

**DIVERSITY OF BRAIN SIZE IN FISHES:
PRELIMINARY ANALYSIS OF A DATABASE
INCLUDING 1174 SPECIES IN 45 ORDERS**

by

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ABSTRACT. - Absolute and relative values of brain weight are now available for 1174 species of fishes, representing 45 taxonomic orders. The original FishBase "Brains" data was assembled by the research team of Bauchot and colleagues, to which the present report adds data for species representing several additional major taxonomic groups. This database is part of the FishBase 97 package which provides researchers with a tool to explore the functional meaning of absolute and relative brain size diversity, in comparison with phylogenetic position, life history mode, locomotion, habitat, and other behavioral parameters. Several results are provided as an example of the use of these data. Galeomorph sharks and batoid rays possess the largest brains among fishes, and elongate forms with anguilliform locomotion (e.g., hagfishes, lampreys, true eels, carapids, zoarcids) possess the smallest relative brain sizes. Among teleost fishes, Osteoglossomorphs possess the largest relative brain sizes. Brain size correlations with oxygen consumption suggest that larger brains consume proportionately more oxygen, or that active fish with higher metabolic rates have larger brains.

RÉSUMÉ. - Diversité de la taille de l'encéphale chez les poissons: analyse préliminaire d'une base de données comprenant 1174 espèces appartenant à 45 ordres.

Les poids absolus et relatifs de l'encéphale sont connus chez 1174 espèces de poissons appartenant à 45 ordres. Ce rapport complète les données de départ rassemblées par l'équipe du Pr. R. Bauchot pour la partie "Encéphales" de FishBase. La base de données présentée est intégrée à la version FishBase 97 qui fournit aux chercheurs un outil pour explorer le rôle fonctionnel de la diversité des tailles absolue et relative de l'encéphale. Cette exploration peut se faire par rapport à la position phylogénétique, au mode de vie, à la locomotion, à l'habitat et à d'autres paramètres comportementaux. Plusieurs exemples d'exploitation des données sont présentés. Les plus gros encéphales sont observés chez les requins Galéomorphes et les raies. Les formes allongées à locomotion anguilliforme (myxines, lamproies, anguilles, carapidés, zoarcidés) possèdent, en taille relative, les encéphales les plus petits. Chez les Téléostéens, ce sont les Ostéoglossomorphes qui possèdent l'encéphale le plus gros. L'étude des corrélations entre la consommation d'oxygène et la taille de l'encéphale suggère deux hypothèses. La première est qu'une consommation supérieure d'oxygène est nécessaire lorsque l'encéphale est plus gros. La deuxième est que les poissons possédant une activité et un taux métabolique plus élevé ont un encéphale plus grand.

Key-words. - Myxiniformes, Petromyzontiformes, Chondrichthyes, Actinopterygii, Dipnoi, Coelacanthiformes, Brain size, Comparative morphology, Physiology, Ecology, Evolution.

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There have been numerous studies documenting patterns of brain size diversity within circumscribed groups of fishes (Table I). These investigations have been enriched and also complicated by the enormous diversity of fishes, which constitute the majority of vertebrate species. In one form or another fishes inhabit most of the aquatic habitats on earth, surviving and reproducing in the intense pressure and darkness of the deepest marine trenches (10 km), subzero Antarctic waters, torrential mountain rivers, desert hot-springs and nearly anoxic swamps. In addition to changes in body size and shape, the brains of fishes have also been modified during the course of phylogeny to suit these various life history modes and environments. It is therefore sometimes possible to use brain size difference among fishes to investigate the relationships of brain evolution with physiological and other morphological data, and to draw inferences on their ecology and life-history requirements (Bauchot *et al.*, 1989).

The "Brains" table of the FishBase 97 (Froese and Pauly, 1997) database allows inferences of this sort. This database allows researchers to address the following kinds of questions: What kinds of variation in brain size are present within and among closely related species? How much of the range of phenotypic variation observed among all fishes is represented in individual groups? What ecological and life history variables are associated with changes in relative brain size? This report provides a brief introduction to the "Brains" table of the FishBase 97 package, and illustrates several examples of how it may be used as a research tool.

Table I. - Sources of data used from surveys of brain size diversity within circumscribed groups of fishes.

Taxon	Source
Actinopterygii	Platel <i>et al.</i> , 1977; Northcutt and Braford, 1980
Catostomidae	Miller and Evans, 1965
Chaetodontidae	Bauchot <i>et al.</i> , 1989a
Cichlidae	Huber <i>et al.</i> , 1997; van Staaden <i>et al.</i> , 1997
Craniata	Crile and Quiring, 1940
Cyprinidae	Evans, 1952; Masai <i>et al.</i> , 1982; Kortschal and Junger, 1988; Kortschal and Palzenberger, 1992
Elasmobranchii	Bauchot <i>et al.</i> , 1976; Northcutt, 1977
Escoidae	Means and Lannoo, 1996
Gymnotiformes	Albert, 1999
Myxinoidei, Petromyzontidae	Ebinger <i>et al.</i> , 1983; Platel and Delfini, 1981, 1986
Notothenioidea	Eastman and Lannoo, 1996
Osteoglossidae	Bauchot <i>et al.</i> , 1994
Sarcopterygii	Northcutt <i>et al.</i> , 1978
Teleostei	Ito, 1978; Bauchot and Bauchot 1986; Bauchot <i>et al.</i> , 1979, 1989b; Ridet and Bauchot 1990a, b, 1991

MATERIALS AND METHODS

The majority of the data on brain size was assembled by the research team of Bauchot and colleagues (Bauchot *et al.*, 1979, 1989, 1994; Ridet and Bauchot, 1990a, 1990b), to which the authors have added data for species representing several additional taxonomic groups. Data are presently available for 1174 species of fishes, representing 45 taxonomic orders, including 14 perciform suborders (taxonomy following Eschmeyer *et al.*, 1997). Most of these data are available in the "Brains" table of FishBase 97 (Froese and Pauly, 1997), and some of the newer additions will be available in FishBase 98, due for release in 1998. The fishes examined were collected from all over the world over a period of many years, from such localities as the Hawaiian and Marshall Islands, New Caledonia, Queensland (Australia), Northern Marianas islands (Guam and Rota), the Philippines, Sulawesi (Indonesia), southwest India, Mauritius and Réunion, Gulf of Oman, northern Red Sea, Senegal, the Caribbean, the Sea of Cortez (Mexico), the Amazon river of Brazil and Peru, the Orinoco river of Venezuela, Honshu (Japan), many localities in the United States, France, and the North Atlantic sea. Data newly reported in the present study are listed in table II.

All fish were weighed before removal of the brain and their standard and/or total lengths taken. The brain was cut from the spinal cord at the first spinal nerves, the meninges removed, the brain blotted and weighed, and then preserved in Bouin solution. Brain size data were obtained by immersing fixed brains in fixative and weighing on an analytical balance. The accuracy of ten repeated measurements estimated on a small brain (c. 0.2 mg) was $\pm 0.5\%$. Cranial nerves were transected at the base of the brain and neither they nor the meninges, blood vessels or choroid plexus were included in the weights. The original research reported for this report was performed under guidelines established by the Japanese Society for Neuroscience.

Some specimens for some species were acquired from museum collections, commercial aquarium dealers and fishers. These include the megamouth shark *Megachasma plagios* (Ito *et al.*, 1999), the lungfish *Protopterus annectens*, the bichir *Polypterus palmus*, the sturgeon *Acipenser transmontanus*, several osteoglossomorphs, cypriniforms, tetras (Characiformes), catfishes (Siluriformes), American electric fishes (Gymnotiformes), ricefishes and needle fishes (Beloniformes), and zoarcoid percomorphs. Additional data were compiled from the literature for hagfishes, lampreys, some sharks, and several groups of non-teleost ray-finned fishes (Ito *et al.*, unpubl. data). The phylogeny of fishes used in analyses of higher level taxa was compiled from numerous sources (see Stiassny *et al.*, 1997, and references therein).

Juveniles have a larger brain relative to body weight than adults (Bauchot *et al.*, 1979) and therefore adult fishes were preferred for weight determinations. Data were also available for a size series in some species, ranging from juveniles to large adults, thus allowing the study of ontogenetic changes in brain size. In the Brains table records are presented with the following fields: Genus and Species, Species Code, Stock Code, Locality, Number, Year, Body Weight (g), Brain Weight (mg), Encephalization Coefficient 1 (EC_1), Encephalization Coefficient 2 (EC_2), Standard Length (SL in cm), Total Length (TL in cm), and Remarks. Encephalization coefficient 1 is a calculated field; $EC_1 = \text{Log}_{10}[\text{brain weight} \times 1000/\text{body weight}]$. Encephalization Coefficient 2 is also a calculated field, which standardizes brain weights over the range of body sizes according geometric considerations: $EC_2 = \text{Log}_{10}[\text{brain weight} \times 1000/\text{body weight}^{2/3}]$ (Snell, 1892; Bauchot *et al.*, 1989; Froese and Pauly, 1997).

Table II. - Body and brain weight data in grams for 41 species representing 14 orders newly reported in the present study. Taxonomy following Eschmeyer (1994). Maximum values reported for species with multiple records. N = number specimens examined.

Genus / species	Order	Body	Brain	N
<i>Megachasma plagios</i>	Lamniiformes	1,004,000.000	19.100	1
<i>Protopterus annectens</i>	Lepidosireniformes	7.660	0.224	1
<i>Polypterus palmus</i>	Polypteriiformes	65.140	0.096	1
<i>Acipenser transmontanus</i>	Acipenseriformes	3,520.000	0.650	6
<i>Lepisosteus osseus</i>	Lepisosteiformes	35.860	0.200	1
<i>Heterotis niloticus</i>	Osteoglossiformes	343.300	1.600	2
<i>Osteoglossum bicirrhosum</i>	Osteoglossiformes	2.900	0.100	1
<i>Scleropages formosus</i>	Osteoglossiformes	11.000	0.300	1
<i>Scleropages jardinii</i>	Osteoglossiformes	17.300	0.300	3
<i>Pollimyrus isidori</i>	Mormyriiformes	2.070	0.115	1
<i>Esox lucius</i>	Esociformes	11,500.000	0.285	1
<i>Umbra krameri</i>	Esociformes	6.440	0.028	1
<i>Oncorhynchus mykiss</i>	Salmoniformes	280.000	0.428	1
<i>Parodon gesteri</i>	Characiformes	3.070	0.043	1
<i>Pygocentrus nattereri</i>	Characiformes	8.480	0.058	1
<i>Adontosternarchus balaenops</i>	Gymnotiformes	7.020	0.117	2
<i>Apteronotus albifrons</i>	Gymnotiformes	34.800	0.171	5
<i>Apteronotus leptorhynchus</i>	Gymnotiformes	25.210	0.150	10
<i>Brachyhyopomus brevirostris</i>	Gymnotiformes	11.460	0.090	1
<i>Gymnotus carapo</i>	Gymnotiformes	96.000	0.266	5
<i>Orthosternarchus tamandua</i>	Gymnotiformes	13.040	0.219	1
<i>Porotergus compsus</i>	Gymnotiformes	14.150	0.127	14
<i>Steatogenys duidae</i>	Gymnotiformes	5.650	0.078	1
<i>Steatogenys elegans</i>	Gymnotiformes	11.960	0.093	3
<i>Sternarchella orthos</i>	Gymnotiformes	12.150	0.131	5
<i>Sternarchella sima</i>	Gymnotiformes	32.800	0.258	5
<i>Sternarchorhamphus nuelleri</i>	Gymnotiformes	22.100	0.208	1
<i>Sternarchorhynchus curvirostris</i>	Gymnotiformes	13.000	0.179	1
<i>Diplomystes nahualbutensis</i>	Siluriformes	2.010	0.047	3
<i>Ictalurus punctatus</i>	Siluriformes	54.000	0.162	10
<i>Noturus flavis</i>	Siluriformes	23.200	0.088	10
<i>Pimelodus pictus</i>	Siluriformes	2.350	0.057	10
<i>Dermogenys megarhamphus</i>	Beloniformes	0.611	0.019	1
<i>Nomorhamphus towoeti</i>	Beloniformes	0.589	0.018	1
<i>Oryzias celebensis</i>	Beloniformes	0.452	0.015	3
<i>Oryzias duncena</i>	Beloniformes	0.242	0.014	3
<i>Oryzias latipes</i>	Beloniformes	0.315	0.012	5
<i>Oryzias natanensis</i>	Beloniformes	0.614	0.016	5
<i>Oryzias marmoratus</i>	Beloniformes	0.644	0.017	5
<i>Oryzias profundicola</i>	Beloniformes	0.594	0.016	5
<i>Lycenchelys</i> sp.	Perciformes	4.520	0.009	2

The analysis of interspecific quantitative data is the subject of a large literature which this report does not attempt to review (see Ridet and Bauchot, 1990b; Harvey and Pagel, 1991; Purvis and Rambaut, 1995). Here it is sufficient to note that methods which treat species values as statistically independent points violate the assumption of sampling independence, because closely related species tend to share characters through common descent rather than only through independent evolution. This phylogenetic correlation may result in characteristics co-occurring among species without there being any interesting reason. Among fishes, for instance, there is a strong tendency for species with spines to be covered with scales, a spurious correlation resulting from the non-independence of species.

RESULTS AND DISCUSSION

Relative brain weights among the major groups of fishes are expressed as minimum convex polygons in figure 1. Figure 2 shows all data points in FishBase 97, including 3218 records representing 1174 species, plotting EC_1 against the Log_{10} of body weight. Figure 2 illustrates an output option of Fishbase 97, which can superimpose the relative brain weight of individual taxa (in this case gymnotiform electric fishes as black dots) on the cloud of all FishBase 97 data points (gray dots).

The qualitative results of our analysis of brain size differences among the major groups of fishes is similar to that of van Dongen (1998). Data on brain size diversity in FishBase 97 range over 5 orders of magnitude, from that of the gobiid teleost *Pandaka lidwilli* (body weight = 0.1 g, brain weight = 1.6 mg) to that of the lamniform shark *Megachasma pelagios* (body weight = 1,004 kg, brain weight = 19.1 g). Since body size diversity in fishes ranges by about 7 orders of magnitude brain size diversity is less than that of body size diversity. A study of the data in FishBase 97 also reveals that much of the diversity in brain size in fishes occurs among relatively closely related species (i.e., confamilials). There are, however, also trends that emerge in comparisons at higher taxonomic levels. Gnathostomes in general possess much larger brains than do the jawless fishes. Among fishes, chondrichthyans possess the largest brains, both absolutely and in proportion to their body sizes (Fig. 1). Especially enlarged brains have evolved in at least two groups of cartilaginous fishes; galeomorph sharks and batoid rays (Northcutt, 1977).

Figure 3 depicts comparisons of relative brain weight in 9 teleost taxa for which a range of brain size data are available. In this plot relative brain weight is measured by EC_2 . To assess the effect of body size differences on relative brain size, data for Osteoglossidae are combined from two species (*Heterotis niloticus* and *Scleropages jardinii*) and for *Acanthurus* from 12 species. These data demonstrate that brain size in many teleosts scales with body size very close to the theoretical $2/3$ expected from geometrical considerations (Snell, 1892). As a result, the size of the brain in adult specimens of many large bodied teleosts (e.g., *Thunnus albacares* and *Gadus morhua*) is attained by following a common growth curve.

Figure 3 also illustrates that certain teleost species with elongate bodies possess relatively smaller brains at larger body sizes than do most teleosts, a pattern resulting from the disproportionate growth of their bodies with respect to their heads. This is especially pronounced in fishes which use anguilliform locomotion (Webb and Weihs, 1983), including true eels (Anguilliformes; e.g., *Conger conger*) and zoarcoid percomorphs (e.g.,

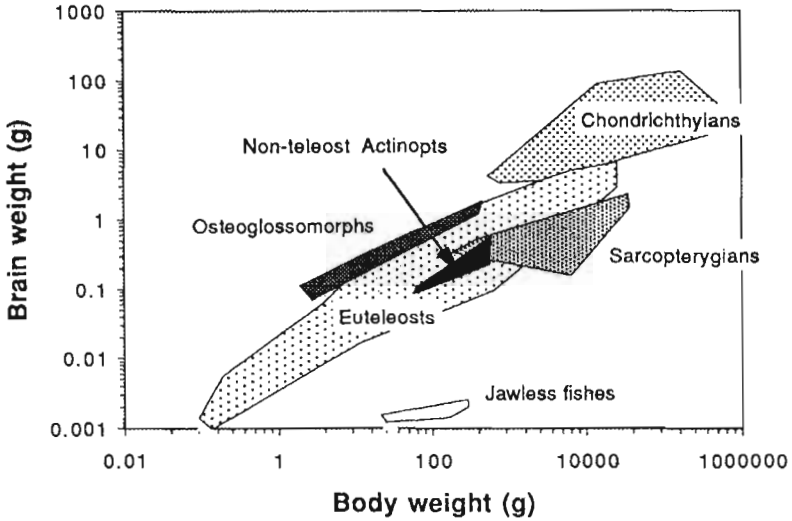


Fig. 1. - Relative brain weight among the major groups of fishes, expressed as minimum convex polygons. Data sources are summarized in tables I and II.

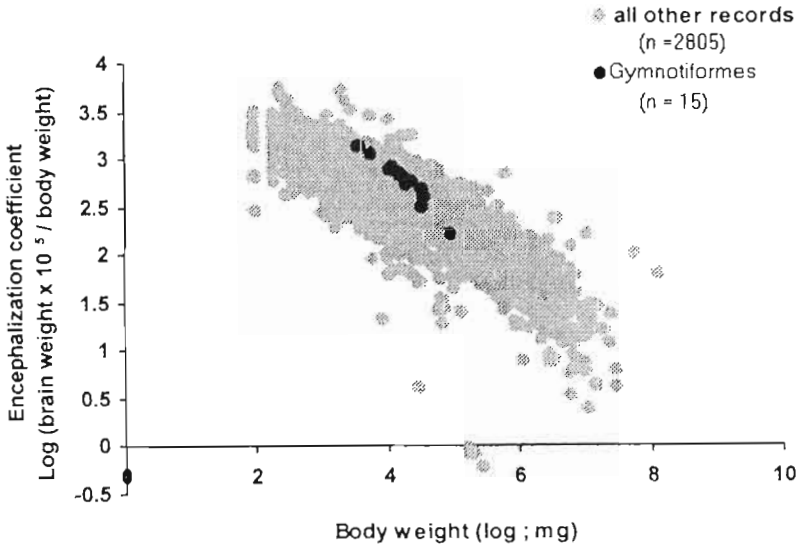


Fig. 2. - Relative brain weight of gymnotiform electric fishes (black dots) superimposed on the cloud of all FishBase 97 data points (gray dots). Use of double log format following Bauchot *et al.* (1989b) and Froese and Pauly (1997). A total of 3218 records are plotted, representing 1174 species. Relative brain weight measured by Encephalization Coefficient I ($EC_1 = \text{Log}_{10}[\text{brain weight} \times 1000/\text{body weight}]$).

Anarhichas lupus, *A. denticulatus*). Elongate fish species which do not use anguilliform locomotion (e.g., the gymnotiform electric fish *Porotergerus compsus*) do not possess

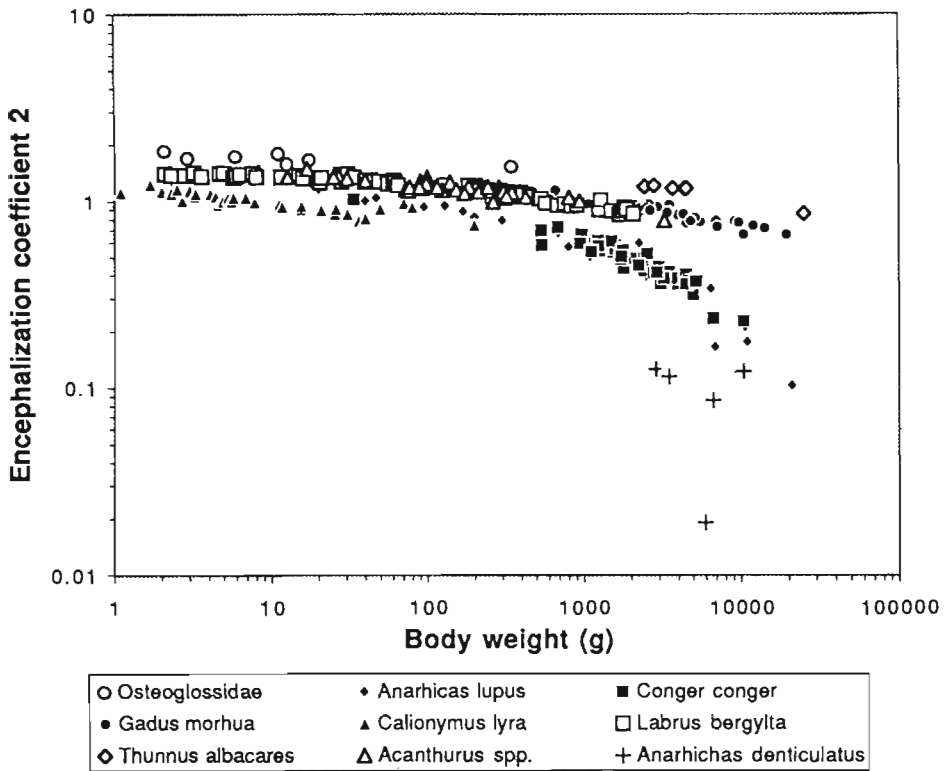


Fig. 3. - Comparisons of relative brain weight in some teleost species for which a range of brain size data are available. Relative brain weight measured by Encephalization Coefficient 2 ($EC_2 = \text{Log}_{10}[\text{brain weight} \times 1000 / \text{body weight}^{2/3}]$).

relatively smaller brains. This pattern resembles the “fat old fish” phenomenon, which refers to a tendency in fishes close to their maximum size to divert from isometric growth and increase fatty tissues rather than muscles, bones, and brain. The data shown for *Thunnus albacares* and *Gadus morhua* do not show this effect due to the absence of very large specimens.

Figure 4 depicts another application of the FishBase 97 package, which permits the comparison of data from different tables. In this case, data from the “Brains” are related with metabolism, using data from the “Oxygen” table. Both datasets present measurements on individual fish which are strongly correlated with body weight. The slope (exponent) of the log-log relationship between oxygen consumption and relative brain weight over all available data was used to correct the individual values for the effect of weight. In this plot each data point represents the average of the available values for species with at least three records. Figure 4 shows that there is sizable variance in the regression of oxygen consumption against brain weight. These data do not refute the hypotheses that large brains consume proportionately more oxygen, or that active fish with higher metabolic rates have larger brains. The variance in these data is anticipated to be reduced once the Oxygen table has been thoroughly proofed.

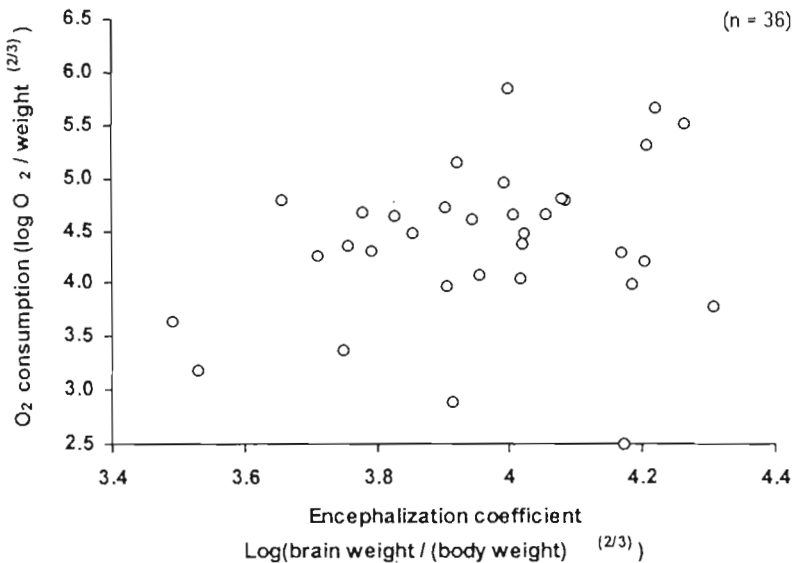


Fig. 4. - Brain weight vs oxygen consumption for several teleost species. Brain weight measured by Encephalization Coefficient 2 (Fig. 3). Note that these data do not refute the hypotheses that large brains consume proportionately more oxygen, or that active fishes with higher metabolic rates have larger brains.

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