Fig. 1. The body weights of fishes span altogether 10 orders of magnitude, with 2-3 orders of magnitude per size group. Most species have medium body size, while about 5,000 species each have small or large body size. The fewer than 100 very large fish show up as outliers beyond

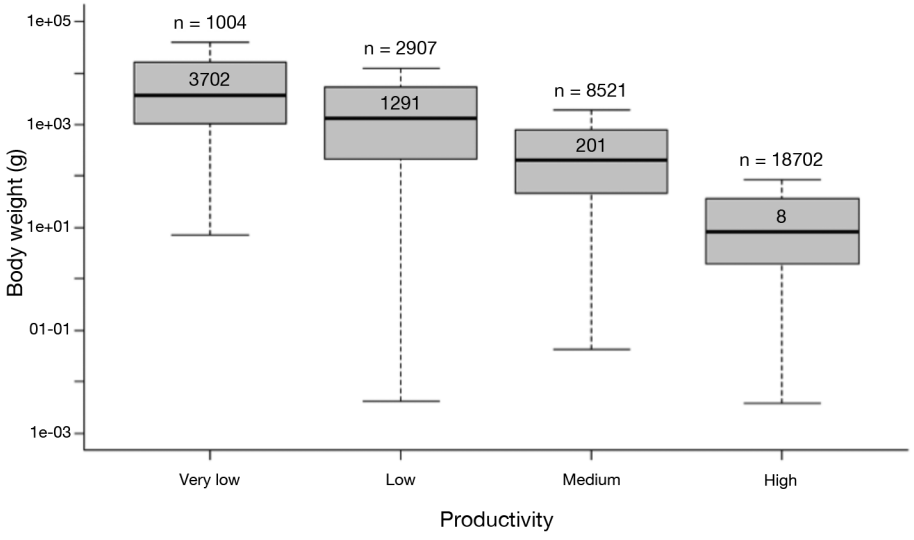

Figure 3. – Boxplot of body weights by productivity group, with indication of number of species (n) and median body weight in grams.

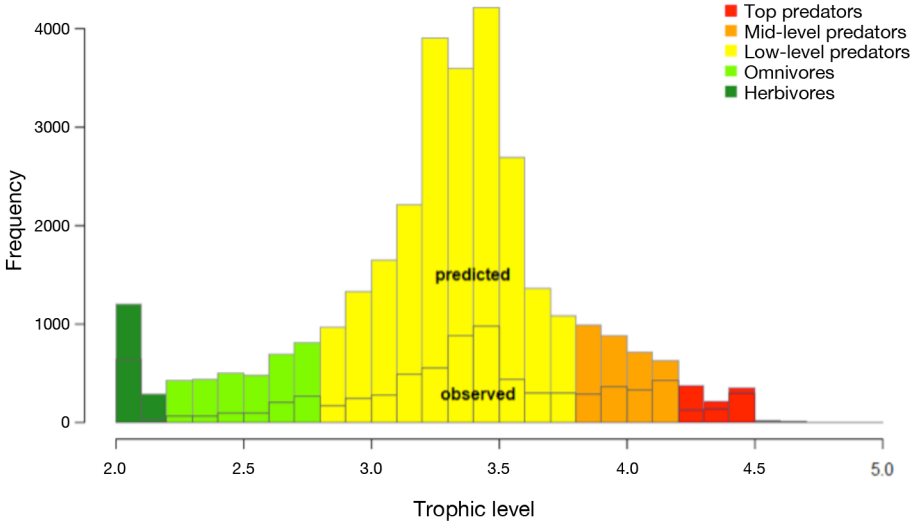

Figure 4. – Histogram of observed (lower bars) and predicted (upper bars) trophic levels. Note that the Herbivores group includes detritivores.

three standard deviations in the tail of the lognormal distribution of body weights (Fig. 1).

Productivity

Productivity and body size of fishes are inversely related, with the range of body weights within productivity groups spanning up to 6 orders of magnitude (Fig. 3). Small fishes with high productivity are the most common group, with close to 20,000 species, while about 1,000 species have very low productivity and large to very large body size.

Trophic groups

For the purpose of this study, species were assigned to 5 trophic groups from herbivores (including detritivores) to top predators, based on their respective trophic level (Tab. II, Fig. 4). The most common trophic group among fishes are mostly zooplankton-feeding low-level predators with over 22,000 species, whereas only over 1,200 species are herbivores, and less than 1,000 species top predators (Fig. 5). Trophic level and body size are correlated such that herbivores/detritivores tend to be slightly larger than omnivores and low-level predators, and mid-level and top predators tend to be larger than the other groups. The range of body weights within trophic groups spans 4-5 orders of magnitude (Fig. 5). Median body weight increases by an order of magnitude from low-level to top predators, as predicted by predator-prey size ratios in fishes (Ursin, 1973; Pauly, 2000; Brose *et al*., 2006).

Contrasting trophic level with productivity shows a slight decline in median trophic level from about 3.7 in species with very low productivity to 3.2 in species with high productivity (Fig. 6). Trophic levels within productivity groups reach from omnivore to top predator for very low productivity, from herbivore to top predator for low and medium pro-

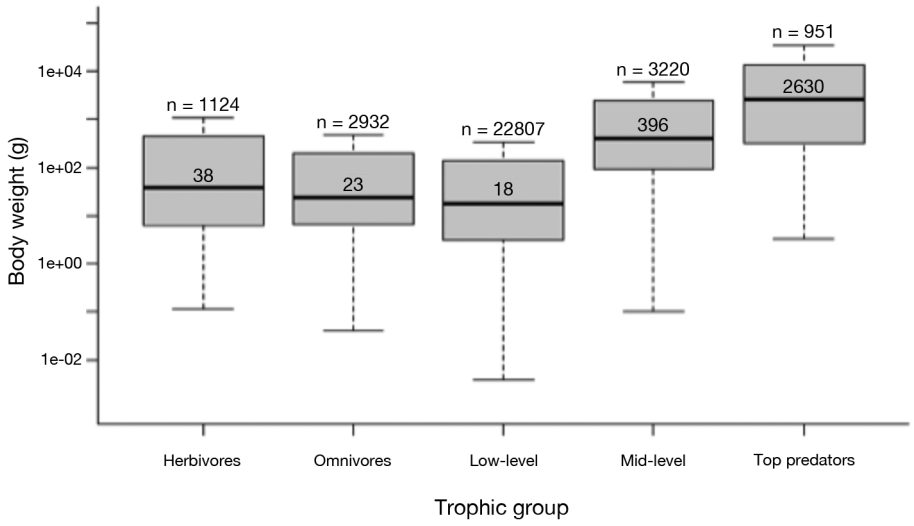

Figure 5. – Body weight distributions by trophic group, with indication of number of species (n) and median body weight in grams. Note that herbivores group includes detritivores.

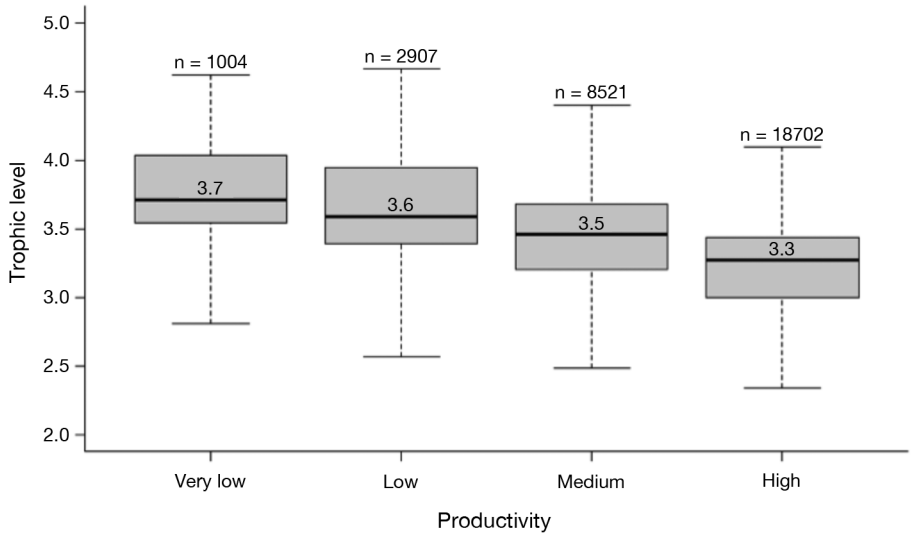

Figure 6. – Boxplot of trophic levels by productivity group, for 31,148 species of fishes, with indication of median trophic level and number of species (n).

ductivity, and from herbivore to mid-level predator for high productivity.

Phylogeny and life history strategies

In FishBase, the fishes of the world were assigned to eight Classes, 93 Orders, 601 Families, 5,176 Genera, and 34,836 Species (see https://www.fishbase.ca/tools/Classification/ClassificationTree.php), largely following Eschmeyer's Catalog of Fishes (Fricke *et al*., 2022). Information about body size, productivity, trophic level and body shape were available for 31,134 (89%) of these species and were used in this study (Tab. III).

Viable combinations of maximum body size, productivity, and trophic level

The number of categories for maximum body size (4), productivity (4), and trophic level (5) allow for 80 theoretical combinations, which are proposed as main life-history strategies. In order to facilitate visualization and exploration of the use of these life history strategies by extant species of fishes, a new type of functional biodiversity plot was developed, with a four-by-four size-productivity matrix, with each of the resulting 16 cells showing coloured horizontal bars representing trophic groups from herbivores/detritivores (dark green) to top predators (red). The width of the bars is proportional to the number of species within that trophic group. At the bottom of each cell, there is an indication of the phylogenetic Classes the species in the cell belong to, ordered by decreasing frequency. The number in the upper right corner of each cell indicates the number of species. A second number below that indicates the median age of the Orders to which the species belong, as an indication whether the species in the cell are mostly recently evolved or evolutionary old.

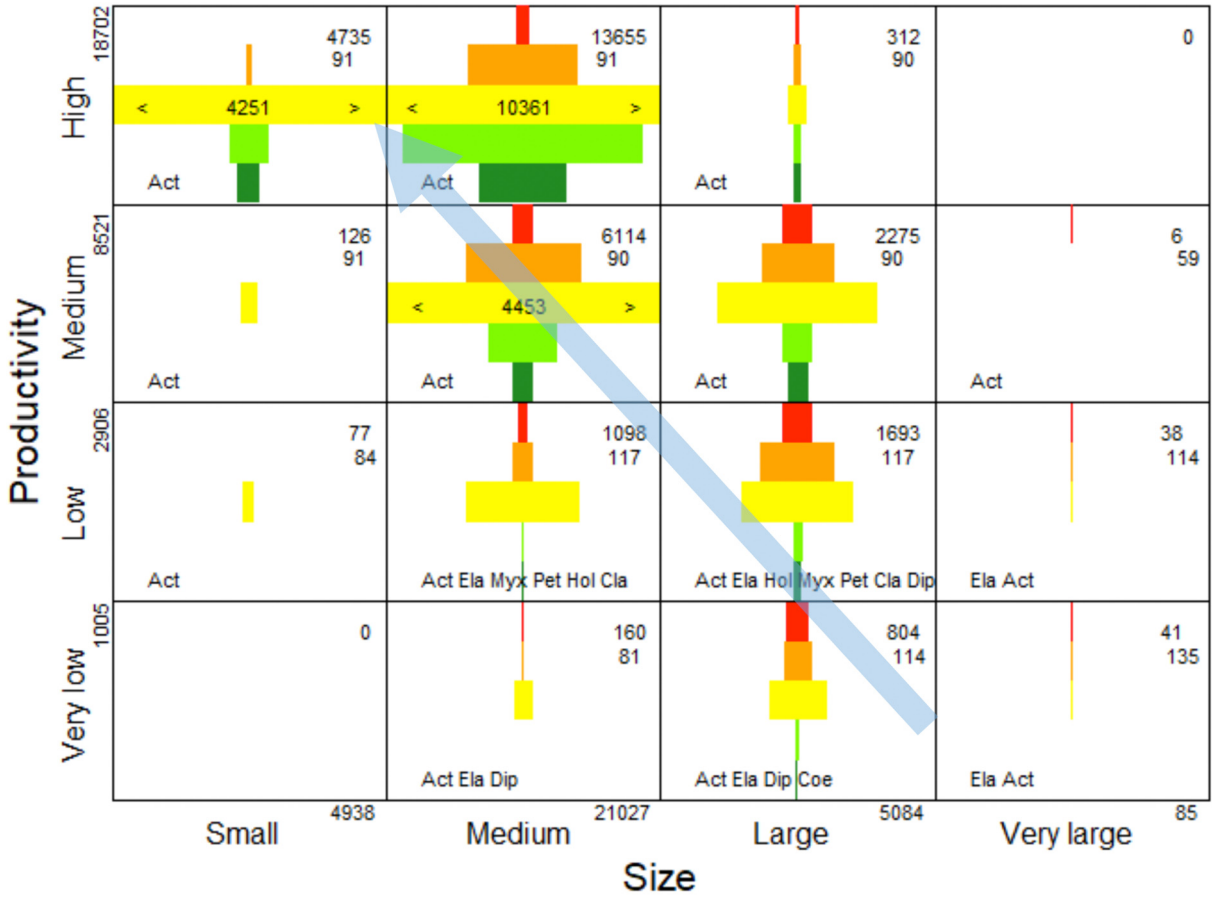

Figure 7. – Functional biodiversity plot for 31,134 species of fishes with body weight, productivity and trophic level information in FishBase. The colours indicate the trophic groups from herbivore (dark green) to top predator (red) as described in Fig. 4. The width of the bars reflects the number of species in a trophic group, with cell width representing 2,000 species. Larger numbers per group are indicated by a number within pointy brackets. The numbers in the upper-right corners indicate the number of species assigned to a cell and the median evolutionary age (in millions of years) of the Orders the species belong to. The numbers left of the rows and below the columns indicate the sum of the respective species. The blue arrow indicates an evolutionary axis from few large and old species with low or very low productivity to many small and medium-sized recently evolved species with high productivity.

The SPT-plot for all of the 31,134 species of fishes with available data suggests that the most used strategies follow a diagonal axis (blue arrow in Fig. 7) from large fishes with very low productivity to small and medium-sized fishes with high productivity. This lower-right to upper left axis seems evolutionary in origin, as indicated by (1) the presence of evolutionary old Classes in the mid- and lower right cells, (2) a decrease in median evolutionary age of the Orders to which the species belong along the axis, and (3) an 18-fold increase in species numbers, also along the axis. All trophic levels from herbivory/detritivory to top predators are used in the cells along the axis. In contrast, species numbers drop off steeply to the left and right of the evolutionary axis, with only few trophic groups being used there. Along the axis, trophic groups from low-level to top predators show the expected pyramid form of declining species numbers with increase in trophic level, as is also visible in Fig. 4. In contrast, in cells further away from the evolutionary axis, herbivores/detritivores and omnivores are mostly absent and the trophic pyramid from low-level to top predators is much less pronounced or incomplete.

Low-level predators are the most common trophic group, overall (Fig. 4) as well as across the 16 size-productivity strategies. Herbivory/detritivory is the least used trophic group across the 16 size-productivity strategies, although the number of herbivores/detritivores is slightly higher than the number of top predators (Fig. 5). Digestion of plant material requires maintenance of low pH levels in the stomach, which consumes metabolic energy that is more readily available in species with high productivity, where indeed levels of herbivory and omnivory are highest (see Fig. 7 and discussion below).

Among the species deviating from the evolutionary axis are, for example, small mid-level predators with high productivity (Fig. 7). Among them are small stargazers that hide in the mud to prey on small fish and invertebrates, small

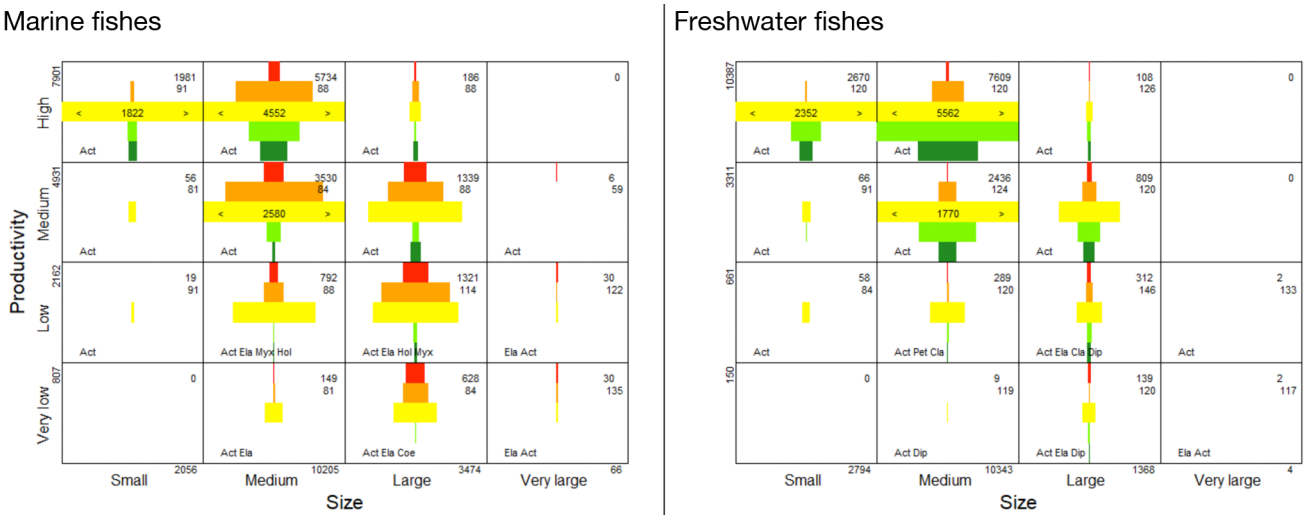

Figure 8. – Comparison of live history strategies of 15,801 marine and 14,509 freshwater species of fishes. Cell-width represents 1,000 species. See legend of Fig. 7 for description of the various labels and numbers.

reef-associated predators of fish eggs and larvae, parasitic catfishes, cleaner wrasses and false cleaner wrasses that use mimicry to bite skin pieces out of much larger fish, *i.e.*, all species that have a higher trophic level than expected from their body size. Another group deviating from the axis are medium-sized top predators with very low productivity. This includes small deep-water lantern sharks and small catsharks with very low fecundity as well as deep-sea grenadiers and polar fish-hunting eelpouts. Twenty-seven combinations of size, productivity and trophic group (out of 80 possible combinations, *i.e.*, 34%) are not used by extant species, such as combinations of small size and very low productivity and very large size and high productivity.

Life history strategies of marine versus freshwater species

A major distinction between species of fishes is their salinity tolerance (Berra, 2001) and thus their occurrence in freshwater or marine habitats. For a comparison of life history strategies, data were available for 15,801 primarily marine and 14,509 primarily freshwater species, excluding diadromous and purely brackish water species (Fig. 8). While the numbers of small- and medium-sized fishes are similar in marine and freshwater habitats, there are only few very large fish and only about half as many large fish in freshwater compared to marine waters. Similarly, while there are about the same numbers of marine and freshwater species with medium or high productivity, there are fewer freshwater species with very low or low productivity. While the numbers of low-level predators are about the same, there are more mid-level and top predators in marine waters and more herbivores and omnivores in freshwater (Fig. 8). Note also that the median evolutionary age of the Orders of freshwater fishes is higher than that of marine fishes, overall (120 *vs* 88 million years) as well as in most of the cells in Fig. 8.

Impact of climate change on functional biodiversity in the Arctic

Polar seas are predicted to see major changes in environmental conditions caused by climate change (Cheung *et al.*, 2009; Bennett *et al.*, 2015). Recent community composition, labelled here as year 2000, shows the presence of 92 species of marine fishes in Arctic waters, with a general increase in species numbers from few large or very large species with very low productivity to medium-sized fishes with medium productivity (Fig. 9). Small-sized species or species with high productivity are absent, as are herbivores or omnivores. Zooplankton-feeding low-level predators are the most common trophic group, same as across all species of fishes. The two very large species present in 2000 are the Greenland shark *Somniosus microcephalus* (Bloch & Schneider, 1801) and Atlantic halibut *Hippoglossus hippoglossus* (Linnaeus, 1758). Ray-finned fishes and elasmobranchs are the only Classes of fishes that are represented. Median evolutionary age in Arctic fishes (81 million years) is slightly lower than in all-marine fishes (88 million years, Fig. 8).

In 2100, the number of Arctic fish species is predicted to nearly triple to 263, with chimaeras and hagfish as additional Classes. As additional very large species, basking shark *Cetorhinus maximus* (Gunnerus, 1765), king of herrings *Regalecus glesne* Ascanius, 1772, and ocean sunfish *Mola mola* (Linnaeus, 1758) are predicted to expand their range north of 75° latitude. While most of the species predicted to be present in 2100 are still medium-sized zooplankton-feeding low-level predators, the number of top predators is predicted to increase more than five-fold from 5 to 27. Some small fish are predicted to extend their range into Arc-

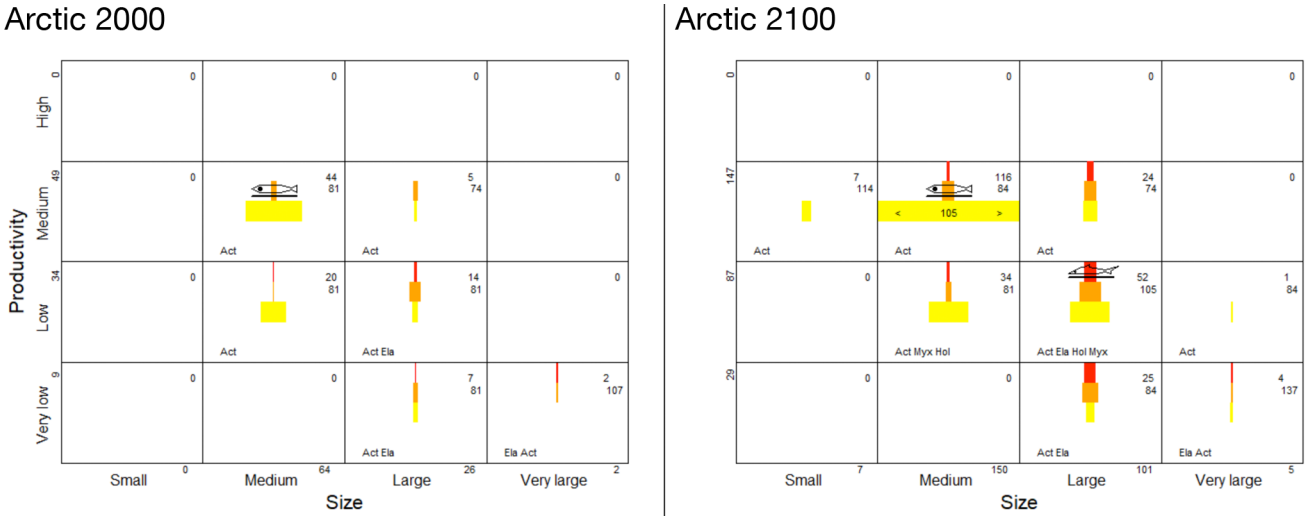

Figure 9. –Life history strategies of 92 marine fish species present in Arctic waters north of 75° latitude in around the year 2000 compared with the functional biodiversity of 263 species of fishes predicted to be present in the year 2100. Cell-width represents 100 species. The pictogram of an elongated benthic species of medium body size, medium productivity and mid-level predator trophic level represents the endemic saddled eelpout (*Lycodes mucosus* Richardson, 1855), whereas the pictogram of a benthic shark represents several large top-predator shark species that are predicted to newly arrive in Arctic waters in 2100.

tic waters, as a first in this currently unoccupied size group. The number of herbivores or omnivores predicted for 2100 remains zero.

Body shape

The SPT-plot can also be used to explore the frequency distribution of other traits of extant fish species within SPT-space. The example used here is the form factor $a_{3.0}$ (Equation 2). The overall median form factor is 0.011. It indicates fusiform body shape, as displayed by the vast majority of fishes, and is dominant along the evolutionary axis in herbivores to midlevel predators (Fig. 10). Left and right of the axis, as well as in top-predators and most very large fish, the form factor tends to fall below a value of 0.08, indicating a more elongated body shape as displayed by sharks, barracudas, or pikes (Froese, 2006). An elongated to eel-like body shape (median $a_{3.0}$ = 0.0038) is dominant in the 160 low-level to top predators with medium body size and very low productivity. That group of species consists mostly of small sharks, grenadiers, and other deep-sea species.

DISCUSSION

The purpose of this study was to present a new functional biodiversity plot that facilitates the visualization and exploration of a combination of traits for a large number of species. The new plot provides a framework of body size, productivity, and trophic level, with additional indication of phylogenetic classes and evolutionary age. For demonstration purposes this framework was applied to 31,134 species of fishes for which information was available in FishBase, as well as to subsets thereof, such as marine versus freshwater species and recent versus future occurrence of fish species in Arctic waters. As an example of the analysis of additional traits, the median form factor was explored as an indicator of the distribution of body shapes in SPT-space. Because of the demonstration purpose of this study, the discussion of the results below is exemplary, short, preliminary, and by no means exhaustive. It is meant to demonstrate the usefulness of the SPT-framework and to instigate further research of functional biodiversity in fishes.

With over 31,000 species of fishes examined, the data used in this study are close to a census of all known fishes (see Table II), meaning that observed differences in species numbers between categories are more likely real than being caused by random sampling effects. Therefore, no sample statistics such as confidence limits or *t*-tests were applied and only substantial differences in median values were considered and their practical significance discussed. Also, no attempt was made to produce new estimates for parameters *a* and *b* of the general $Y = a\ W^b$ power law that relates most traits (*Y*) to body weight (*W*) (Huxley, 1932; Peters, 1983; Brown *et al.*, 2004). Rather, the purpose of this study is to present a new framework that allows visual detection, examination and single-species-level verification of functional biodiversity patterns across phylogeny, ecosystems, and evolutionary as well as current time spans. Rather than trying to understand and properly interpret the output of complex, multidimensional statistical methods, the approach followed in this study is to present the known traits in a simple framework that illustrates their actual interaction through their co-

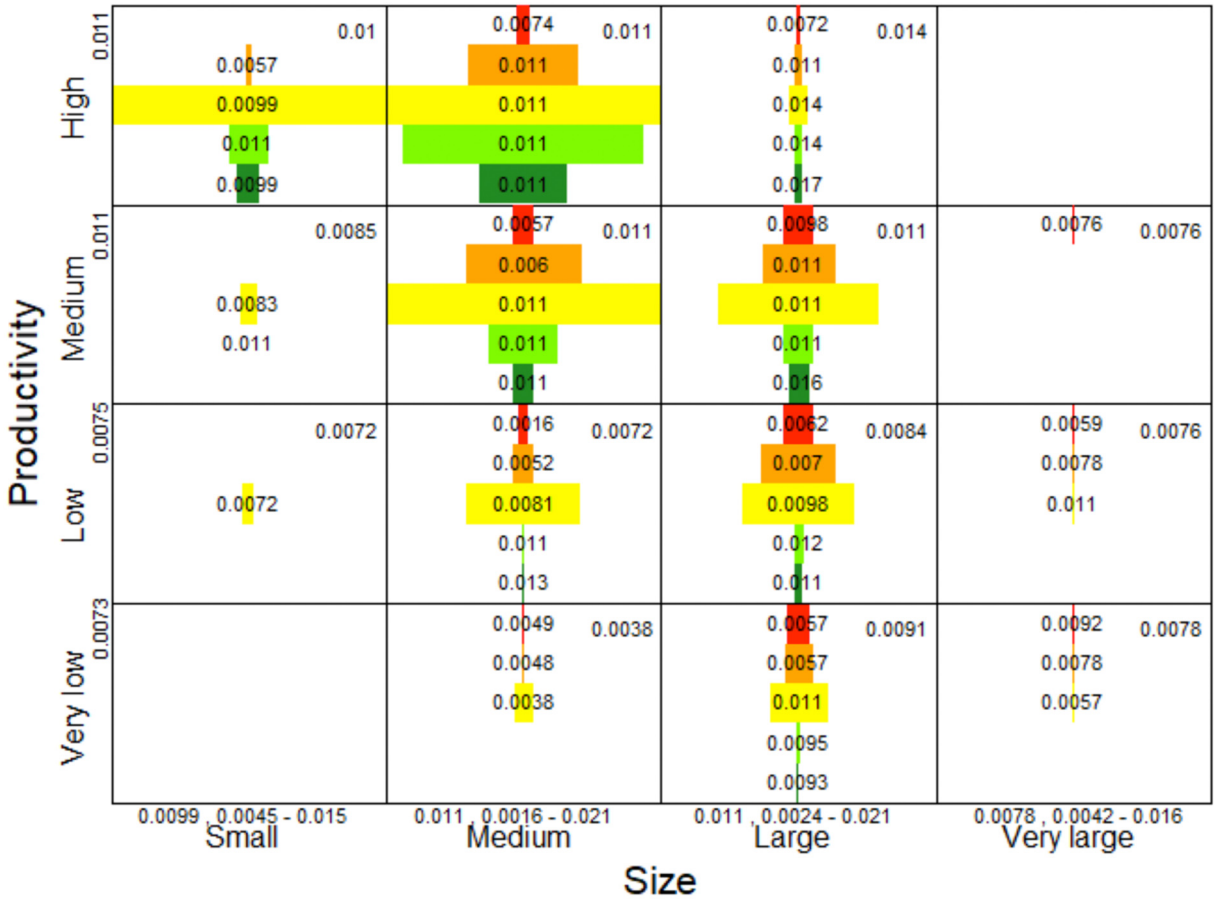

Figure 10. – Distribution of body shapes in SPT-space for 31,134 species of fishes, where body shape is expressed by the median form factor (Equation 2). The numbers within the trophic level bars give the median form factors for that level, the numbers in the upper right corners are the median form factor for each cell, the numbers left of the rows indicate the median form factor, and the numbers below the columns indicate the median form factor as well as the 5th and 95th percentiles. Numbers, ages and Classes of species per cell are the same as in Fig. 7. Cell-width represents 2,000 species.

occurrence in species. In other words, the emphasis of the SPT-framework is to facilitate exploration and development of hypotheses about functional biodiversity as a prelude to formally testing such hypotheses with more sophisticated multidimensional statistical methods (*e.g.*, Magneville *et al.*, 2022).

Maximum body size, productivity and trophic level

There is an amazingly wide range of traits with power law correlations with body weight, including many well-known correlates such as age, growth rate, swimming velocity and various flux rates. Lesser-known attributes such as duration of sleep, survival of starvation, and lower critical temperatures are also correlated with body weight (see lists in Peters, 1983 and examples in Brown *et al.*, 2004). In fishes, body weight displays a well-formed lognormal distribution around a peak of about 37 g (Fig. 1), spanning 10 orders of magnitude from about 0.04 g to 34 tonnes, with only a few species of whales being heavier. We surmise that the lower size limit may be caused by the complex vertebrate body plan with its endoskeleton losing its advantage in 1 cm long species (close to larval-size), where exoskeletons or muscle-supported body walls provide a much simpler structural solution. Another reason may be the typical diameter of fish eggs of about 1 mm (Pauly and Pullin, 1988) (Fig. 11), which is about the same as the body diameter in very small fishes and which may pose a lower body size limit for fish who need to produce several such eggs for successful reproduction.

Referring to insects, May (1978, 1986) proposed that highest species richness occurs among small, but not the smallest species. That pattern certainly holds true in fishes (Figs 2, 7) in marine and freshwater habitats (Fig. 8), and also in cold Arctic waters (Fig. 9), lending support to the hypothesis that smaller fish with higher metabolic rates have shorter generation times, faster evolutionary dynamics and higher rates of speciation (Brown *et al.*, 2004).

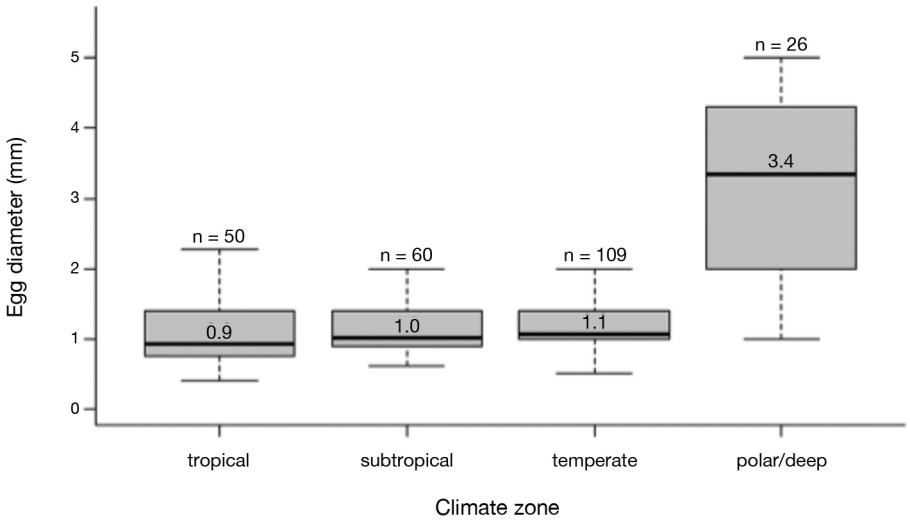

Figure 11. – Boxplot of egg diameters (n = 245) of 156 species of ray-finned fishes by climate zone, as compiled in FishBase. Numbers within the boxes indicate the median diameter. The smallest reported diameter for polar/deep fishes is 1 mm.

Mean trophic level is the measure of choice for expressing the position of an organism in the food web (Christensen and Pauly, 1992). The histogram of trophic levels (Fig. 4) shows a roughly normal distribution with a peak of zooplankton-feeding fishes at about 3.3, but with raised lower tails at 2.0 for herbivores (because plants and detritus have the lowest trophic level of 1 by definition, and feeding only on those gives trophic level 2) and at 4.4-4.5 for top predators. A scatterplot of trophic levels over body weight (Fig. 2) reveals constraints of body size on trophic level: very small fish species do not feed on µm-sized phytoplankton, algae, or higher plants. Instead, they feed on mm-sized zooplankton, presumably because they do have neither mouths large enough to consume other fish, nor body cavities large enough for the long gut typically required to extract nutrients from algae and higher plants (Fig. 2), giving them a trophic level slightly above 3.

Viable combinations of maximum body size, productivity, and trophic level

Maximum body size, productivity and trophic level are main life history traits with roughly lognormal or normal frequency distributions (Figs 1, 2, 4). These traits have co-evolved as is clearly visible in their respective one-on-one relations (Figs 3, 5, 6). However, there is a high degree of variability in the combinations that are realized. Of 80 theoretically possible combinations of traits, here referred to as life history strategies, only 53 (66%) are occupied by extant species of fishes. Usage of these 'viable' life history strategies varies from 6 very large top predators with medium resilience to 13,655 medium-sized low-level predators with high resilience (Fig. 7). These six very large top predators are three billfishes, Istiophoridae (Blue marlin, *Makaira nigricans* Lacepède, 1802, Black marlin *Istiompax indica* Cuvier, 1832, Striped marlin *Kajikia audax* Philippi, 1887), the Swordfish *Xiphias gladius* Linnaeus, 1758, Xiphiidae, and two tunas, Scombridae (Atlantic bluefin tuna *Thunnus thynnus* Linnaeus, 1758, Pacific bluefin tuna *Thunnus orientalis* Temminck & Schlegel, 1844). Their combination of traits has evolved only recently, having the lowest median age of the Orders in our analysis. The late evolution may be explained by the ecology of large scombroids, which requires evolving extremely sophisticated gills whose huge surface area is made possible by gill lamellae being so thin that 1 mm of gill filament can include up to 120 of them (Muir and Hughes, 1969). This singular adaptation enables large scombroids to roam the oceans, but they cannot inhabit coastal waters, which contain grit that would clog their gills. Thus Ellis (2008) mentions that, after a storm battered an Australian southern bluefin tuna (*Thunnus maccoyii* Castelnau, 1872) farming operation, the fish "were suffocated as their gills became clogged in swirling clouds of silt, excreta, and sediment. Between 65,000 and 75,000 tunas died".

There is an apparent development from a few evolutionary old large to very large predators with very low productivity towards many evolutionary younger small to medium sized fishes with high productivity using the full range of trophic groups. The change in size from large to small body size seems to contradict Cope's (1887) rule that animal lineages tend to evolve toward larger sizes over time, as recently shown for tetraodontiform fishes (Troyer *et al.,* 2022); however, the opposite trend was found in hammerhead sharks (Family Sphyrnidae) (Lim *et al.,* 2010). Our results represent a current across-lineages snapshot in evolutionary time, where mostly large species of the old lineages have survived and many new lineages with mostly small to medium-sized species have appeared. In other words, the within-lineages trend towards larger size and lower productivity (Cope's rule) is superseded by the across-lineages (and sometimes within, see Lim *et al.,* 2010) trend towards small to medium

sized fishes with high productivity. The evolutionary trend as hypothesized here must be tested further, in particular to take into account the size of species at the time of speciation.

Species numbers are highest and traits are more fully used along the proposed evolutionary axis indicated by a blue arrow in Fig. 7. Species numbers and used traits decrease steeply to the left and right of the evolutionary axis, with the extreme corners of small size with very low productivity and very large size with high productivity remaining unoccupied, presumably representing non-viable combinations of viable traits or abandoned evolutionary pathways.

Productivity is a proxy of the intrinsic rate of population growth (Tab. I) and ultimately of whole-body metabolism, which is known to decline with increase in body weight (Blueweiss, 1978; Brown *et al*., 2004; Pauly and Froese, 2021), thus explaining the lower-right to upper-left direction of the evolutionary axis in Fig. 7.

Comparison of life history strategies of marine versus freshwater fishes

Comparing body size of marine and freshwater fishes shows only few very large freshwater fish and about half as many large fish. Plate tectonics, mountain ranges and waterfalls have created hard boundaries between continental freshwater habitats (Matthews, 1998) that do not occur between marine habitats, where the global distribution of home-ranging reef fish such as the lined surgeonfish *Acanthurus lineatus* (Linnaeus, 1758) may reach from East Africa to the Hawaiian Islands (Randall, 1986). The smaller freshwater habitats provide less niche space for large and very large species, as predicted by the hypothesis of shorter trophic chains in smaller ecosystems (Schoener, 1989; Rao *et al*., 2015; Sommer *et al*., 2018).

There are nearly twice as many herbivorous species in freshwater (793) than in marine waters (402), presumably because of a much larger diversity of plants and fruits in and around freshwaters providing food to the fish of lakes and rivers. Another likely explanation is the typically lower pH of freshwater, meaning that the low pH required in the stomach for digestion of plant material (pH 2-3; Lobel, 1981) is less costly to maintain in freshwater (pH about 6-8) than in seawater (pH about 8.1).

Also note that many fish species inhabiting tropical coastlines readily enter freshwaters, which can lead to rivers and lakes in some countries being dominated by marine fishes (Herre, 1959; Pauly *et al*., 1990). This phenomenon may be due to the cost of osmoregulation increasing less than overall metabolic rate with temperature (Edwards and Marshall, 2012), which would result in osmoregulation representing a smaller fraction of their overall metabolism than in fish from colder climate.

A major feature of freshwater fish is the frequent occurrence of air-breathing. While this mode of respiration is limited in marine fishes to a few coastal species (notably the mudskippers of the Family Oxudercidae) and to a few diadromous fishes such as tarpon (*Megalops* spp.), there are many species and families of freshwater fishes whose adults are facultative or obligatory air breathers, such as lungfishes, labyrinth fish, bichirs, ropefish, bowfins, gars, and clariid catfish (Johansen, 1970; Graham, 1997). Air-breathing not only allows hypoxic freshwater bodies to be inhabited by fish, but also allows them to attain sizes and growth rates which rival those of the fastest growing marine fish. One example in FishBase is the air-breathing Mekong giant catfish (*Pangasianodon gigas* Chevey, 1931), with VBGF parameters W_∞ = 345 kg and K = 0.085 year^{-1}, which are comparable to those of Atlantic bluefin tuna (*Thunnus thynnus*). In other words, air-breathing may result in higher productivity than found in species with similar size and fecundity (Tab. I).

Vega and Wiens (2012) suggest that, although the ancestors of all fish were marine, recent ray-finned marine fishes are derived from freshwater ancestors. That hypothesis is consistent with the data shown in Fig. 8, where overall and in most cells, evolutionary age of marine fishes is younger than that of freshwater fishes.

Impact of climate change on functional biodiversity of Arctic fishes

The Arctic Ocean is a large, cold, ice-covered ecosystem consisting of deep basins and intercontinental ridges, with very little, if any, daylight from October to March. Metabolic theory (Brown *et al*., 2004) predicts that the low kinetics of biochemical reactions in such cold environments result in slow ecological and evolutionary dynamics with low speciation rates. The metabolic restrictions may also explain the reduced range of functional biodiversity among the few fish species in this large ecosystem. The strategies used in this extreme environment are not specialist or rare strategies that may incur additional energetic cost, but rather are among the most common and presumably least-energetic-cost strategies represented along the evolutionary axis proposed for all fishes. The low abundance of herbivores and omnivores is due to the winter-long absence of light and thus of plants, and the presence of only few top predators is due to the scarcity of mid-level predators as prey. The low kinetics of biochemical reactions in Arctic waters also explain the complete absence of species with high productivity or small body size. Another reason for the lack of small fishes may be the increased diameter of eggs in polar waters (Marshall, 1953) (Fig. 11), which requires females to be large enough to produce a sufficient number of such large eggs. Marshall (1953) proposes that the production of large eggs hatching into large larvae is correlated with the low concentration of planktonic food in polar waters: larger larvae have lower food requirements in relation to body size and their increased powers of swimming allow them to search a wider range for suitable food.

The Arctic Ocean is among the most rapidly warming marine ecosystems on Earth, turning it from a permanent to a seasonally ice-covered ocean (Post *et al*., 2019; Snoeijs-Leijonmalm *et al*., 2022). The warming will allow many species of fishes to extend their northern ranges into Arctic waters. We predict the future Arctic species composition based on the assumption that observed environmental preferences of fish species in adjacent waters will be unchanged in 2100, that no other factors prevent such northward extension, and that the environmental changes predicted by the RCP8.5 scenario (Kaschner *et al*., 2019) will apply. If these assumptions hold true, the number of fish species in Arctic waters is predicted to about triple in numbers and the number of top predators is predicted to increase five-fold. In other words, current Arctic fishes may be outcompeted by new arrivals at a ratio 2:1 overall and 4:1 with regard to top predators, which could cause the extinction of endemic species with low competitive or predator-avoidance skills. At the same time, the spatial range of environmental conditions currently preferred by Arctic species will shrink drastically (Kaschner *et al*., 2019; Brito-Morales *et al*., 2020). The number of herbivores or omnivores is predicted to remain low, because other than temperature, the long absence of daylight and thus plant growth will remain. In summary, the impact of climate change on functional biodiversity will be extraordinarily strong in Arctic waters, with a high probability that several endemic species may go extinct.

Body shape

Body shape as represented by the median form factor was used here as an example of presenting and exploring the distribution of other traits in SPT-space. The null-hypothesis of equal distribution of body shapes is refuted by the tendency of top predators such as billfishes and swordfish as well as very large fishes and medium sized fishes with very low productivity to be elongated rather than fusiform. Ryabov *et al*. (2021) explored the relationship between body shape and species diversity in phytoplankton. They found that in phytoplankton the greatest variations in body shape occurred in medium sized species, whereas small and large species tended to have a narrow variety of mostly spherical or cubic body shapes. The difference in variation of body shapes with size is confirmed in fishes, where medium-to-large sized fishes have a median fusiform form factor of 0.011, with 90% of the form factors falling between eel-like 0.0016 and spherical 0.021 (Fig. 10). In contrast, small fishes have a slightly elongated fusiform median body shape of 0.0099, with a much narrower 90% range of 0.0045-0.015, and very large fishes have an elongated body shape with 0.0078, and with a similar narrow range from 0.0042-0.016. The difference of spherical/cubic body shape in small and large phytoplankton organisms versus fusiform-elongated body shape in small and very large fishes is probably due to different forms of propulsion, with passive drifting or limited propulsion with flagella in phytoplankton versus fin and whole-body movements in most fishes. This exploration of body shapes in SPT-space is an example of the power of the simple SPT-framework to explore existing hypotheses and to formulate new ones, which then can be explored by more sophisticated methods such as the multidimensional functional biodiversity tool (mFB) (Magneville *et al*., 2022).

There are many traits whose distribution in SPT-space could be explored in a manner similar to the form factor, such as mean environmental temperature, or mean depth, or fecundity, or predator-prey size ratios, to name a few.

Placing of individual species within the functional biodiversity framework

The SPT-framework can be used to show the combined traits of a single species against the background of all other species or the other species in its respective ecosystem. For example, the position of the endemic saddled eelpout (*Lycodes mucosus* Richardson, 1855), one of very few medium-sized mid-level predators with medium productivity in Arctic waters, is shown against the functional biodiversity of all other Arctic species in the year 2000. The used pictogram indicates the elongated body shape of the species and its demersal habitat (Fig. 9, panel for 2000). Very few top-predators are present in 2000 to potentially feed on it. In contrast, in the year 2100, the number of potentially competing species in its SPT-space is predicted to double, and the number of top-predators is predicted to increase 5-fold, as indicated by the pictogram of benthic sharks in the top-predator group of large species with low productivity (Fig. 9, panel for 2100). Such body-shape-habitat pictograms can be placed in SPT-graphs for any ecosystem to discuss functional biodiversity at the species level.

Additional thoughts about the usage of size-productivity space

One of the vacant spaces in the SPT plot (Fig. 7) is very large body size combined with high productivity. It is widely recognized that metabolism scales as less than unity with body size, during ontogeny as well as across species of different body size (Blueweiss *et al*., 1978; Brown *et al*., 2004; Pauly and Froese, 2021). Oxygen consumption is often used to measure metabolic rate and thus follows the same < 1 scaling. Such scaling means that an organism growing to a larger body size increases its metabolic rate less than the relative increase in body size, thus reducing its oxygen consumption per unit of body size. Consequently, increase in body size must end once relative oxygen consumption reaches the minimum required for maintenance metabolism (Pauly, 2021). This also means that adults of very large species, having reduced their relative metabolism during ontogeny, must have lower relative metabolic rates and productiv-

ity than their juvenile stages, which have similar metabolic requirements as other species with similar maximum body size. Therefore, very large fish can only have less than high productivity (Fig. 7).

The same metabolic reasoning also explains the scarce use of medium body size and very low productivity (Fig. 7): the small juveniles of the medium sized adult fish must have had higher than 'very low' productivity, which was reduced as a consequence of growth from small to medium size. In simplifying, one can imagine these juveniles as occupying the small-size-low-productivity space from which they grew into the medium-size-very-low-productivity space. No such development option is available for small species with less than 2 g body weight and where very low productivity would mean low metabolism, slow growth, late maturation, low fecundity, and low rate of natural mortality. No such species exists, although some cavefishes may get close.

Another insight may be gained by looking at the persistence of species around the proposed evolutionary axis. Iñiguez *et al*. (2022) show that, in any ranking of entities in natural, social, economic, and infrastructural systems, comprising millions of elements and timescales from minutes to centuries, entities near the top of the list tend to remain at their position much longer than entities at lower ranks. For example, if songs are ranked by the number of copies sold in the previous week, then the number one song is more likely to stay at number one than the number 50 song is to stay at number 50. If we think of the species in Fig. 7 being ranked by their inverse perpendicular distance to the evolutionary size-productivity axis, then this general property of ranking would suggest that species with the highest rank and thus closest to the axis will persist longer in evolutionary time than the more distant species. This hypothesis cannot be refuted by the median evolutionary ages of the Orders to which the species in the cells belong, and which tend to be lower with increased distance from the axis. A more robust test of the ranking hypothesis would require a better representation of the evolutionary time of persistence of species near and far from the evolutionary axis. In other words, in this example the simple SPT-framework was used to get a first assessment of the probability of a hypothesis, which here looks promising and thus may be more formally tested with better data and statistical methods.

More generally, the snapshot of recent occupancy of SPT-space by extant species makes it difficult to understand the evolution of functional biodiversity from the Cambrian to the present. Ideally, we would like to compare the recent snapshot with similar snapshots representing selected periods in geological time. Body size is readily available in fossils and productivity and trophic groups in the broad categories of the SPT-framework could be inferred from 'living fossils' or evolutionary old extant species. Such exploration was beyond the scope of this study.

CONCLUSIONS

This study presents a simple framework for exploration of functional biodiversity in size-productivity-trophic-space for small or high numbers of species. Preliminary results show an across-lineages evolutionary axis in SPT-space from few, evolutionary old, large species with very low productivity to many, evolutionary younger, medium sized species with high productivity, effectively reversing the within-lineage trend to larger size and lower productivity (Cope's rule). Trophic levels from herbivores to top-predators are only fully used close to that evolutionary axis. The axis is present across 89% of extant fish species recorded in FishBase, in marine waters and freshwaters, and in present and future Arctic waters. The existence and direction of the axis is in concordance with metabolic theory (Brown *et al*., 2004).

Functional biodiversity patterns are similar in marine and freshwater habitats, with however a substantially higher proportion (72%) of small and medium sized species with high productivity in freshwater, compared to 50% in marine waters. The Arctic Ocean was used to showcase the suitability of the SPT-framework for exploring future changes in species composition and functional biodiversity, as predicted by climate change scenarios, suggesting a loss of endemic species due to strong increase of top predators. Body shape was used as an example for studying the distribution of other traits in SPT-space. Body-shape-habitat pictograms were employed to discuss functional biodiversity at the species level in a given ecosystem.

In-depth exploration of the preliminary findings was beyond the scope of this study, which instead aimed at presenting the SPT-framework as a new simple tool for display, discussion and formulation of hypotheses which then can be tested with more sophisticated statistical tools.

Acknowledgements. – We thank Helmut Hillebrand for critical comments and Nele Rabenhorst for programming the first version of the SPT-plots in Mathematica. We thank Rachel Atanacio for creating the pictograms shown in Fig. 9. Rainer Froese and Marco Scotti acknowledge support by the German Federal Agency for Nature Conservation (BfN) with funds from the Federal Ministry of the Environment, Nature Conservation and Nuclear Safety (BMU), under grant agreement FKZ: 3521532201. The authors thank two anonymous reviewers for their useful comments.

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