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FRESHWATER ANIMAL DIVERSITY ASSESSMENT

Global diversity of fish (Pisces) in freshwater

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Abstract The precise number of extant fish species remains to be determined. About 28,900 species were listed in FishBase in 2005, but some experts feel that the final total may be considerably higher. Freshwater fishes comprise until now almost 13,000 species (and 2,513 genera) (including only freshwater and strictly peripheral species), or about 15,000 if all species occurring from fresh to brackishwaters are included. Noteworthy is the fact that the estimated 13,000 strictly freshwater fish species live in lakes and rivers that cover only 1% of the earth's surface, while the remaining 16,000 species live in salt water covering a full 70%. While freshwater species belong to some 170 families (or 207 if peripheral species are also considered), the bulk of species occur in a relatively few groups: the Characiformes, Cypriniformes, Siluriformes, and Gymnotiformes, the Perciformes (noteably the family Cichlidae), and the Cyprinodontiformes. Biogeographically the distribution of strictly freshwater species and genera are, respectively 4,035 species (705 genera) in the Neotropical region, 2,938 (390 genera) in the Afrotropical, 2,345 (440 genera) in the Oriental, 1,844 (380 genera) in the Palaearctic, 1,411 (298 genera) in the Nearctic, and 261 (94 genera) in the Australian. For each continent, the main characteristics of the ichthyofauna are briefly outlined. At this continental scale, ichthyologists have also attempted to identify ichthyological ''provinces'' that are regions with a distinctive evolutionary history and hence more or less characteristic biota at the species level. Ichthyoregions are currently identified in each continent, except for Asia. An exceptionally high faunal diversity occurs in ancient lakes, where one of the most noteworthy features is the existence of radiations of species that apparently result from intralacustrine speciation. Numerous fish-species flocks have been identified in various ancient lakes that are exceptional natural sites for the study of speciation. The major threats to fish biodiversity are intense and

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have been relatively well documented: overexploitation, flow modification, destruction of habitats, invasion by exotic species, pollution including the worldwide phenomena of eutrophication and sedimentation, all of which are interacting.

Keywords Fish · Freshwater · Distribution · Diversity · Ichthyoregions · Global scale

General issues

The word fish is applied to a heterogeneous grouping of aquatic chordates comprised of hagfishes and lampreys, sharks, rays and chimaeras, and the finned bony fishes. The latter is by far the most diverse group and is well represented in freshwaters, while the others are predominantly marine groups.

Each continent has a distinctive freshwater fish fauna and the observed patterns of fish distribution (see summary in Berra, 2001) are the result of physical barriers disrupting past fish dispersal, as well as to difference in temperature adaptations amongst the different groups. Most species occur in the tropical and subtropical regions and there is an overall reduction in diversity towards temperate and polar regions. Although some temperate regions, particularly those that were never glaciated are relatively rich in species, the continental areas that have experienced glaciations, such as northern North America, Europe and Asia, tend to have relatively depauperate fish faunas.

The freshwater fishes of the equatorial zone are extremely diverse and are not readily characterised by any particular clades. While the freshwaters of the northern temperate/cold regions are characterised by salt-tolerant salmonids, sturgeons, smelts, northern lampreys and several primary families including pikes, leuciscine cyprinids and perches. The southern temperate/cold regions have a low diversity of fishes including salt-tolerant galaxids and southern lampreys. Most oceanic islands are inhabited by species of predominately marine groups that have adapted to (or remained in) freshwaters.

Freshwater fishes, which tend to be more-or-less confined to drainage systems, provide a relatively conservative system for examining patterns of distribution that may reflect the imprint of past continental and climate changes.

Global species and taxonomic diversity

Fresh, brackish and saltwater fishes

Ichthyologists used to distinguish three major groups of freshwater fish according to their tolerance to saltwater and their hypothesised ability to disperse across marine barriers (Myers, 1949): the *primary division* fish being strictly intolerant of salt water; the *secondary division* able occasionally to cross narrow sea barriers; and the *peripheral division* including representatives of predominantly marine families that have colonised inland waters from the sea. This classification scheme has been challenged partly because of the subjectivity in distinguishing between divisions. However, the scheme is still widely used by many fish biogeographers and has the advantage of common usage. The popular internet site FishBase (http://www.fishbase.org) adheres to a slightly different classification with fresh and brackishwater fish species falling into three categories: (1) exclusively freshwater, (2) occurring in fresh and brackishwaters, (3) or in fresh, brackish and marine waters. The first category covers more or less the primary and secondary divisions of Myers, while categories 2 and 3 cover the peripheral division.

Global estimates of fish species diversity

The precise number of extant fish species remains to be determined. However, since Linneaus' listing of 478 species of teleost fish in 1758, our knowledge has increased considerably and some global estimates are available.

The Catalog of Fishes established by Eschmeyer (2005) provided an estimate of 27,300 valid fish species, with a prediction of about 31,500 species when all inventories are completed (Berra, 2001). In September 2005, 28,900 species were already listed in FishBase. Nelson (2006) suggested a total of almost 28,000 species (freshwater and marine), which is 51% of the 54,711 then recognised living vertebrate species. The eventual number of extant fish species may be projected to be close to, conservatively, 32,500 (Nelson, 2006). At the global scale, the fresh and brackishwater fish belong to 207 families and 2,513 genera.

Tables 1 and 2 provide an estimate of the number of fish species inhabiting inland waters, by continents

Table 1 Fresh and brackishwater fish species richness by continents or large sub-continental units (based on Fishbase, September 2005)

	Freshwater		Brackish/salt		Total	
	Families	Species	Families	Species	Families	Species
Africa	48	2,945	66	295	89	3,240
Asia	85	3,553	104	858	126	4,411
Europe	23	330	36	151	43	481
Russia	28	206	28	175	40	381
Oceania	41	260	74	317	85	577
North America	74	1,411	66	330	95	1,741
South America	74	4,035	54	196	91	4,231
Total		12,740		2,322		15,062

or large sub-continental units, recorded in FishBase. Nelson (2006) listed only 11,952 strictly freshwater species, and 12,457 using freshwater. FishBase uses Eschmeyer's classification and the difference with Nelson's estimate may result differing views on the definition of species. The unclear status "brackish species" may probably explain the differences in the total number of fish species using freshwaters (12,457 according to Nelson) or inhabiting fresh and brackishwaters (15,062 according to Fishbase) (Table 2).

Following Nelson (2006) and Eschmeyer (2005) about 40–43% of all fishes occur in, or almost always in, freshwaters. The current data from FishBase provide an even higher figure of 45%. Whatever the precise number, it is noteworthy that the estimated 13,000 freshwater species live in lakes and rivers that cover only 1% of the earth's surface, while the remaining 16,000 species live in marine habitats which cover a full 70%.

Taxonomic diversity

Table 2 provides an evaluation of the number of families and species, of inland water fishes in different taxonomic orders. Altogether fresh and brackishwater species are included in about 207 families (170 for strictly freshwater fish). The bulk of families and species occur in a few groups: the ostariophysan Characiformes, Cypriniformes, Siluriformes and Gymnotiformes, the Perciformes (including the family Cichlidae) and the Cyprinodontiformes. While supraspecific taxonomic ranks such as that of "family" are arbitrary, nonetheless family diversity is generally a reasonable indicator of taxonomic (i.e. species) diversity.

At the level of the biogeographic realms (Tables 3, 4) and taking into account only fully freshwater fish families (i.e. the primary and secondary divisions), the largest number of families by far (43) is found in the Neotropical region, with a high proportion of endemic families (33% or 77%) mainly belonging to the orders Characiformes and Siluriformes. Then, follows the Oriental region (33 families, 15 endemic) and the Afrotropical region (32 families, 17 endemic). The Nearctic and Palaearctic regions are relatively depauperate, as a result of Quaternary climatic events: 22 families in the Nearctic region (nine endemic) and 17 families in the Palaearctic (with a single endemic family). Figure 1 provides an approximation of the worldwide distribution of selected freshwater fish groups and illustrates the existence of groups distributed only in the North, and groups more-or-less widely distributed in the inter-tropical zone.

For strictly freshwater fishes, at the generic and species levels in the different biogeographic realms (Fig. 2A) the overall pattern is quite similar to that at the family level with 4,035 species (705 genera) in the Neotropical region, 2,938 (390 genera) in the Afrotropical, 2,345 (440 genera) in the Oriental, 1,844 (380 genera) in the Palaearctic, 1,411 (298 genera) in the Nearctic, and 261 (94 genera) in the Australian.

When taking into account the fresh and brackishwater fishes (Tables 3, 4; Fig. 2B), the figures are, respectively, 4,231 species (769 genera) in the Neotropical region, 3,272 (542 genera) in the Afrotropical, 2,948 (609 genera) in the Oriental, 2,381

Table 2 Number of families and species for fish orders with representatives in fresh and brackishwater. Data from FishBase (September 2005)

Class	Order	Fresh			Fresh–brackish		
		FishBase, 2005		Nelson, 2006	FishBase, 2005		Nelson, 2006
		Families	Species	Species	Families	Species	Species
Holocephali (chimaeras)	Chimaeriformes	1	1	0	1	1	0
Cephalaspidomorphi (lampreys)	Petromyzontiformes	1	33	29	2	57	38
Elasmobranchii (sharks and rays)	Carcharhiniformes			1	1	13	8
	Orectolobiformes			0	1	2	0
	Pristiformes			0	1	24	1
	Pristiophoriformes			0			1
	Rajiformes	2	24	0	3	35	2
	Myliobatiformes			23			28
Sarcopterygii (lobe-finned fishes)	Ceratodontiformes[a]	2	8	6	2	8	6
Actinopterygii (ray-finned fishes)	Acipenseriformes	2	8	14	2	56	27
	Albuliformes			0	1	5	0
	Amiiformes	1	1	1	1	1	1
	Anguilliformes	2	8	6	5	76	26
	Atheriniformes	7	181	210	7	224	240
	Batrachoidiformes	1	5	6	1	9	7
	Beloniformes	3	71	98	3	132	104
	Characiformes	17	1794	1674	17	1801	1674
	Clupeiformes	5	72	79	5	209	85
	Cypriniformes	7	3451	3268	7	3664	3268
	Cyprinodontiformes	9	964	996	9	1096	1008
	Elopiformes			0	2	12	7
	Esociformes	2	15	10	2	20	10
	Gadiformes			1	2	10	2
	Gasterosteiformes	2	13	21	2	30	43
	Gobiesociformes	1	9	0	1	9	0
	Gonorynchiformes	2	31	31	3	36	32
	Gymnotiformes	5	133	134	5	133	134
	Hiodontiformes			2			2
	Lepisosteiformes	1	4	6	1	7	7
	Lophiiformes			0	1	2	0
	Mugiliformes			1			7
	Ophidiiformes	1	4	5	1	6	6
	Osmeriformes	3	31	82	5	82	86
	Osteoglossiformes	7	219	218	7	221	218
	Perciformes	34	2402	2040	51	3368	2335
	Percopsiformes	3	9	9	3	9	9
	Pleuronectiformes	4	23	10	5	81	20
	Polyptériformes	1	16	16	1	17	16
	Salmoniformes	1	161	45	1	295	66
	Scorpaeniformes	4	75	60	6	105	62
	Siluriformes	34	2835	2740	34	2992	2750

Table 2 continued

Class	Order	Fresh			Fresh–brackish		
		FishBase, 2005		Nelson, 2006	FishBase, 2005		Nelson, 2006
		Families	Species	Species	Families	Species	Species
	Synbranchiformes	3	90	96	3	105	99
	Syngnathiformes	1	20	0	1	61	0
	Tetraodontiformes	1	29	14	1	48	22
Total		170	12740	11952	207	15062	12457

[a] Ceratodontiformes include Lepidosireniformes

Table 3 Number of fresh and brackishwater fish species per biogeographic realm (data from Fishbase, September 2005)

Order	PA	NA	NT	AT	OL	AU
Chimaeriformes	–	–	1	–	–	–
Petromyzontiformes	17	24	2	1	–	1
Carcharhiniformes	3	2	2	2	3	3
Orectolobiformes	1	–	–	1	1	1
Pristiformes	4	4	4	5	4	4
Pristiophoriformes[a]						
Rajiformes	1	1	18	4	9	3
Myliobatiformes[b]						
Ceratodontiformes[c]	–	–	1	7	–	1
Acipenseriformes	23	10	1	1	–	–
Albuliformes	1	1	1	1	1	1
Amiiformes	–	1	–	–	–	–
Anguilliformes	9	2	4	14	29	23
Atheriniformes	2	55	31	15	76	41
Batrachoidiformes	–	4	5	–	–	–
Beloniformes	9	12	14	4	83	14
Characiformes	1	88	1493	212	–	3
Clupeiformes	34	24	32	38	60	17
Cypriniformes	1394	392	17	539	1381	15
Cyprinodontiformes	30	377	346	309	10	12
Elopiformes	4	1	1	3	3	3
Esociformes	7	9	–	1	–	–
Gadiformes	3	4	–	–	–	–
Gasterosteiformes	11	7	–	1	3	–
Gobiesociformes	–	6	3	–	–	–
Gonorynchiformes	1	1	1	32	1	1
Gymnotiformes	–	7	126	–	–	–
Hiodontiformes[d]						
Lepisosteiformes	–	7	–	–	–	–
Lophiiformes	–	–	–	–	1	1
Mugiliformes[a]						

Table 3 continued

Order	PA	NA	NT	AT	OL	AU
Ophidiiformes	–	5	1	–	–	–
Osmeriformes	31	10	7	1	9	25
Osteoglossiformes	–	2	3	208	7	1
Perciformes	348	455	413	1274	604	327
Percopsiformes	–	9	–	–	–	–
Pleuronectiformes	14	11	21	9	24	8
Polypteriformes	–	–	–	17	–	–
Salmoniformes	161	47	11	6	1	7
Scorpaeniformes	61	31	–	–	4	4
Siluriformes	189	121	1666	496	535	45
Synbranchiformes	5	4	2	52	43	3
Syngnathiformes	10	6	2	12	24	12
Tetraodontiformes	7	1	2	7	32	4
Total	2381	1741	4230	3272	2948	580

[a] Mugiliformes & Pristiophoriformes are considered as stricly marine in Fishbase

[b] Myliobathiformes are included in Rajioformes in Fishbase

[c] Ceratodontiformes include Lepidosireniformes

[d] Hiodontiformes are included in Osteoglossiformes in Fishbase

(551 genera) in the Palaearctic, 1,741 (402 genera) in the Nearctic, and 580 (1,232 genera) in the Australian.

Some general characteristics of the fish fauna at the global scale

Many hypotheses have been proposed to explain spatial variability species richness at broad spatial scales (see for example Ricklefs, 2004 for a review). These may be grouped into three main hypotheses: the first, the "area" hypothesis, states that species richness increases as a function of surface area through size-dependent extinction/colonisation rates (MacArthur & Wilson, 1967) and/or habitat diversity (MacArthur, 1964). The second, the "productivity" hypothesis (Wright, 1983) predicts that species richness of a region will be positively correlated with the total energy available. The third, the "historical" hypothesis, which includes many variants (Ricklefs, 2004), explains diversity patterns by differential speciation or extinction rates, coupled with dispersal limitation, due to historical contingency. Concerning freshwater fishes it is clear that area per se explains a large portion of richness variability. In rivers, species richness increases with area (basin area and amount of discharge) as it generally does in terrestrial biomes (Hugueny, 1989; Oberdorff et al., 1995; Guégan et al., 1998) (Fig. 3). Nevertheless, when area is controlled for, energy availability and history also explain a significant part of the observed richness patterns, even if the contribution of the latter is generally weaker (Oberdorff et al., 1995, 1997; Tedesco et al. 2005).

Phylogeny and historical processes

The present distribution of freshwater fishes has been shaped by millions of years of changes in the global water cycle. In relation to climate change, the nature and dynamics of surface freshwater systems have evolved continuously, at various spatial and temporal scales. Many of the surface freshwater systems have, therefore, been transient; their fauna and flora usually disappeared when the systems disappeared, or were able to survive by developing adaptations to the changing circumstances. The dual processes of speciation and extinction have interacted with climatic and geological events that have both isolated fish populations and provided opportunities for migration and colonisation of new habitats.

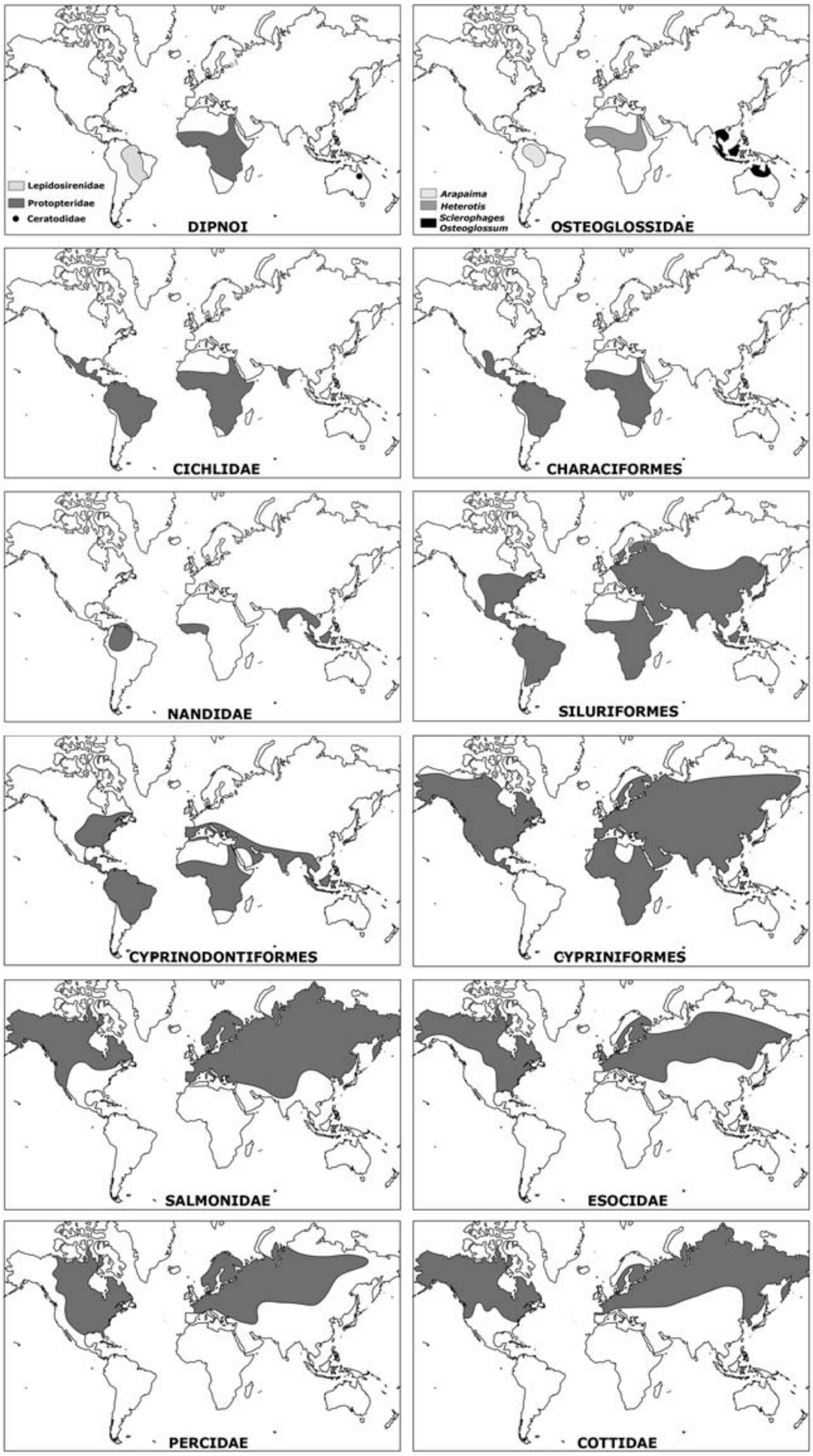

Fig. 1 Geographical distribution of selected fish groups (adapted from Berra, 2001). These maps represent only a simplified approach and need checking and refining

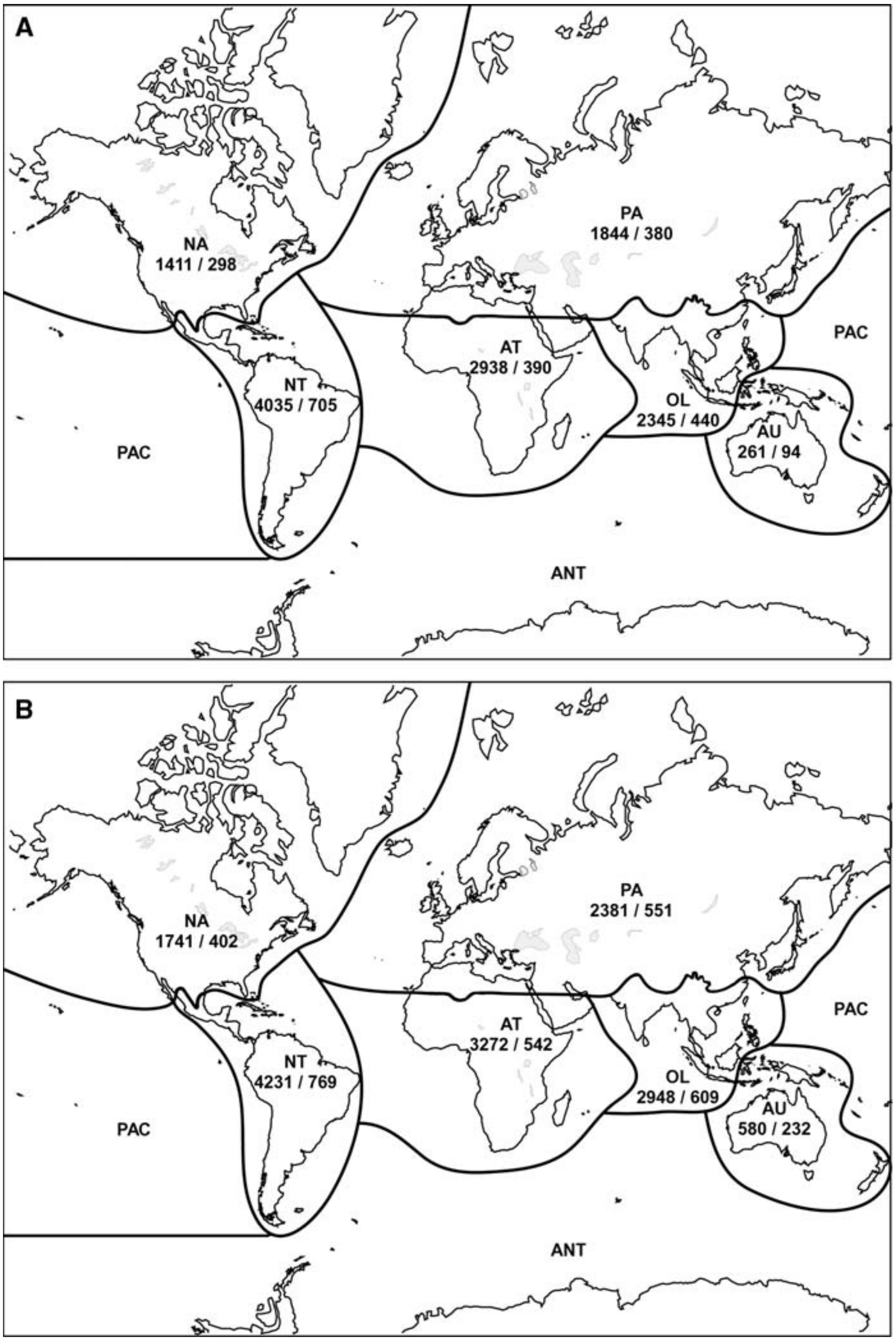

Fig. 2 Freshwater fish diversity: current number of species and genera (Sp/Gn) per zoogeographic region for strictly freshwater fishes (**A**) and for fresh and brackishwater fishes (**B**) (data from Fishbase, September 2005). PA—Palaearctic; NA—Nearctic; NT—Neotropical; AT—Afrotropical; OL—Oriental; AU—Australasian; PAC—Pacific Oceanic Islands, ANT—Antarctic

Some major groups of jawed fishes (chondrichthyes, dipnoi, some chondrostei) presently living were in existence by the middle of the Devonian, more than 350 Myrs ago and the relationship between continental drift and freshwater fish distribution has been widely discussed.

Several freshwater fish lineages appear to have a Gondwanan origin i.e. members of the lineage were present on Gondwana prior to its fragmentation. Consequently they have widespread distributions with living representatives and/or fossils present on different continents. Such is the case for the Dipnoi

Table 4 Number of fresh and brackishwater fish families and genera per biogeographic realm (some families and genera may be found in several realms) (data from Fishbase, September 2005)

Order	PA		NA		NT		AT		OL		AU	
	Families	Genera	Families	Genera	Families	Genera	Families	Genera	Families	Genera	Families	Genera
Chimaeriformes	–	–	–	–	1	1	–	–	–	–	–	–
Petromyzontiformes	1	5	1	5	1	2	1	1	–	–	1	1
Carcharhiniformes	1	3	1	2	1	2	1	2	1	3	1	2
Orectolobiformes	1	1	–	–	–	–	1	1	1	1	1	1
Pristiformes	1	2	1	1	1	1	1	2	1	2	1	2
Pristiophoriformes[a]												
Rajiformes	1	1	1	1	1	3	1	4	2	4	2	3
Myliobatiformes[b]												
Ceratodontiformes[c]	–	–	–	–	1	1	1	1	–	–	1	1
Acipenseriformes	2	5	2	3	1	1	1	1	–	–	–	–
Albuliformes	1	1	1	1	1	1	1	1	1	1	1	1
Amiiformes	–	–	1	1	–	–	–	–	–	–	–	–
Anguilliformes	5	5	1	1	2	2	4	6	5	10	4	7
Atheriniformes	2	2	2	8	2	5	2	4	5	15	3	7
Batrachoidiformes	–	–	1	1	1	4	–	–	–	–	–	–
Beloniformes	2	3	3	4	2	5	1	3	3	13	3	7
Characiformes	1	1	9	37	15	233	3	42	–	–	2	3
Clupeiformes	3	15	3	9	3	15	4	25	4	23	3	11
Cypriniformes	6	253	3	78	1	11	3	45	5	226	2	13
Cyprinodontiformes	4	6	7	56	4	47	3	28	3	3	3	7
Elopiformes	2	2	1	1	1	1	2	3	2	2	2	2
Esociformes	2	3	2	4	–	–	1	1	–	–	–	–
Gadiformes	2	2	2	3	–	–	–	–	–	–	–	–
Gasterosteiformes	1	3	1	4	–	–	1	1	1	1	–	–
Gobiesociformes	–	–	1	1	1	1	–	–	–	–	–	–
Gonorynchiformes	1	1	1	1	1	1	3	6	1	1	1	1
Gymnotiformes	–	–	4	4	5	30	–	–	–	–	–	–
Hiodontiformes[d]												
Lepisosteiformes	–	–	1	2	–	–	–	–	–	–	–	–
Lophiiformes	–	–	–	–	–	–	–	–	1	1	1	1
Mugiliformes[a]												
Ophidiiformes	–	–	1	2	1	1	–	–	–	–	–	–
Osmeriformes	3	11	1	5	1	3	1	1	2	5	2	5
Osteoglossiformes	–	–	1	1	2	2	5	24	2	3	1	1
Perciformes	38	138	20	91	19	89	29	252	39	172	36	122
Percopsiformes	–	–	3	7	–	–	–	–	–	–	–	–
Pleuronectiformes	3	5	3	6	2	9	4	7	3	7	3	6
Polypteriformes	–	–	–	–	–	–	1	2	–	–	–	–
Salmoniformes	1	11	1	7	1	4	1	4	1	1	1	3
Scorpaeniformes	5	19	1	3	–	–	–	–	2	3	2	3
Siluriformes	13	40	11	45	16	291	10	64	16	88	6	15
Synbranchiformes	2	4	1	3	1	1	2	4	3	12	1	2
Syngnathiformes	1	4	1	3	1	1	1	5	1	4	1	2

Table 4 continued

Order	PA		NA		NT		AT		OL		AU	
	Families	Genera	Families	Genera	Families	Genera	Families	Genera	Families	Genera	Families	Genera
Tetraodontiformes	1	5	1	1	1	1	1	2	1	8	1	3
Total	106	551	95	402	90	768	90	542	106	609	86	232

[a] Mugiliformes & Pristiophoriformes are considered as stricly marine in Fishbase

[b] Myliobathiformes are included in Rajioformes in Fishbase

[c] Ceratodontiformes include Lepidosireniformes

[d] Hiodontiformes are included in Osteoglossiformes in Fishbase

(lungfishes) a monophyletic group that first appeared in the Devonian, diversified in the Mesozoic, and is now represented by a few extant species in Africa, Australia and South America (Fig. 1) (Lundberg, 1998; Lundberg et al., 2000) and the Osteoglossomorpha, a distinctive clade of teleosts, at least late Jurassic in age, whose subgroups are scattered among tropical freshwater regions and North America (Fig. 1).

The Polypteridae (bichirs and reedfishes) also had a large distribution; however, today, living species occur only in Africa, while fossils have been identified in South America (Gayet & Meunier, 1991).

The Otophysi (superorder Ostariophysi) is a monophyletic group that includes very speciose families in freshwater: the Siluriformes (catfishes), Gymnotiformes (knifefishes), Cypriniformes (minnows) and Characiforms (characins) whose current distribution present some interesting contrasts (see Fig. 1). They do not occur in Australia, Madagascar or the West Indies. Recent molecular studies supported the hypothesis that Cypriniformes are the sister group to the remaining three orders (Saitoh et al., 2003). The divergence time of cypriniforms from the otophysan stock has been estimated at 250 mya (Kumazawa et al., 1999).

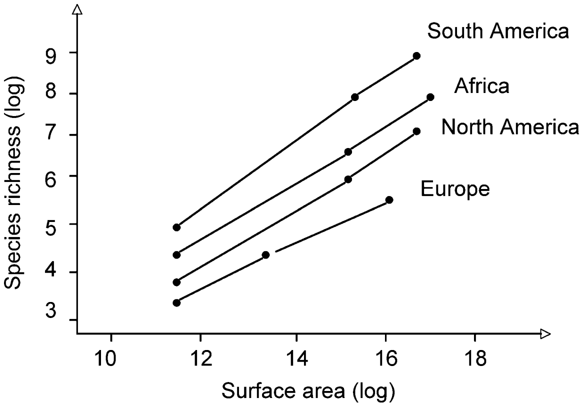

Fig. 3 Intercontinental comparison of species–area relationships. Each line links, respectively, the estimated species richness in a 10,000 km^2 drainage basin, the species richness of the largest continental river (i.e. Danube river for Europe, Mississippi river for North America, Congo river for Africa, and Amazone river for South America), and the continental species richness. Modified after Hugueny (2003) using data from Oberdorff et al. (1995)

The understanding of Otophysan biogeography has been a matter of debate, since the beginning of the 20th century. Asia, where the group is the most speciose, was long considered to be the centre of origin of the Cypriniformes. However, current evidence argues for a hypothesis that the cypriniforms, and probably also the siluriforms, originated in South America and migrated to Asia in the late Jurassic (ca 150–160 Myrs ago) along the northern shore of theThethys sea (Briggs, 2005). Diogo (2004) also supported the origin of catfishes in the South American region during the late Cretaceous period, at a time when there were still some remaining Pangean connections between Gondwana and Laurasia. Then catfishes would have dispersed to other areas with some subgroups migrating via predrift dispersion to Laurasian regions (Sullivan et al., 2006).

Recent palaeontological studies demonstrated that several archaic fish families disappeared from South America during the Cretaceous and the entire Cenozoic. Much diversification of modern Neotropical fishes occurred during the 70 Myrs period from the late Cretaceous through the Miocene (Lundberg, 1998). By the late Miocene (10 Myrs) the fish fauna was essentially modern. Fish diversification continued but at finer-taxonomic levels. Apparently geological events during the Pliocene and Pleistocene played little role in forging the great diversity of genera and families (Lundberg, 1998).

Present distribution: main characteristics of the ichthyofauna at the continental level

North America

Spanning the continent from Alaska and Canada in the north to the Transvolcanic Axis just south of the Mexican plateau, North America harbours some 1,050 freshwater fish species. Compared with other temperate zone regions this is an extremely species-rich area, and the continental US alone, with a little over 800 species, ranks seventh in World. As elsewhere, these fish species are not evenly distributed over the continent. Watershed boundaries, local geological and climatic forces shape the landscape and hydrology, and historical factors, particularly the imprint of past glaciations, have moulded ichthyofaunal distributions. Fish richness is greatest in the southeastern US where some 500 species reside, with a focus of endemism in the upland regions of southern Appalachia, where at least 350 species are concentrated. At the continental scale species richness tends to decline markedly to both the north and west of these southeastern foci. The extraordinary diversity of the southeastern US is probably the result of a combination of factors including a diverse physical geography, a favourably moist climate, and a long but dynamic history of zoogeographical interactions. Furthermore, and perhaps most critically, these southeastern regions escaped the repeated Pleistocene glacial advances that effectively denuded ichthyological landscapes in the northern third of the continent. In the southwest aridity and a harsh climatic regime, perhaps accounts for the relatively low levels of species richness, although locally high levels of endemism characterise much of the Pacific south western US. Diversity over the Mexican plateau is high with an estimated 250 species of which over 200 are considered endemic, and the majority of which have neotropical affinities.

Main characteristics

- Around 35 strictly freshwater families are represented in North American waters, 13 of which are endemic to the region. Numerically dominant families include the Cyprinidae, Percidae, Poeciliidae and Catostomidae, which together comprise over 50% of the total number of fish species.
- Radiations of freshwater species belonging to otherwise predominantly marine families (e.g. Cottidae, Atherinidae, Clupeidae and Moronidae) form an important component of the North American freshwater fauna.
- Anadromous trouts and salmons, particularly along the Pacific Coast, seasonally dominate freshwater ichthyofaunal communities mediating a significant nutrient passage between the ocean and inland areas. Similarly, at least historically, catadromous anguillid eels, *Alosa* and *Brevoortia* formed an important component of the coastal and inland waters of the Atlantic Seaboard.
- North America harbours a relatively rich representation of living basal actinopterygian fishes including sturgeons, paddlefish, gars and the enigmatic bowfin, *Amia calva*, as well as the only extant northern hemisphere osteoglossomorphs in the endemic Hiodontidae.
- The North American fauna includes a predominance of elements with Eurasian affinities, such as the Esocidae, Umbridae, Cottidae, Cyprinidae, Catostomidae, Percidae and Gasteosteidae, but Neotropical elements are also clearly represented, particularly in southern regions, for example the Cichlidae, Characidae, Pimelodidae, Rivulidae, Anablepidae and Synbranchidae.

Smith in Lundberg et al. (2000) provides an excellent summary review of fish diversity and notes that compared with tropical regions species diversity in North America is relatively well documented. While a few new species continue to be discovered and described each year, in general the potential for significant biodiscovery is probably limited to the Mexican regions in the south and overall the North American ichthyofauna can be considered to be well known. In addition to numerous regional works on the ichthyofauna the treatises of Mayden (1992) and Hocutt & Wiley (1986) provide excellent overviews.

Abell et al. (2000) provide a regional assessment of the conservation status of the fauna.

South and Central America

South and most of Central America corresponds to the Neotropical realm of bio-geographers. Its freshwater fish fauna is the most diversified in the world (around 3,600 freshwater fish species according to Reis et al. 2003, 4,164 according to FishBase). Despite the proximity of the Neotropical region to North America, there seems to be little relationship with the Nearctic fish fauna, and more with the Afrotropical region.

The aquatic fauna of Central America, from the isthmus of Tehuantepec to the border of Panama/Columbia, consists of a mixture of North American and South American lineages, and includes some endemic groups of cyprinodontiform and many members of peripheral fish families. Only two North American families (Catostomidae and Ictularidae) occur in the Central America freshwater fish fauna.

Main characteristics

- The great majority of Neotropical fishes belong to five dominant groups: Characiforms (some 1,500 described, probably 2,000), Siluriforms (at least 1,400 known species, probably 2,000), Gymnotiforms (some 180 species), Cyprinodontiforms (some 400 species) and cichlids (some 450 species). There is a spectacular radiation of characoids and siluroids in South America.
- South America lacks many of the rather primitive fish families endemic to Africa, with the exception of Lepidosireniformes and Osteoglossiformes.
- There are no native Cypriniformes.
- The Gymnotiforms are electroreceptive fishes, showing a remarkable convergence with the unrelated mormyrids of Africa, and the notopterids of Africa and Asia.
- Characteristic of the Neotropical fish fauna is the abundance of very small species (size from 20 mm to 30 mm) among characiforms, siluriforms and cyprinodontiforms. At the other end of the scale, some very large fish occur here as well, such as the goliath catfish *Brachyplatystoma* in the Amazon (up to 3 m long and 140 kg), or the osteoglossid *Arapaima gigas*, (up to 4.5 m long and 200 kg).

Vari & Malabarba (1998) pointed out that some 800 new freshwater species have been described during the last two decades from South America, and they anticipate an increase in the rate of description. They forecasted a final total of some 8,000 Neotropical fish species. Lundberg et al. (2000) gave estimates of 5,000–8,000 species for the Neotropical ichthyofauna. Only 4,500 species are currently known (see Table 1) but many new species have been described recently, and many more await description.
At the moment no comprehensive review exists for the Neotropical fish fauna as a whole. Much of the available information was summarised and published in a symposium volume (Malabarba et al., 1998).

Europe

The European freshwater fish fauna is impoverished compared to other continents, as a result of recent glaciations. Biogeographic evidence indicates that the glaciated areas were recolonised (north and westward dispersal) during the interglacial and post-glacial periods mainly from the Ponto-Caspian region, and particularly from the middle and lower sections of the Danube basin, which served as a major refugia (Banarescu, 1992; Griffiths, 2006). Other refugia during the last ice age were located in the southern peninsulas of Iberia, Italy, the Balkans and Greece. However, post-glacial northern expansions of fishes from these regions, or recolonisation of these regions from the north, were prevented by mountain ranges (Pyrenees, Alps, for example). This geographical isolation explains the high level of endemism found in the southern regions (Banarescu, 1992; Durand et al., 2003; Reyjol et al., 2007).

Main characteristics

- Twenty families but the major groups are Cyprinidae—more than 50% of the species, (Revenga & Kura, 2003; Reyjol et al., 2007), Salmonidae, Coregonidae, Gobiidae and Cobitidae.
- Very few endemic species; the largest numbers are all located in areas which have served as major refugia in the last ice age (see above).

- The river Danube with about 90 species has the most diverse fauna of the continent.

In Europe, according to Maitland (2000) there are over 250 native freshwater fish species, while Kottelat (1997) recognised 358 species west of the former USSR. The species level taxonomy of salmonoids (Salmonidae and Coregonidae), which is far from resolved, may partly explain this difference.

Africa and Madagascar

Most of the African continent has remained above sea level since the Precambrian, more than 600 Myrs ago, though large areas such as the Sahara, Somalia and Ethiopia, have been at times inundated by the sea (Lévêque, 1997) Such a long period of exondation may explain why Africa has a diverse fish fauna and an unparalleled assemblage of archaic, mostly endemic, families.

Main characteristics

- There are about 48 families of freshwater fishes in tropical and southern Africa, 15 of which are endemic. The African ichthyofauna has fewer families and species than South America but it includes a higher number of basal and archaic families.
- The archaic groups include the Polypteridae, recorded since the Cretaceous only from Africa; the Denticipidae, considered as the sister group of Clupeiformes (Lavoué et al., 2005); and the Phractolemidae, Kneriidae, Cromeridae and Grasseichthydae.
- The African fauna also includes remnants of archaic elements of wider distribution, such as the Protopteridae, Notopteridae and Osteoglossidae. Three other families of the predominantly Gondwanan Osteoglossomorpha are endemic to Africa: the speciose family Mormyridae, and the monotypic Gymnarchidae and Pantodontidae.
- Two large lineages of secondary division freshwater fishes are present in Africa: the Cyprinodontiformes and the Cichlidae, both extremely diversified.
- Peripheral freshwater fish families are relatively poorly represented in African inland waters in comparison to other continents. Only a few families include exclusively freshwater genera or several freshwater resident species: Clupeidae, Ariidae, Synbranchidae, Latidae (ex Centropomidae), Gobiidae, Eleotridae, Mugilidae, Syngnathidae and Tetraodontidae.
- True diadromous species are rare in Africa. The genera *Anguilla* occurs in the Maghreb and five species are known from the east coast. However, the genus is completely absent from western and central Africa. This is also the case for many gobioids (e.g. *Sicydium*).

Madagascar's freshwater fish fauna contrasts with the continental Africa one (Sparks & Stiassny, 2003). Of a total of 135 native fish species, 84 are endemic to the island itself. Many new species have been described during the last decade and many more are waiting identification. The origins of the freshwater fish fauna remains unclear. Most of the species belong to widely distributed peripheral families. Many of the major groups of freshwater fish present in Africa, as well as those present in Africa and Asia (anabantids, bagrids, clariids, mastacembelids, notopterids, etc.), are absent in Madagascar (Stiassny & Raminosoa, 1994). Noteworthy is the absence of primary freshwater families such as the cyprinids, characins and mormyrids. Only three secondary freshwater families (Aplocheilidae, Cichlidae and Poeciliidae) have been recorded from the island. Many Malagasy species are phylogenetically basal within their respective families, and the ichthyofauna is apparently of relict nature.

Currently 3,255 species of fresh and brackishwater fish species have been described from Africa, belonging to 95 families. Numerous others are awaiting description.

Asia

Tropical Asia covers the Oriental region extending from the Indus basin to South China and Indonesia. In addition to continental areas the region includes many large islands such as Borneo, Sumatra and Java, as well as numerous smaller islands.

Main characteristics

- High number of fish families: 121 recorded from inland waters including 34 primary and secondary division freshwater fishes (18 endemic to South-east tropical Asia) and 87 peripheral usually represented only by a few species (Lundberg et al., 2000).

- The dominant primary groups are Cypriniforms including Cyprinidae (about 1,000 spp.), Cobitidae (about 100 spp.) and Balitoridae (about 300 spp.), Siluriforms including Bagridae (about 100 spp.) and the Osphronemidae (85 spp.).
- On oceanic islands and in coastal river basins, peripheral families dominate the fish communities. In Sulawesi, the Moluccas and most Philippine islands, there are no primary freshwater fishes. The dominant peripheral group is the Gobiidae (about 300 spp.).
- As in South America, the discovery of miniature species is fairly common. *Boraras micros* from northern Thailand is adult at about 12 mm SL, and *Paedocypris progenetica*, recently described from peat swamp pools in Indonesia, is sexually mature at 7.9 mm SL. At the opposite extreme, the Mekong stingray *Himantura chaophraya*, has a disk width of 2 m, a total length of 4 m, and used to weigh up to 600 kg. *Pangasianodon (Pangasius) gigas* of the Mekong is also one of the largest freshwater fishes with historical records of up to 3 m and 300 kg.

An estimated total number of 3,000 species has been suggested (Lundberg et al., 2000), but incomplete surveys in many countries render this a probable under-estimate. FishBase records 3,553 freshwater species or some 4,400 species if peripheral species are included.
Knowledge of the fish fauna of tropical Asia is still in its exploratory phase particularly in China and India where survey work is incomplete. Many species have still to be described or to be discovered.

Oceania

Australia, Tasmania, New Guinea and the islands of the Australian continental shelf represent a well-delimited biogeographic entity. New Zealand belongs to this realm as well.

The terrestrial connections between Australia and other continents broke some 100 Myrs ago. The last 15 Myrs have seen increased drying, resulting in decreased surface water in drainages mostly established during the Palaeocene (Unmack, 2001). Most patterns of distribution were almost certainly established in the distant past, perhaps as early as Miocene. Pleistocene glaciations were geographically limited, with probably little effect on the aquatic biota (Unmak, 2001).

Main characteristics

- The freshwater fish fauna of Australia is depauperate and lacks all Otophysan primary freshwater families found elsewhere in the world.
- The majority of freshwater fishes are representatives of marine families with many catadromous species.
- The only primary freshwater fishes are the Australian lungfish, *Neoceratodus* and some osteoglossids of the genus *Scleropages*. Neoceratodus is restricted to Queensland where it survives in swamps and permanent rivers.
- High endemicity in several provinces: most provinces in southern, central, and western parts of the continent have a large proportion of endemics, whereas Northern and Eastern provinces have few. The pattern results in part from isolation, due to aridity and drainage divides.

New Zealand has no primary freshwater fishes and low species richness: only about 50 species, belonging to seven families (e.g. Galaxiidae, Eleotridae, Anguillidae) that probably colonised New Zealand by sea. More than 60% fish species are diadromous. The degree of endemism is high.

Continental ecoregions and main areas of endemicity

At continental scales, ichthyologists have attempted to identify biogeographic or ichthyological ‘‘provinces’’ based on their distinctive evolutionary history and more-or-less characteristic biota at the species levels (e.g. Abell et al., 2000; Thieme et al., 2005). The present pattern, however, may also be the imprint of a long evolutionary history that has resulted in differentiation at higher taxonomic levels.

Main ecoregions in North America

Based mainly upon distribution data for freshwater fishes, mussels and crayfish, Abell et al. (2000) recognise 10 regional complexes (herein designated as provinces) for North America within which 76 ecoregions are delineated. In North America fishes, mussels and crayfish tend to display rather similar distributional patterns and here we take the basic map of Abell et al. (2000), as a reasonable surrogate for a regional subdivision of North America into ichthyofaunal provinces (Fig. 4):

1. Pacific Coastal province (ca. 40 endemic fish species). Comprised mainly of temperate coastal rivers, lakes and springs. With xeric elements in the Sonoran and southern Pacific regions.
2. Great Basin province (23 endemic fish species). Comprised mainly of endoreic rivers, lakes and springs.
3. Colorado province (20 endemic species). A mix of the large temperate Colorado River and xeric region rivers, lakes and springs.

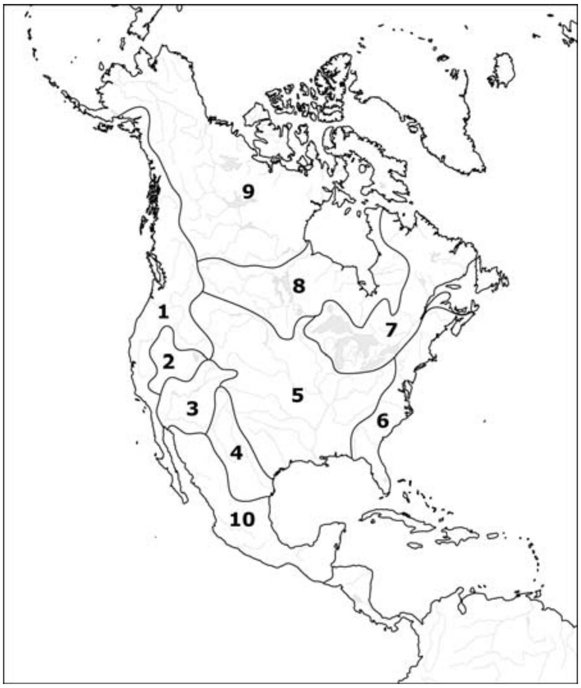

Fig. 4 Main ichthyological provinces in North and Central America (modified after Abell et al., 2000). See text for ecoregions

4. Rio Grande province (ca. 80 endemic species). Comprised mainly of the Upper and Lower Rio Grande River and a mosaic of xeric rivers, lakes and springs.
5. Mississippi province (ca. 130 endemic species). The largest river in the US, the Mississippi drains a basin of about one eighth the area of North America. Its mainstream, tributary systems, headwaters, embayments and karsts harbour at least 375 fish species. This basin has provided a refuge during times of glaciation and acted as a source for northern recolonisations.
6. Atlantic province (ca. 65 endemic species). A mosaic of subtropical coastal rivers, lakes and springs in the south, extending northward along the Atlantic seaboards temperate coastal rivers and lakes into maritime Nova Scotia.
7. St. Lawrence province (at least three endemic species). Temperate coastal rivers and lakes of northern Nova Scotia and the Gulf of St Lawrence, and the Great Lakes.
8. Hudson Bay province (no endemic species). Temperate headwaters and lakes of southern Canada, extending east to the Arctic rivers and lakes of the Hudson and James Bays.
9. Arctic province (four endemic species). Arctic rivers and lakes of the Yukon and Alaskan Arctic and Arctic islands.
10. Mexican Transition Bioregion (ca. 200 endemic species). A mosaic of xeric rivers, lakes and springs, and subtropical coastal rivers, volcanic crater lakes, sink holes and extensive wetlands.

Main ecoregions in Central America

More than 350 species are found in Central America, an area lying between the isthmus of Tehuantepec to the north and the Colombian border to the south. Based on the work of Bussing (1998) and supported by a preliminary analysis of freshwater fishes distribution at the basin scale (Tedesco et al., unpublished data), four ichthyofaunal provinces are recognised (Fig. 4):

1. The Usumacinta province comprises Atlantic rivers from Honduras, Guatemala, Belize and southern Mexico including the relatively large Usumacinta drainage.

2. The Pacific province includes coastal streams of the Pacific versant from Costa Rica to Mexico.
3. The San Juan province includes rivers of the Atlantic versant of Nicaragua and Costa Rica.
4. The Isthmian province sharing various species with the Magdalenean province from South America. Includes Pacific and Atlantic rivers from Panama and some Pacific rivers of Costa Rica.

Main ecoregions in South America

Based on a preliminary analysis of freshwater fishes distribution at the basin scale (Tedesco et al., unpublished data) and on the work of Gery (1969), 10 ichthyofaunal provinces are recognised for South America (Fig. 5):

1. South Patagonian province (12 species, 1 endemic). Southern Argentinean rivers extending from Tierra del Fuego to the Chubut river.

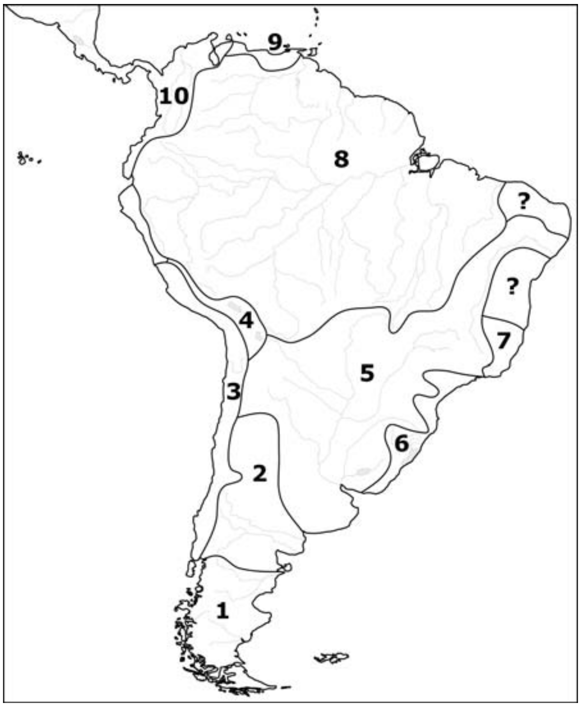

Fig. 5 Main ichtyofaunal provinces in South America. See text for ecoregions

2. North Patagonian province (23 species, 5 endemics) includes the Colorado and Negro rivers from Argentina.
3. Trans-Andean (South) province (19 species, 13 endemics) includes all the small coastal rivers from Chile.
4. Lake Titicaca province (32 species, 30 endemics). Endorheic drainages from the Bolivian and Peruvian Andes where sympatric speciation of the genus *Orestias* seems to be ongoing.
5. Paranean province (847 species, 517 endemics). Mainly including coastal rivers from central Argentina and two large rivers, the La Plata drainage and the Sao Francisco drainage from Brazil.
6. South-East Brazilian province (194 species, 90 endemics) comprised southern Brazilian coastal streams and a large coastal lagoon system.
7. East Brazilian province (131 species, 50 endemics) includes coastal rivers from eastern Brazil. Existing information is scarce.
8. Amazonian province (2,416 species, 2,072 endemics). This great province includes the Amazon and the Orinoco drainages, and the coastal rivers from the Guyanas and northern Brazil. Many new discoveries are anticipated.
9. North Venezuelan province (61 species, 9 endemics).
10. Trans-Andean (North)/Magdalenean province (423 species, 326 endemics). Includes rivers from Ecuador, Colombia and the Maracaibo drainage from Venezuela.

Main ecoregions in Europe

The only study using Europe-wide data at the basin scale was performed by Reyjol et al. (2007). These authors used species list from 406 basins (233 species) fairly evenly distributed across Europe to define geographical regions (provinces) having homogenous fish fauna. Figure 6 illustrates these provinces:

1. Ponto-Caspian Europe province (98 species, 36.7% endemic),
2. Northern Europe province (42 species, 9.5% endemic),

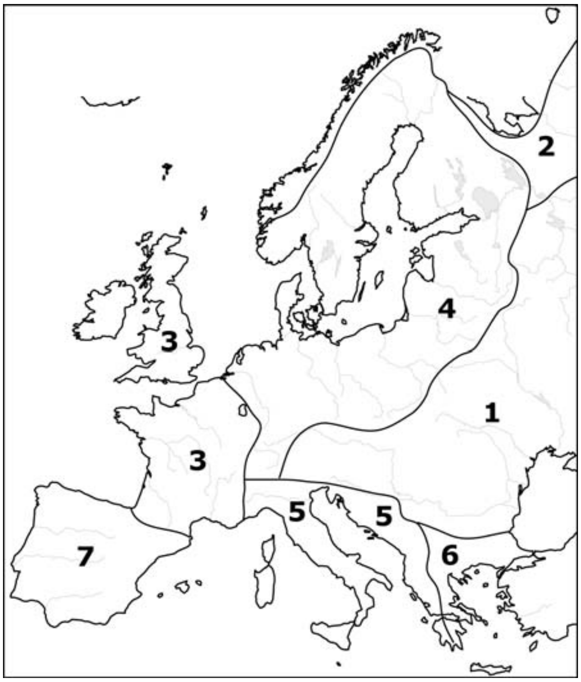

Fig. 6 Main ichthyological provinces in Western Europe. See text for ecoregions. Modified after Reyjol et al. (2007)

3. Western Europe province (47 species, 6.4% endemic) and
4. Central Europe province (57 species, 1.8% endemic).
5. Central peri-Mediterranean province (93 species, 64.5% endemic),
6. Eastern peri-Mediterranean province (64 species, 31.2% endemic),
7. Iberian Peninsula province (50 species, 60% endemic).

Main ecoregions in Africa

Several ichthyological provinces have been identified in Africa (Roberts, 1975; Levêque, 1997; Thieme et al., 2005) (Fig. 7):

1. The Maghreb has a very depauperate fauna with Paleartic affinities.
2. The Nilo Sudan province extends from the Atlantic coast to the Indian Ocean and includes the major drainage basins of the sahelian zone: Nile, Chad, Niger, Senegal, Volta. The fish fauna is relatively rich (Paugy et al., 2003).

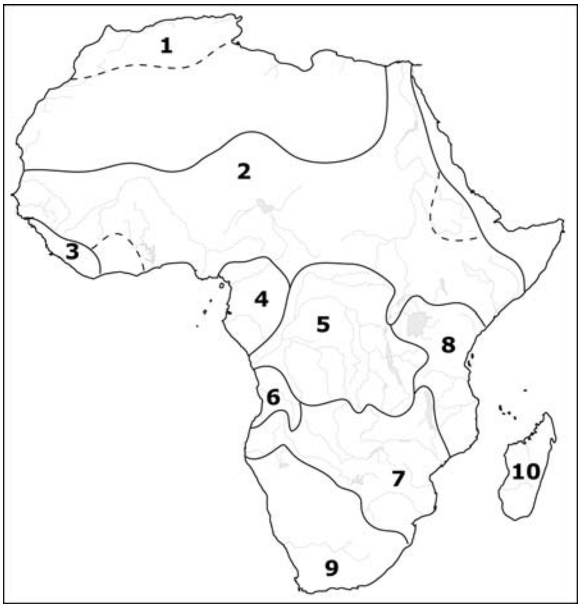

Fig. 7 Main ichtyological provinces in Africa (Lévêque, 1997, modified from Roberts, 1975). See text for ecoregions

3. The Upper Guinea province includes the coastal rivers from Guinea to Liberia and exhibits faunistic affinities with the Lower Guinea Province and the Congo. Fauna well diversified with many endemic taxa (Paugy et al., 2003).
4. The Lower Guinea covers coastal rivers from Cameroon to the mouth of the Congo river, with a well diversified fauna (Stiassny et al., in press).
5. The Congo province includes the entire Congo basin, which is the largest in Africa. The ichthyofauna is rich and diversified, but existing information needs to be synthetised and many new discoveries are anticipated.
6. The Quanza province which covers the Angolan coastal drainages is still extremely poorly known.
7. The Zambezi including the river Cunene, Okavango and Limpopo has a moderately rich fauna and is fairly well documented (Skelton, 2000)
8. The East Coast covers the coastal drainages from the Juba in the North to the Zambezi in the south. The fauna is moderately rich and a new synthesis is needed.
9. The Southern province includes the basins of the Orange-Vaal and all the coastal systems to the south. The fauna is moderately rich and well known (Skelton, 2000).

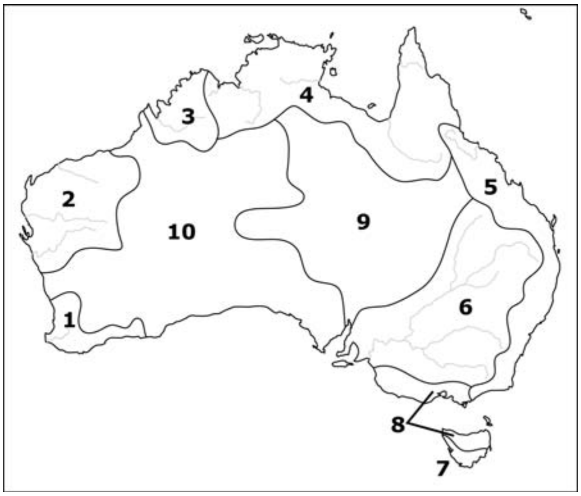

Fig. 8 Freshwater fish biogeographic provinces in Australia (from Unmack, 2001). See text for ecoregions

Ecoregions in Asia

We present no information about ecoregions in Asia, as work is in progress under the leadership of WWF-USA and will be published soon.

Main ecoregions in Australia

In a recent work, Unmack (2001) identified 10 biogeographical provinces (Fig. 8). Most patterns were almost certainly established in the distant past, perhaps as early as Miocene. Influences of Plio–Pleistocene events on broad patterns of freshwater fish distributions seem minimal (Unmack, 2001).

1. *South-western* province has few species, and no species in common with any other, suggesting long-term isolation. Faunal relationships, although distant, lie with south-eastern Australia;
2. *Pilbara* province is one of the hotest in Australia. Five of 12 recorded species are endemic, the remainder are widespread in Australia;
3. *Kimberley* province is characterised by high endemicity. Only 16 species, out of 29 are widespread;
4. *Northern* province has 38 endemic species (25 shared with New Guinea) out of 75 (50% endemic). A strong relationship exists between Fly River, New Guinea and the Northern Province of Australia, with 34 out of 75 freshwater fishes (45%) in common (Allen, 1991).
5. *Eastern* province is distinctive for its lack of faunal breaks, its boundary with the Northern Province being due to a sharp decline in richness. Fifteen out of 47 species (31%) are endemic.
6. *Bass* province has a depauperate fauna;
7. *Southern Tasmanian Province* has no shared species, all eight being endemic including three *Galaxias* and three *Paragalaxias*. All have restricted ranges, often one or a few lakes and/or streams.
8. *Murray-Darling* province appears to have experienced mixing of faunas from surrounding regions, while maintaining a high degree of endemism.
9. *Central Australian* province (30 species);
10. *Palaeo* province contains former connections to surrounding drainages now dried. Only one species recorded from this vast region.

Endemism and fish species flocks in ancient lakes

Exceptionally high faunal diversity occurs in certain ancient lakes ("long-lived" lakes that are more than 100,000 years old). One of the most noteworthy features is the existence of "species-flocks" that are aggregates of disproportionally high numbers of species, sharing a common ancestor and endemic to each lake (Table 5). The longevity of ancient lakes, compared to younger lakes, may explain the abundance of endemic evolutionary radiations they harbour. However, the processes accounting for these radiations are a matter of debate, but there is a growing body of evidence that suggests that in addition to intra-lacustrine allopatric speciation sympatric speciation may have also occurred (Schliewen et al., 2001). At present, several rich fish-species flocks have been identified in various ancient lakes that are exceptional natural sites for the study of speciation processes.

In Africa, the most striking feature of the Eastern African Great Lakes (Victoria, Tanganyika, Malawi) is that each has its own highly endemic lacustrine cichlid fauna that apparently evolved independently from riverine ancestors. Some 550 endemic haplochromine cichlids occur in Lake Victoria, probably more than 800 in Lake Malawi (Fryer, 1996), and 325

Table 5 Current fish species flocks in selected ancient lakes

	AFRICA					ASIA	SOUTH AMERICA			ASIA	EUROPE
	Matawi	Victoria	Tanganyika	Kivu	Tana	Lanao	Titicaca	Chapala	Chichancanab	Baïkal	Ohrid
Salmoniformes											
Salmonidae											■
Cypriniformes											
Cyprinidae					■	■					
Siluriformes											
Bagridae			■								
Mochokidae			■								
Atheriniformes											
Atherinidae								■			
Cyprinodontiformes											
Cyprinodontidae							■		■		
Synbranchiformes											
Mastacembelidae			■								
Scorpaeniformes											
Cottidae										■	
Comephoridae										■	
Abyssocottidae										■	
Perciformes										■	
Cichlidae	■	■	■	■							
Centropomidae			■								

in Lake Tanganyika ans some 1,000 species are still awaiting scientific description((Snoeks, 2000). Intra-lacustrine cichlid speciation has also occurred, to a lesser extent, in other smaller lakes of the Rift Valley (Kivu, Albert, Edward and Turkana), and in certain crater lakes of Cameroon (Stiassny et al., 1992; Schliewen et al., 1994). Rates of speciation in cichlids can be extremely fast, with some estimates at about 100,000 yrs (e.g. Verheyen et al. 2003).

The non-cichlid fauna of the East African Lakes is less speciose and has lower levels of endemism, but is still noteworthy. For instance, Lake Tanganyika harbours small species flocks within a few other families: 7 mastacembelid species, 6 species of the clarotid *Chrysichthys*, 7 species of the mochokid *Synodontis* and 4 species of the latid, *Lates* (De Vos & Snoeks, 1994).

A species flock of lacustrine cyprinids has recently been discovered in Lake Tana, Ethiopia, where Nagelkerke & Sibbing (1996, 2000) carried out detailed studies of the morphology, reproduction and feeding habits of the large hexaploid barbs belonging to the species complex, *Labeobarbus intermedius*. They identified at least 15 biologically distinct species differing in food niche and habitat preferences, as well as in spawning grounds.

In South America, the native fish fauna of Lake Titicaca includes 24 *Orestias* species (Cyprinodontidae) (Lauzanne, 1992). Lake Chapala, located in Mexico is a remnant of a series of Tertiary lakes where atherinids (silversides) of the genus *Chirostoma* are prominent with eight species (Echelle & Kornfiel 1984). In the Laguna Chichancanab in the Yucatan Peninsula (Mexico), a flock of six species of the genus *Cyprinodon* (pupfishes) has also been identified (Echelle et al., 2005).

In northern Asia, lakes existed in the Baikal Rift zone (East Siberia) for at least the last 60 million years. Since about 28 Myrs, one or more continuous large lakes have evolved into the extant lake (Mats, 1993). Today, Lake Baikal hosts a very diverse fauna, with some 2,500 described animal species (most of them endemic) including 56 species and subspecies of fish belonging to 14 families (Sideleva, 1994). Noteworthy is the presence of a sculpine (Cottotoidei) species flock, comprising 29 species (11 genera) of sculpins endemic to the lake. Through adaptive radiations, sculpins have colonised the most diverse habitats such as the abyssal and the pelagic zones of the lake. According to recent molecular studies sculpine fish comprise a fairly young species cluster, which have most likely diverged since the beginning of the Pleistocene (2 Myrs) when the climate in the region generally became much cooler (Yu Sherbakov, 1999).

In tropical Asia, Lake Lanao (Philippines) was formed 3.6–5.5 Myrs ago. The cyprinid flock is a widely acknowledged example of adaptive radiation while its age is a matter of debate (Rainboth, 1991). Unfortunately over-exploitation and exotic introductions have decimated the fauna, so that now only three or fewer endemic cyprinids are still surviving (Harrison & Stiassny, 1999). In central Sulawesi (Indonesia) a series of tectonic lakes host a fauna of 26 native species (22 endemic) (Kornfield & Carpenter, 1984).

The tectonic Lake Biwa is the largest and oldest lake in Japan. The Old-Biwa lake was established as a small, shallow lake about 5–6 million years ago (Kawanabe, 1996) with the present deep basin forming around 300,000 years ago. At present there are 71 species and subspecies of freshwater fishes in the lake and its tributaries (Yuma et al., 1998). More than half belong to the family Cyprinidae (37 species) and the rest to Cobitidae (6), Gobiidae (6), Salmonidae (5), Siluridae (3) among others.

Human related issues and conservation

The number of fish species able to use freshwaters, totals to about 13–15,000 species, which is 40–45% of the global fish diversity estimated at about 29–30,000 described species. Fish inhabiting freshwaters comprise therefore ca. 25% of living vertebrates (about 55,000 described species) and represent 13–15% of the 100,000 freshwater animal species currently known (Lévêque et al. 2005).

It is often claimed that freshwater ecosystems are the most endangered ecosystems in the world (Sala et al., 2000). The particular vulnerability of freshwater fish to global changes reflects the fact that both fish and freshwater are resources humans need and that have been heavily impacted by human usage and regulation. Asia supports over half of the global human population, with enormous consequent pressures on inland waters and freshwater fish biodiversity vities (Dudgeon et al., 2006). Conversely, in areas such as the Amazon and Congo basins with lower population densities, human impacts are relatively less marked although increasing nonetheless.

The major threats to fish biodiversity have been well identified: overexploitation, flow modification, destruction of habitats, invasion by exotic species, pollution including the worldwide phenomenon of eutrophication (Harrison & Stiassny, 1999; Dudgeon et al., 2006), all of which are interacting.

Freshwater fishes are important and valued resources for food, sport and ornament. Overexploitation occurs all over the world with the use of more and more sophisticated fishing gear, and the decrease of many fish stocks has been documented as a result of expanding fisheries (Allan et al., 2005). Illegal fishing using pesticides, electrofishing, dynamite, etc. are also major threats to fish diversity all over the world.

Other serious threats are flow modifications of running waters (diversion, extraction, storage) and water engineering such as impoundment by dams. The loss, or modification of aquatic habitats, are both responsible for extinction of native species (Harrison & Stiassny, 1999). The demand for reliable sources of fresh water and flood control has encouraged prolific dam-building (45,000 large dams and possibly 800,000 smaller ones—mainly since the last century) that has resulted in fragmentation and destruction of habitat, and loss of species (e.g., Vörostmary et al., 2006).

Over the past decades, excessive nutrient loading has emerged as an important direct driver of freshwater ecosystem change. World consumption of nitrogenous fertilisers grew nearly eightfold between 1960 and 2003, from 10.8 million tons to 85.1 million tons (MEA, 2005). Eutrophication is probably the most widespread problem affecting lake and reservoir waters. A direct impact of eutrophication is a change in the structure of fish species communities, or even elimination of fish populations (Seehausen et al., 1997).

Species have been introduced throughout the world for different purposes including stocking of fishes for aquaculture and fisheries, sport fishing, use of baitfish and their release after fishing, intentional or unintentional releases of aquarium species, environmental management for pest/weed control etc. In Europe, translocations are believed to date from Roman times, when carp, *Cyprinus carpio*, from the River Danube were reared in ponds in Italy and western and southern Greece (Balon, 1995). According to historical sources, it seems likely that during Roman times and later in the Middle Age, other freshwater fish species were moved from one system to another. Carp was probably not always introduced alone and other species were likely included in the carp transportations, as has been the case with the worldwide translocation of tilapias in the past century.

Biotic homogenisation, the process of gradual replacement of native biotas by non-indigenous and locally expanding non-native species is rapidly diminishing the regional distinctiveness of aquatic systems (Olden & LeRoy Poff, 2004). Such a process is well documented in United States where Rahel (2000) showed that states share, on average, 15.4 more species than before the European settlement. In documented cases, states that formerly had no species in common, now share an average of 25.2 species.

Inventories of freshwater biodiversity are incomplete in many parts of the world, especially the tropics, and rates of species loss may be higher than currently estimated. Today, hundreds of freshwater fish are close to extinction. Large tropical lakes like those in Eastern Africa, but also the Palaearctic Lake Baikal, have a very high heritage value. They are natural laboratories to study evolution and they should be given high priority for conservation. Maintenance of freshwater fish biodiversity is a critical test of whether water use and ecosystem modifications are sustainable. However, to be fully effective, protection of freshwater requires control over the upstream drainage network, the surrounding land, the riparian zone, and—in the case of migrating aquatic fauna—downstream reaches. Such prerequisites are hardly ever met!

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