

## An assessment of animal species diversity in continental waters

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### Abstract

There is a need for monitoring the status and trends of freshwater biodiversity in order to quantify the impacts of human actions on freshwater systems and to improve freshwater biodiversity conservation. Current projects carrying assessment of freshwater biodiversity focus mainly on leading-better-known groups such as fish, or identify keystone species and/or endemic freshwater systems for conservation purposes. Our purpose is to complete these existing projects by providing quantitative estimates of species number for all freshwater groups on each continent and/or major eco-regions. This article presents the results of the first implementation phase carried out from September 2002 to June 2003 and which addressed only freshwater animal species. The project consisted of: (1) compiling existing data from literature, web sites and museum collections; (2) contacting scientific experts of each group to provide a 'to the best of their knowledge, estimates of species numbers. In this study, we consider as true freshwater species, those that complete part or all of their life cycle in freshwater, and water-dependant species those that need freshwater for food or that permanently use freshwater habitats. The current order of magnitude for known freshwater animal species world wide is 100 000, of which half are insects. Among other groups, there are some 20 000 vertebrate species; 10 000 crustacean species and 5000 mollusc species that are either true freshwater or water-dependant species. The study highlighted gaps in the basic knowledge of species richness at continental and global scales:

- (1) Some groups such as Protozoa, nematodes or annelids have been less studied and data on their diversity and distribution is scarce. Because current richness estimates for these groups are greatly biased by knowledge availability, we can expect that real species numbers might be much higher.
- (2) Continents are not equal in the face of scientific studies: South America and Asia are especially lacking global estimates of species richness for many groups, even for some usually well-known ones such as molluscs or insects.

The second phase of the project will address freshwater plants and algae. The present status should be considered as a first sketch of the global picture of freshwater biodiversity. We hope that this project will initiate interactive exchange of data to complete and update this first assessment.

### Introduction

It is widely recognised that freshwater biodiversity and habitats are increasingly being affected by human activities (Stiassny, 1999). Available data

suggest that around 30% of fish species are threatened (IUCN Red List of Threatened Species, Khlphake et al., 2001). The extinction rate for freshwater animals in North America is estimated to be five times higher than for terrestrial fauna,

with 123 freshwater animal species recorded as extinct since 1900 (Ricciardi & Rasmussen, 1999). All estimates of biodiversity loss are conservative considering the lack of knowledge for many groups of species and for extended areas in the tropics and high latitudes (Lévêque & Mounolou, 2003). Consequently, the number of threatened species is expected to be much higher. In addition to species loss, also habitat degradation, eutrophication and species introduction affect freshwater bodies world wide. Despite the signs of rapid and destructive changes in freshwater ecosystems, freshwater biodiversity remains of low priority in global conservation initiatives carried by governmental and intergovernmental organization, (Stiassny, 1999; Balmford et al., 2002; Shumway, 1999). For example, lakes and their watersheds are dramatically under-represented both in protected areas and in Conservation measures although they are experiencing serious degradation (Duker & Borre, 2001). The lack of conservation and management strategies to avert damaging changes in freshwater habitats occurring around the globe increases the potential for permanent loss and ignorance of much of our planet's rich aquatic biota (Lundberg et al., 2000)

Scientists are faced with the challenge to provide baseline studies on freshwater biodiversity at regional and global scales to international policy makers (Postel, 2001). Indeed, monitoring the status and trends of freshwater biodiversity is essential to quantify impacts of human activities on freshwater systems and to improve freshwater biodiversity conservation. Estimating global trends for freshwater biodiversity will also be a critical asset for management strategies considering that studies on climate change and water resources and data management systems are currently being developed at a global scale (GWSP).<sup>1</sup>

Current projects on the assessment of freshwater biodiversity focus mainly on a few better-known groups, such as fish or molluscs, or identify keystone species and/or endemic freshwater systems for conservation purposes (Groombridge & Jenkins, 1998; Lévêque, 2002; Revenga & Kura, 2002). Our aim is to complete these existing projects by providing quantitative estimates of species numbers for all freshwater groups on each

continent and/or major eco-regions. The results should highlight gaps and help prioritising the groups and geographical areas where additional investigations are needed.

The first phase of the project has been implemented from September 2002 to June 2003 and has addressed only freshwater animal species. The project consisted of: (1) compiling existing data from literature, web sites and museum collections and reporting the most recent number of known (described) species for each group; (2) contacting scientific experts of each group to provide a 'to-the-best-of-their-knowledge' estimate of species number. The results of this first phase are reported here and were also presented at the conference on 'Aquatic biodiversity: Past-Present-Future, an International Scientific Meeting' held in Antwerp, Belgium, in August 2003. A second project phase should address the plant, fungi and algal species.

### What is a freshwater species?

The first problem encountered in assessing freshwater biodiversity is the actual definition of a freshwater species.

Indeed, many animal species dependency upon freshwater habitats in many different ways:

- Some species depend on freshwater for all stages of their life cycle, r, i.e. many freshwater fishes (except diadromous species that migrate between marine and freshwater environments), freshwater crustaceans or rotifers;
- Some species need freshwater to complete part of their life cycle, such as many amphibians and insects;
- Some species need humid habitats such as some Collembola;
- Some species are closely dependant on freshwater for food or habitat such as most of the so-called aquatic birds and some mammals, but also parasites whose 'food and habitat' is then a freshwater animal host.

In the present paper, we consider as freshwater species both the 'true freshwater species' and the 'freshwater dependant species'. The latter include for example many aquatic birds, and several mammals or reptiles. In the case of parasites, if

<sup>1</sup>Global Water System Programme, web site <http://www.gwsp.org/>

they have a freshwater stage, they are considered as true freshwater species; if they have only internal parasitic stages, they would fall into the freshwater dependent species.

### **An assessment of freshwater invertebrate species diversity**

#### **PHYLUM PORIFERA**

**Habitat and Diversity:** The entire phylum Porifera consists of more than 5000 species world wide. Only 197 of these are known to occur in freshwater; a total of less than 300 sponge species are expected to be non-marine (Ruppert & Barnes, 1995). The *Spongillidae* is a major family of freshwater sponges, represented by about 170 species world wide (Smith, 2001), with 27 species being reported from North America (Thorp & Covich, 2001).

**Distribution:** Of the currently known freshwater sponges, 77 species occur in Eurasia 49 in Africa 27 in North America, 51 in South America and 31 in Oceania (Manconi & Pronzato, 2002; Pronzato & Manconi, 2002). There are likely to be various undescribed species, particularly in tropical regions that have not been thoroughly investigated. **Endemicity:** The diversity of sponges in freshwater is low in comparison with those of marine habitats from which they have evolved but there are some valuable hot-spots of endemicity because freshwater sponges have undergone adaptive radiation in ancient lakes such as lakes Baikal and Tanganyika, and in South America (Dumont, 1994b). One sponge family, the Lubomirskiidae, is endemic to Lake Baikal and comprises 14 species (Timoshkin, 1997).

#### **PHYLUM CNIDARIA**

**Habitat:** Also the Cnidaria are a primarily marine phylum with a few freshwater representatives that belong to the class Hydrozoa. There are sessile polyp forms, which are usually colonial and free-swimming medusae, which usually represent the sexually reproducing, dispersal phase.

**Diversity and endemicity:** The total number of freshwater cnidarians is low, about 30–45 species

are estimated to occur world wide (Vervoort, pers. com.). Few comprehensive data could be reported on endemic freshwater cnidarian. In Lake Baikal, one of the two described *Hydra* species is endemic. **Distribution:** Fifteen cnidarian species are reported from Europe (Fauna Europaea, 2002) and 22 species are report from freshwaters of North America (Smith, 2001). There are altogether about 10–14 freshwater species of medusa. No freshwater medusa appears to have evolved in Europe and the Americas, but one is currently present there: *Craspedacusta sowerbii* has apparently managed to colonize all continents except Antarctica, in the course of the 20th century (Dumont, 1994b). *Limnocoidea* and *Craspedacusta* are the two main genera of cnidarians from continental waters, with a free-swimming medusa in their life cycle. They originated in tropical-subtropical areas, *Limnocoidea* is also found in Africa (Williams et al., 1991); *L. tanganyicae* is endemic to Lake Tanganyika (Coulter, 1991).

#### **PHYLUM PLATYHELMINTH**

There are four classes in this phylum: the Cestoda (tapeworms), Trematoda (flukes), Monogenea and Turbellaria (planarians).

**Habitat:** The turbellarians are mostly marine with several freshwater orders. Most freshwater turbellarians are free-living and occur in various aquatic systems such as ponds, lakes, streams, hyporheic water, ditches, and temporary puddles. A few freshwater turbellarian species are ectoparasitic on crustaceans. The cestodes, the trematodes and the monogenes are all internal parasites. **Diversity and Endemicity:** There are about 20 000 platyhelminth species world wide (Pennak, 1989). The Microturbellaria include 400 species in freshwaters and about 100 species of Macroturbellaria (Triclad or planarians) occur world wide (Giller & Malmqvist, 1998). Free-living platyhelminthes (Turbellaria) comprise 150 described species in Lake Baikal of which about 130 are endemic; several dozens of Baikalian turbellarian species are still awaiting description (Timoshkin, 1997).

**Distribution:** The total number of non-marine turbellarians reported from Europe is 623 species of which 577 are affiliated to freshwater and 46 species are strictly terrestrial (Faubel, pers. com.; Fauna Europaea, 2002). About 350 microturbel-

larian species have been recorded from Europe, and approximately 150 from North America; 40 macroturbellarian species have been recorded from North America (Smith, 2001).

### PHYLUM ROTIFERA

**Habitat:** The phylum Rotifera is mainly represented by freshwater species, widely distributed in all types of inland waters, and by a few marine species.

**Diversity:** The phylum currently comprises 1817 valid species, but the total number is doubtlessly higher. There are only 50 exclusively marine species, and a few terrestrial and parasitic species. The Monogononta is the largest group (1441 sp.), followed by Bdelloida (374 sp., Segers, 2002). The latter group is highly enigmatic, as it constitutes the highest taxonomic level of exclusively asexually reproducing multicellular eukaryotes.

**Distribution:** Rotifers are generally cosmopolitan, with a preponderance of thermophilic or tropicopolitan representatives. Nevertheless, some taxa like *Synchaeta* and *Notholca* are more diverse on higher latitudes. The fauna of tropical South America and Asia, and that inhabiting the freshwaters of Northeast North America are particularly diverse and rich in endemics; the same may hold for Southwest Australia. The fragmentary nature of our knowledge on the rotifer fauna of tropical Africa and Madagascar precludes any reliable assessment (Segers, 1996, 2001, 2003). The number of known rotifer species from Australia is close to 600 spp. (Shiel & Koste, 1986). In Asia, 477 species are recorded in China in 84 genera and 28 families (Zhuge et al., 1998). Only 3% of the Chinese rotifer fauna is restricted to the area, with 15 endemic taxa. Rotifer diversity is also high in Thailand with 310 taxa on record, although some of them may be questionable (Segers, 2001). The majority of rotifers recorded from Southeast Asia are widely distributed and occur in the tropical regions of the old world, Australia and the Austro-Malayan region (Segers, 2001). Remarkably, although the total number of valid species recognised in Rotifera stands at a relatively low 1817 (Monogononta: 1441), local diversity may be fairly high: Dumont & Segers (1996) estimate that some 250 species of Monogononta may co-occur in a single lake.

**Endemicity:** For a long time, the prevailing idea was that rotifers had a cosmopolitan distribution. However, recent work has demonstrated that the degrees of cosmopolitanism and endemism vary between groups. The same is true for long distance, passive dispersal, and vicariance events, which all play key roles in structuring distribution patterns (Segers, 1996, 2003). Lake Baikal, holds 26 endemic species on a total of 186 rotifer species (Timoshkin, 1997).

### PHYLUM NEMERTEA

**Habitat:** Most nemerteans are marine organisms, and a small minority is terrestrial or lives in freshwater (Moore & Gibson, 1985). They are benthic forms, hermaphroditic and often proteandric.

**Diversity and endemicity:** Amongst the 900 known species, 20 nemerteans inhabit freshwaters (Gibson, pers. com.). No comprehensive data could be reported about possible nemertean endemicity.

**Distribution:** Three nemertean species are found, in North America (Gibson, 1995; Thorp & Covich, 2001), and 15 species are reported from Europe (Fauna Europaea, 2002).

### PHYLUM NEMATODA

**Habitat:** Many nematods are free-living but they also include parasitic species, a number of which affect humans directly or indirectly through their domestic animals (Malakhov, 1994). It is difficult to identify the exact diversity of freshwater nematode species, because some terrestrial nematods live in the water-film surrounding plants or soil particles. In addition, some species are generalist, occurring across wide areas and in many habitats while others are much more specialised. Many of them are terrestrial, but some genera contain obligate freshwater species (or at least, part of their life cycles occurs in freshwater habitats).

**Diversity:** There are currently about 14 000 known nematode species, about half of which is considered to be non-marine (Bongers, pers. com.), but the true number may be closer to 100 000 as suggested by Coomans (2000). About 3000 nematode species have been recorded in freshwater, but some of these might also be found under terrestrial conditions (Bongers, pers. com.).

Distribution: Andr assy (1978) listed 605 species of freshwater nematodes in a checklist for European inland water, Jacobs (1984) listed 327 species of freshwater nematodes in Africa and Thorp & Covich (2001) estimated the number of freshwater nematodes in North American waters at about 300–500, but again the real numbers are expected to be much higher.

Endemicity: Shoshin (1999) registered about 300 (mostly undescribed) species at only six near shore sampling localities in Southern Baikal. Several hundreds of species are awaiting description.

### PHYLUM NEMATOMORPHA

Habitat: Most nematomorph species exist in freshwater habitats, except for the genus *Metonema* which comprises pelagic marine species. Nematomorph life cycles involve a short-lived non-feeding adult stage and a more persistent larval stage that commonly parasites arthropods.

Diversity and endemicity: There are currently around 32 described species (Ruppert & Barnes, 1995), which might be a considerable underestimation. For example, Dudgeon (1999) estimated that there are over 100 species of Gordioidea, an order of Nematomorpha confined to freshwaters. No comprehensive data are available on distribution and possible endemicity of Nematomorpha.

### PHYLUM GASTROTRICHA

Habitat: Gastrotrichs are free-living in aquatic environments, either marine or freshwater (Boaden, 1985). The freshwater gastrotrich species mainly inhabit the sediment surface and the submerged vegetation in eutrophic waters (Ricci & Balsamo, 2000). Gastrotrichs are amongst the few animal groups commonly found in (near-) anaerobic environments.

Diversity and endemicity: There are 250 known freshwater gastrotrich species; the vast majority of these belong to the order Chaetonotida. (Smith, 2001). This total number is likely to be a considerable underestimation, due to lack of investigations in many geographical areas. We could not find comprehensive data on possible gastrotrich endemicity.

Distribution: Fewer than 100 species of gastrotrichs are reported from North America (Thorp & Covich, 2001) and around 200 species from Europe (Fauna Europaea, 2002).

### PHYLUM BRYOZOA

Habitat: Bryozoans are aquatic organisms, living mostly in colonies of interconnected individuals, also called zooids. Most bryozoans are marine, although brackish- and freshwater forms are moderately common. These freshwater forms are generally restricted to warm water, both in lakes and rivers.

Diversity and endemicity: The phylum *Bryozoa* remains largely unknown, although it is a very diverse group with about 5000 living species. The number of freshwater bryozoans world wide is around 70–75 species (Massard, pers. comm.). We could not find comprehensive data on possible gastrotrich endemicity.

Distribution: There are about 15–16 bryozoan species in Europe (Fauna Europaea, 2002) and 24 bryozoan species are found in North America (Thorp & Covich, 2001).

### PHYLUM TARDIGRADA

Habitat: Tardigrades, water bears, are present in freshwater, marine and terrestrial habitats (Nelson & McInnes, 2002). All tardigrades are dependent on water to feed, breathe, reproduce and move. In terrestrial habitats, limno-terrestrial tardigrades live in the water film that surrounds litter, moss and lichens where they share a micro-world with other organisms (Collembola, mites, rotifers, and nematodes) and endure extreme environmental conditions from flood to drought. Hydrophilous tardigrades are aquatic species that live only in permanent freshwater habitats, mostly in the littoral zone.

Diversity and distribution: Tardigrades include approximately 800 species world wide of which limno-terrestrial species account for the largest part. In North America, five species are strictly freshwater and 13–14 typically freshwater (Thorp & Covich, 2001), but the actual number is probably much higher. In Europe, there are 1000 species of limno-terrestrial and freshwater tardigrades (Fauna

Europaea, 2002). We could not find comprehensive data on possible tardigrade endemicity.

## PHYLUM ANNELIDA

Three classes of annelids occur in freshwaters: Polychaeta or tube worms, Oligochaeta or aquatic earthworms, and Hirudinea including the leeches and blood suckers.

### Class Polychaeta

**Habitat:** Polychaetes are typically marine and only a few of the more than 80 families have freshwater representatives.

**Diversity and endemicity:** There are 9000 polychaete species currently recognised (Rouse and Pleijel, 2001), but no estimates are available for freshwater species. Four freshwater polychaete species have been described from Lake Baikal (Timoshkin, 1997), but no additional data have been reported on freshwater polychaete endemicity or distribution.

### Class Oligochaeta

**Habitat and Diversity:** The oligochaetes are well-represented in both marine and freshwater environments. Oligochaetes display the greatest diversity of the freshwater annelids with about 700 species world wide (Tim, 1985; Dudgeon, 1999) and are considered to be cosmopolitan (Brinkhurst & Wetzel, 1984).

**Distribution:** The total number of freshwater oligochaetes is distributed over the following regions: 419 Holarctic species, 170 Sino Indian, .83 Ethiopian, 133 Neotropical, 85 in Antarctica (Tim, 1985; Dudgeon, 1999). Regional estimations gave figures of 50 species in Southern Africa (Day & De Moor, 2002), 73 in North America (Brinkhurst & Gelder, 1991) and 85 species in Europe (Minelli, pers. com.).

**Endemicity:** Lake Baikal is a centre of diversity and endemicity for oligochaetes, with 164 endemic species out of a total of 194 described species (Timoshkin, 1997).

### Class Hirudinea

**Habitat:** Leeches and blood-suckers are found in fresh and marine waters, but many terrestrial species occur in tropical regions. Leeches form an important component of the benthos of most lakes

and ponds (Sawyer, 1986). They are either predators of macroinvertebrates or temporary ectoparasites of freshwater fishes, turtles, amphibians, water birds and occasional mammals (aquatic or terrestrial).

**Diversity and endemicity:** The total number of Hirudinea world wide might be a little less than 500 species (Minelli, pers. com.). A total of 69 species is recorded in North America (Thorpe & Covich, 1991).

Eleven endemic species of Hirudinea have been described from Lake Baikal out of a total of 13 described species (Timoshkin, 1997). In Lake Tanganyika, 20 Hirudinea species have been described, of which 12 are endemic (Coulter, 1991).

## PHYLUM MOLLUSCA

**Habitat and Diversity:** Molluscs are well distributed in all marine, freshwater and terrestrial habitats. The total number of molluscs from marine, freshwater and terrestrial habitats is estimated to range between 80 000 and 135 000 (Seddon, 2000). In fresh and brackish waters some 5000–6000 species have been identified in 55–60 families of gastropods (snails and slugs) and bivalves (clams and mussels; Taylor, 1988) (Table 1).

**Distribution:** Molluscs occur throughout, the world except Antarctica. The present distribution is primarily controlled by habitat and life history, and means of dispersion, with a strong influence of geologic history. Most families are widespread, but a few are restricted to single lakes. Widely distributed species (cosmopolitan and circum-boreal) are those that can live in an extreme range of habitats.

The highest diversity of freshwater molluscs is recorded in North America (USA 945 sp.; Bogan, 1998). There are currently 177 described molluscan species in Europe (excluding the Mediterranean basin and ex-USSR; Falkner et al., 2001). Data on freshwater mollusc richness are either lacking or scattered for South America and Asia.

**Endemicity:** Endemism of molluscan species occurs in river, spring and lake systems. Groombridge and Jenkins (1998) identified 27 areas of special importance for freshwater mollusc diversity world wide:

Table 1. Global diversity of freshwater molluscs

	North America <sup>1</sup>	South America	Europe <sup>2</sup>	Africa	Asia	Australia <sup>4</sup>	World
Bivalves	344		50 <sup>9</sup>	172 <sup>5</sup>		37	1000
Gastropods	601						4000 <sup>7</sup>
Prosobranchs	439		133	250 <sup>3</sup>		156	
Pulmonates	162		30	91 <sup>3</sup>		c.67	
Total mollusks	945			513	285 SE Asia <sup>8</sup>	260	5000

<sup>1</sup> Bogan (1998).

<sup>2</sup> Excluding the mediterranean Basin and exUSSR (Falkner et al., 2001).

<sup>3</sup> Excluding Hydrobiidae from Northern Africa (Brown, 1994).

<sup>4</sup> Valid described taxa from Ponder (pers. com.) based on (Smith, 1992) and published unpublished data, there are at least 179 undescribed species and nine introduced species.

<sup>5</sup> Daget (1998).

<sup>6</sup> India, Sri Lanka, Pakistan, Nepal, Bhutan, Bangladesh, Afghanistan and Myanmar. *Source*: Naggs (in prep.).

<sup>7</sup> Bogan (1998) and Revenga & Kura (2002).

<sup>8</sup> Continental South East Asia: (Davis, 1982).

<sup>9</sup> Giller & Malmqvist (1998).

- habitats from ancient lakes: Lake Baikal, Lake Biwa and Lake Tanganyika respectively exhibit 70, 52 and 64% of endemic molluscan species (Table 2).
- habitats from lower river basins (Congo, Volta, Mekong, Mobile Bay, Uruguay River and Rio de la Plata): 93% of the total molluscan species found in the Mobile Bay basin (Tombigbee–Alabama rivers-USA) are endemic (Seddon, 2000). Another notable center of endemism is found in the Lower 500 km of the Mekong river basin with 92% of endemic molluscan species (Seddon, 2000).
- habitats from springs and underground aquifers (Australia, New Caledonia, the Balkans, western US, Florida and Cuatro Ciénegas basin in Mexico).

The phylum Mollusca includes two classes: the class Bivalvia (mussels and clams), and the class Gastropoda (snail and slugs).

### Class Bivalvia

**Habitat:** Bivalves are mainly marine organisms with less than 10% of the total number of species being found in freshwater (Bogan, 1998).

**Diversity:** Bivalves comprise approximately 15 000 species world wide, including around 1000, freshwater species which belong to 18 families, nine of

which have radiated (Bogan, 1998). Most freshwater bivalves are included in two orders: Unionoidae and Veneroidae.

**Distribution:** The most diverse freshwater bivalve fauna is found in North America and is dominated by Unionids with 300 described species (Bogan, 1998). Europe has about 48 bivalve species not including invasive species: 16 Unionoidae species and around 32 Veneroidae species (Nagel et al., 1998). The total number of freshwater bivalves for Asia is not known although it is expected that Asia, China and South Asia have a high diversity of Unionoidae species, second only to east and central North America (Banareescu, 1990). The Unionidae include 38 species in China (Liu Yueyin, 1979), 53 described species in India (Subba Rao, 1989), and 33 described species in Thailand (Brandt, 1974).

Ponder (1997) listed 37 described bivalve species in Australia: 18 Hyriidae, two Corbiculidae and 17 Sphaeriidae. Comprehensive data on freshwater bivalve diversity could not be reported for South America, where only local or national checklists exist and where data have not yet been compiled for the two main bivalve families: the Mycetopodidae and the Hyriidae. There are 172 bivalve species recorded in Africa, one family being restricted to the African continent: the Mutelidae (Daget, 1998).

**Endemism:** Lakes Baikal, Victoria, Tanganyika and Biwa are amongst the main critical areas of

Table 2. Number of mollusc species in key areas of endemism: the major ancient lakes of the world and some major river basins (based on Gargominy et al.<sup>1</sup>, Groombridge & Jenkins, 1998; Seddon, 2000)

Lakes	Gastropods (endemic)	Bivalves (endemic)	Total (endemic)
Baikal <sup>2</sup>	150(117)	31(16)	181(133)
Biwa	38(19)	16(9)	54(28)
Sulawesi <sup>3</sup>	ca. 50 (ca. 40)	4(1)	ca. 54 ca. 41)
Tanganyika	68(45)	15(8)	83(53)
Malawi	28(16)	9(1)	37(17)
Victoria	28(13)	18(9)	46(22)
Ohrid	72(55)		
Titicaca	24(15)		
River Basins			
Mobile Bay Basin	118(110)	74(40)	192(150)
Lower Uruguay	54(26)	39(8)	93(34)
River and Rio de la Plata			
Mekong River (lower 500 km) <sup>4</sup>	121(111)	39(5)	160(116)
Lower Congo Basin	96(24)		
Lower Zaire Basin	96(24)		

<sup>1</sup> Hotspots of freshwater molluscan diversity prepared by O. Gargominy, A. Bogan, P. Bouchet, W. Ponder: draft discussion paper from the Mollusc Specialist Group IUCN-SSC.

<sup>2</sup> Timoshkin (1997).

<sup>3</sup> Lake Poso and the Malili lakes system.

<sup>4</sup> Davis (1982).

freshwater bivalve endemism with respectively 40, 50, 53 and 56% of endemic bivalve species (Table 2). Hot spots of endemism for freshwater bivalves are also identified in North America, i.e. Mobile Bay Basin which harbours 54% of endemic bivalves (Table 2).

### Class Gastropods

**Habitats:** Gastropods are among the most ubiquitous organisms, they have widely colonized all marine, freshwater and terrestrial habitats. Freshwater gastropods are especially abundant in shallow littoral zones in lakes and streams.

**Diversity and Endemism:** Gastropods include some 40 000 species of which about 4000 species inhabit freshwater habitats (Bogan, 1998). Gastropods are divided in two sub-classes: Prosobranchia and Pulmonata.

Most endemic species belong to the class Prosobranchia. The ancient lakes represent Key areas of gastropod endemism, the rate of endemism ranging from 50% (Lake Biwa) to 80% (Lake Baikal; Table 2). Caves and springs also are largely colonised by endemic gastropods (mainly prosobranchs-hydrobiids). In addition, some major river basins are rich in endemic populations of gastropods: the lower Congo basin, the lower Mekong, the Mobile Bay basin or the Ohio–Tennessee rivers (Table 2). Isolated areas or islands are also susceptible to harbour endemic populations, i.e. Madagascar exhibits 12 endemic gastropod species of the 30 known species (Groombridge & Jenkins, 1998).<sup>2</sup>

**Distribution:** North America contains the highest diversity of freshwater gastropods with 601 species representing 14 families (Bogan, 1998). Freshwater gastropod diversity is also high in Africa with 341 known species (Brown, 1994), while in western Europe (excluding the Mediterranean basin and ex-USSR) there are only 166 known species (Falkner et al., 2001). We could not report comprehensive data on freshwater gastropod diversity for South America and Asia; however, local diversity estimates for major river basins (Uruguay River and Rio de La Plata, lower Mekong; Table 2) indicate that the diversity of freshwater gastropods on these continents might be very high.

**Prosobranchia. Habitat:** Most Prosobranchia species are marine, but there are also many freshwater taxa and a few terrestrial forms. The freshwater prosobranchs tend to occur in large and old lakes in tropical regions (Bogan, 1998).

**Diversity:** The two most diverse freshwater prosobranch families are Hydrobiidae with 228 known species world wide; and Pleuroceridae with 196 known species world wide (Revenga & Kura, 2002).

**Distribution:** The Afrotropical fauna differs from that of India and Southeast Asia in its richness of species in the families Ampullaridae, Bithyniidae, Thiaridae and Planorbidae. Pleuroceridae are especially diverse in rivers of the Southeast United States (Revenga & Kura, 2002).

**Endemism:** Prosobranchs generated numerous endemic populations. In particular, many Hyd-

<sup>2</sup>Contribution of IUCN Mollusk Specialist Group.



robiidae genera present in subterranean waters and springs radiated into endemic populations (Hersler et al., 1990; Kabat & Hersler, 1993). Among the hot spots of prosobranch (mainly hydrobiids) endemicity in springs and underground aquifers, we can cite: the Balkan region (180 endemic/190 known species), the arid and semi-arid western part of the USA (58/c. 100), Florida (43/84); the Great Artesian Basin in Australia, New Caledonia (65/81) and Western Tasmania (Groombridge-; Jenkins, 1998). Brown (1994) noted the lack of any hydrobioid radiation in the Afrotropical region, contrasting it with the radiations reported for the Mekong river (Davis, 1982).

Endemic prosobranch species are also found in large ancient lakes in tropical regions where they represent most of the endemic gastropod populations, i.e. the Thiaridae show large endemic radiation in Lake Tanganyika. (Banarescu, 1990; Michel, 1994; Mandaville, 2000).

*Pulmonata*. Habitat: The sub-class Pulmonata is mainly composed of terrestrial species (land snails). Freshwater pulmonate species are preferably found in muddy habitats of ponds and eutrophic lakes of small or moderate size (Brusca & Brusca, 1990). Many freshwater Pulmonata species are commonly found in ephemeral habitats (Brusca & Brusca, 1990).

Diversity and endemicity: The pulmonates did not generate as many endemic populations as the prosobranchs but the less numerous taxa are much more widely distributed throughout the world with a particularly high diversity at the northern latitudes. There are 28 000 species of pulmonates in terrestrial, marine and fresh waters (Smith, 2001). The freshwater representatives are all included in two orders: Archaeopulmonata and Basommatophora (Smith, 2001). Pulmonates have spread throughout the world with a limited number of taxa resulting in few endemic species (Banarescu, 1990).

Distribution: Freshwater pulmonates reach their greatest size and diversity at northern latitudes (Smith, 2001). Data on freshwater pulmonate species richness are lacking for South America (56 species in Argentina; Ituarte, pers. com.) and Asia (285 species in South East Asia of which 200 species are from India; Naggs, in prep.).

## PHYLUM ARTHROPODA

### *Class Crustacea*

Most crustaceans are marine but some 10% of the extant species are found in freshwater (Smith, 2001). They spend all, or most of, their life in water, some species being diadromous.

### *Subclass Branchiopoda*

Habitat: Most brachiopods live in fresh or brackish water and a few are found in marine habitats. They occur in stagnant temporary pools and permanent waters, from stagnant to weakly running (Maeda-Martinez et al., 1997).

Diversity: Branchiopods constitute a diverse class of Crustaceans including about 1000 species (Dumont & Negrea, 2002). Over 400 species belong to the 15 or more families of the 'Phyllopoda' (Anostraca, Notostraca, Laevicaudata, Spinicaudata and Cyclestherida), and more than 500 belong to the 15 families of 'Cladocera'.

*Super-order Cladocera*. Habitat: Cladocerans (or water fleas) inhabit almost any kind of freshwater habitats from large lakes to ponds. There are a few estuarine species but this group has not been successful in the oceans. The freshwater cladocerans are a widespread group, living on or near the bottom or on aquatic vegetation. Some species are planktonic in the open water of lakes.

Diversity and distribution: According to Dumont & Negrea (2002), the number of continental Cladocera species is slightly more than 500. The total number of cladoceran species includes 40 cosmopolitan species, 190 restricted to tropical and subtropical lowlands, 150 from cool-temperate and altitudinal zones, and 30 with an unclear status. It is now demonstrated that many species first considered to be cosmopolitan were, in fact, groups or complexes of morphologically similar species, each species having a more restricted distribution than the original group or complex.

### *Super-order Sarsostraca*

*Order Anostraca*. Habitat: The fairy or brine shrimps are usually found in temporary ponds and pools; as well as in freshwater, alkaline or hypersaline lakes.

Diversity: There are 273 recorded species of Anostraca world wide (Belk & Brtek, 1995, 1997;

Dumont & Negrea, 2002). The most familiar members of the Anostraca are species of the genus *Artemia*.

Distribution and endemicity: In South Africa (Africa south of the Zambezi and Kunene Rivers), 46 anostracan species are currently known, including 80% of endemic species (Hamer & Brendonck, 1997). Endemism of fairy shrimps is also abundant in South West Australia (12 endemic/19 total species), in Western USA (13 endemic/26 total species) and in the Southern part of South America (14 endemic/18 total species; Belk, pers. comm. in Groombridge & Jenkins, 1998). In Europe, Italy hosts seven endemic species on a total of 16 species (Belk, pers. comm. in Groombridge & Jenkins, 1998).

#### ***Super-order Conchostraca***

Orders *Laevicaudata*, *Spinicaudata* and *Cyclestherida*. Habitat: Conchostracans are found exclusively in freshwater, usually on the bottom of temporary puddles or sometimes almost entirely dug into the mud. Conchostracans develop very quickly depending on temperature; they are thus well adapted to the extreme conditions of temporary water bodies.

Diversity: Conchostracans or 'clam shrimps' comprise about 130 species described world wide (Dumont & Negrea, 2002).

***Super-order Notostraca and Haplopoda.*** Two other super orders of Branchiopoda: Calmanostraca (order Notostraca) and Leptodorida (Order Haplopoda) lack information about habitat, diversity and distribution. Notostraca (or 'tadpole shrimps') include the genera *Triops* with four species and the genera *Lepidurus* with five species (Dumont & Negrea, 2002). Haplopoda includes to date a single family with a single species, *Leptodora kindtii*.

#### ***Subclass Ostracoda***

Habitat: The class Ostracoda (Seed shrimps or mussel shrimps) contains both marine and freshwater forms. Ostracods occur in practically every aquatic environment, from the abyssal depths to the shoreline. They inhabit estuaries, lagoons as well as freshwater lakes, ponds and streams, salt lakes, hot springs, and even damp vegetation. Ostracods may be free-swimming for all or part of

their life-cycle, but, more commonly, they are benthic, living among aquatic plants or crawling on or through the sediment. A number of interstitial forms are known. Some are parasitic or commensal on other crustaceans, polychaete worms, echinoderms and even sharks.

Diversity: According to Kempf (1980, 1997), there are at present ca 30 000 ostracod species described, of which 8000 are freshwater species and 4500 ostracod genera, including 750 freshwater. However, these figures include nominal species (no synonymies are taken into account), while both living and fossil taxa are included here. From three checklists on recent non-marine ostracod faunas on Europe, Africa and South America (Limnofauna Europaea, Martens, 1984; Martens & Behen, 1994), it follows that presently some 500 described species occur in each of these continents and that they have few species in common. This would mean that there are ca. 3000 extant freshwater ostracod species, belonging to ca. 150 genera. In addition, about 5000 freshwater fossil species belonging to 600 genera have been described.

All freshwater Ostracods belong to the Podocopa, a group which is estimated to comprise around 5000 living species (Dole-Olivier et al., 2000). Most species are found in lakes, but recently it was shown that the diversity of subterranean (Danielopol & Rouch, 1991) and terrestrial ostracod faunas (Pinto et al., in press) is much higher than previously assumed.

Distribution and endemicity: There are few cosmopolitan freshwater ostracod species, most have more restricted distributions. All ancient lakes, for example, hold dozens of endemic species, for Lakes Baikal and Tanganyika these numbers could be up to 200 species for each lake (Martens, 1984). Surprisingly, the levels of endemicity reported for the African ancient lakes are only matched by the temporary pool faunas of South West Africa (Martens, 1998).

#### ***Subclass Copepoda***

Habitat: Copepod habitats range from freshwater to hyaline conditions, from subterranean caves to streams, rivers, and lakes. Copepods may be free-living, symbiotic, or internal or external parasites on almost every phylum of animals in water (2000 described species are parasites of fish).

Table 3. Global diversity of freshwater crustaceans

Group	North America	Europe	Asia	Australia	South America	Africa	World
Branchiopoda							
Cladocera	140 <sup>1</sup>						500 <sup>4</sup>
Phyllopoda	67	72					420
Ostracoda	420 <sup>2</sup>	400 <sup>6</sup>			500 <sup>7</sup>	500 <sup>8</sup>	2000
Copepoda <sup>5</sup>	363	902	927	181	516	524	2085
Branchiura	23						
Malacostraca							4200

<sup>1</sup> Pennak (1989).

<sup>2</sup> Thorp & Covich (1991).

<sup>3</sup> Sternberg & Cumberlidge (2001).

<sup>4</sup> Dumont & Negrea (2002).

<sup>5</sup> D. Defaye (pers. com.).

<sup>6</sup> Giller & Malmqvist (1998).

<sup>7</sup> Martens (1984).

<sup>8</sup> Martens & Behen (1994).

**Diversity:** Among the ca. 13 000 species of copepods (free-living and parasites) more than 2900 species of free-living freshwater copepods are presently identified (Dussart & Defaye, 2002; D. Defaye, pers. com.) (Table 4).

**Distribution:** In freshwaters, three orders are dominant: Calanoida, Cyclopoida and Harpacticoida. Freshwater calanoid species have a relatively restricted distribution and the tropical and temperate species do not generally overlap (Dussart & Defaye, 2002). Two genera are dominant planktonic cyclopids in the tropics: *Mesocyclops* and *Thermocyclops* (Dussart & Defaye, 2002). Harpacticoids are the most numerous, but it is estimated that only 50% of the species have been described in interstitial waters and ground waters (Galassi, 2001).

**Endemicity:** some of the key hotspots of endemicity or copepods are: Lake Baikal (27 endemic/65 total described species; Timoshkin, 1997), and Lake Tanganyika (33/69; Coulter, 1991).

#### **Subclass Malacostraca**

The Malacostraca include about two thirds of all crustacean species, and contain all the larger forms such as shrimps, prawns, lobsters and crabs. There are about 4100 malacostracan species world wide (Table 5).

**Order Mysidacea.** Habitat: Mysids (opposum shrimps) inhabit coastal and open sea waters, as well as continental freshwaters, several taxa occur also in different groundwater habitats (Smith, 2001).

Table 4. Global Diversity of freshwater copepods (from Dussart &amp; Defaye, 2002 updated by D. Defaye)

Order	North America	Europe	Asia	Austr. N. Zeal	South America	Mexico Central America	Africa	World
Calanoida	111	119	294	63	123	37	113	678
Cyclopoida	105	277	308	52	203	118	228	1045
Harpacticoida	147	504	325	66	190	61	183	1260
Gelyelloida		2						2
Total	363	902 <sup>1</sup>	927 <sup>2</sup>	181	516	216	524 <sup>3</sup>	2080

<sup>1</sup> To the Urals, Caucasus not included.

<sup>2</sup> Plus Turkey, Philippines, Indonesia, Malaysia.

<sup>3</sup> Plus Madagascar.

Table 5. Global diversity of freshwater Malacostraca

Order	North America	Europe	Asia	Australia	South America	Africa	World
Mysidacea	3 <sup>1</sup>	20 <sup>1</sup>					43
Cumacea							20
Tanaidacea							2
Isopoda	130						> 660
Amphipoda	150 <sup>3</sup>	350 <sup>3</sup>					1700 <sup>2</sup>
Decapoda							
Brachyura	1	3		30	234 + 90 Central Am	96	950 <sup>4</sup>
Astacidae	342 <sup>5</sup>						600
Caridea	15						221

<sup>1</sup> Pennak (1989).

<sup>2</sup> McAllister (1997).

<sup>3</sup> Giller & Malmqvist (1998).

<sup>4</sup> Sternberg & Cumberlidge (2001).

<sup>5</sup> Thorpe & Covich (2001).

**Diversity and endemism:** Mysids include more than 1000 species (Abele, 1982). Only 25 mysid species occur in freshwaters and 18 additional species live in freshwater caves (Abele, 1982). The major family *Mysidae* shows the highest diversity in the basins of the Caspian, Azov and Black Seas, with 11 endemic genera.

**Distribution:** Mysids are widespread over all the continents. There are only three freshwater species in the US, and about 20 in Europe (Pennak, 1989).

**Order Cumacea.** Habitat: Cumaceans occur from tidal to abyssal depths in marine and brackish waters throughout the world (Pennak, 1989). Only one family has brackish and freshwater species that live in the Ponto-Caspian basin (Banarescu, 1990).

**Diversity and endemism:** There are 20 species in the Caspian Sea (nine endemic species, seven endemic genera).

**Order Tanaidacea.** Habitat: While the vast majority of tanaidaceans are marine, a small number of species are found in brackish water.

**Diversity and distribution:** Two freshwater species are found in very distant locations. *Tanais stanfordi* on oceanic islands and *Nesotanais lacustris* on Rennell Island (Banarescu, 1990).

**Order Isopoda.** Habitat: Isopods or 'sow bugs' are common inhabitants of nearly all environments, aquatic and terrestrial.

**Diversity:** The isopods include approximately 10 000 described species, in 10 suborders. Freshwater species are mainly represented by Asellota with about 660 species world wide and 130 species in the US (Smith, 2001).

**Diversity and endemism:** There are only a few isopod species in Lakes Tanganyika (three species, Coulter, 1991) and Baikal (five species, Hidding et al., 2003) but all of them are endemic.

**Order Amphipoda.** Habitat: A large number of amphipods is found in subterranean waters (Holsinger, 1993). These are stygobionts, and thus restricted to hypogean waters. However, the majority of the amphipods is epibiont.

**Diversity and endemism:** According to McAllister et al. (1997) freshwater amphipods represent 24% of the 7000 known Amphipoda, which would amount to 1700 species world wide. Giller & Malmqvist (1998) provide lower estimates: 900 freshwater amphipod species are thought to be known world wide. The 740 species of subterranean Amphipoda belong to the suborder Gammaridea (with the possible exception of the ingofiellids) and make up approximately 13% of the estimated 5700 gammaridean species (Holsinger, 1993). A large fraction (94%) of the stygobiont Amphipoda occur in only 12 families: the four most important ones are Niphargidae, Crangonyctidae, Hadziidae, and Bogidiellidae (Holsinger, 1993).

There are currently 345 amphipod species recorded from Lake Baikal, only one of these is not endemic to the lake (Timoshkin, 1997). The Baikalian amphipods are an extensive and at least partially adaptive radiation, with representatives having invaded almost every possible niche in the lake, even the pelagic. Kamal'tynov (1999) has raised the level of endemism to that of family by recognising four endemic families, while Väinölä & Kamal'tynov (1999) recognised the existence of many cryptic (but reproductively isolated) species, so that the total specific amphipod diversity of Lake Baikal could exceed 1000 species.

**Distribution:** In Europe, the number of freshwater amphipods is estimated to be around 350 species, while 150 described species are known from North America (Giller & Malmqvist, 1998). About 116 of the latter are groundwater amphipods (Thorp & Covich, 2001; Groundwater Amphipod Database). The current knowledge of the freshwater amphipod fauna in South America is neither up-to-date nor complete.

#### *Order Decapoda*

##### **INFRA ORDER BRACHYURA (TRUE CRABS)**

**Habitat:** Among the Brachyura, there are few freshwater crabs, all of these appear to be restricted to warmer waters.

**Diversity and endemism:** There are about 950 freshwater crabs world wide (Sternberg & Cumberlidge, 2001). Three freshwater crab species can be found in Europe and 1 in North America (Giller & Malmqvist, 1998). In Africa, there are 96 species reported for the entire continent with 32 species in West Africa (Cumberlidge, 1999) and 12 species reported from southern Africa (Day et al., 2001). In Central America, about 90 species are recorded from Mexico to Panama including the Caribbean islands (Groombridge & Jenkins, 1998).<sup>3</sup> In South America, two families of freshwater crabs are present: the Trichodactylidae with 44 species and the Pseudothelphusidae with 190 species (Rodríguez, 1982, 1992). In Asia, the greatest diversity of freshwater crabs is found in Sumatra, Java, Borneo, Sulawesi and the Southern Philippines.

<sup>3</sup>Based on the contribution of N. Cumberlidge and R. von Sternberg.

Over a hundred species is found in Northeast India, Myanmar, Thailand, the Mekong basin in southern Indochina, to the Malaysian peninsula and Singapore (Groombridge & Jenkins, 1998). Thirty species are recorded from New Guinea and Australia (Groombridge & Jenkins, 1998).

Endemic populations of freshwater crabs are mostly found in Asia and Africa. In Asia, South China hosts 160 species, most of which are endemic; the west coast and south part of the Indian peninsula are known to harbour 20 endemic species, while there are 16 endemic species in Sri Lanka (Groombridge & Jenkins, 1998). In Africa, Lake Tanganyika hosts 8 endemic freshwater crab species (10 species in total, Coulter, 1991), a further 10 endemic species inhabit Madagascar, while also the Niger-Gabon area shows 10 endemic species (Cumberlidge, 1999).

**Distribution:** Freshwater crabs dominate tropical freshwaters and warm temperate zones of Central and South America, Southern Europe, Africa and Madagascar, South and Southeast Asia, China, Japan, The Philippines, New Guinea and Australia. They are absent from oceanic islands in Atlantic and Pacific (Revenge & Kura, 2002).

##### **INFRAORDER CARIDEA**

**Habitat:** Most species of Caridea inhabit freshwater habitats or occasionally brackish waters, some species of the genus *Macrobrachium* being marine as juveniles (Jayachandran, 2001). A few troglobitic taxa are restricted to caves.

**Diversity and endemism:** According to Jayachandran (2001), the freshwater representatives belong to three genera: *Palaemon* with one species, *Palaemonetes* with 20 species, and *Macrobrachium* with some 180 valid species and subspecies. There are also nine genera and some 20 troglobitic species. Lake Tanganyika harbours 15 species of which 14 are endemic (Coulter, 1991).

**Distribution:** Ten *Palaemonetes* and five *Macrobrachium* species are reported in North America (Thorp & Covich, 1991). Most species of *Macrobrachium* are pantropical and subtropical. Other freshwater representatives of Caridea belong to the family *Athyidae* represented by three endangered species in North America and by four species in Brazil (Jayachandran, 2001).

**INFRA ORDER ASTACIDEA**

Habitat: Crayfish and true lobsters are represented in freshwater and marine environments. Three families of Astacidea are restricted to freshwater habitats: Astacidae, Cambaridae and Parastacidae.

Diversity and Endemicity: There are 590 freshwater species recognised world wide of which 342 native species of crayfishes have been identified from USA and Canada, (Thorp & Covich, 2001; Hobbs, 1989). More than 65 taxa are known from a single locality or a single river or drainage (Taylor et al., 1996).

There are two well identified centres of species endemism for freshwater crayfishes: the first is located in the southeastern United States (including the eastern and southern Mississippi drainage) where some 80% of the cambarid species can be found (Horwitz, 1990); the second is centred on Victoria (Australia) and Tasmania and houses a large proportion of the parastacid species (K Crandall pers. com. in Groombridge & Jenkins, 1998).

Distribution: In the Northern Hemisphere, the astacids are widespread in Europe and the Western United States while the cambarids occur in Eastern North America and parts of Asia, the latter representing 70% (404 sp.) of all known freshwater crayfish. In the Southern Hemisphere, only the parastacids (156 sp.) are found (Crandall, 2003).

**Class Arachnida**

Habitat: Arachnids (spiders, mites and ticks, scorpions) are mainly terrestrial invertebrates. There are a few freshwater spiders and a large number of water mites in the sub-class Acari. Water mites can be parasitic, for example on insects, as larvae and are predatory as deutonymphs and adult. A few taxa are parasitic on bivalves or crayfish in their post-larval stages (Walter & Proctor, 1999).

Diversity and endemism: The class Arachnida is represented in freshwater by few genera of semi-aquatic true spiders (*Dolomedes*, *Argyroneta*) and a large number of water mites. The freshwater mites belong to five unrelated groups that have independently invaded freshwaters. The Hydracarina or Hydrachnidia is the most diverse group with more than 5000 named species world wide in 300 genera (Smith & Cook, 1991; Giller & Malmqvist, 1998).

Distribution: Over 1500 species are currently estimated to occur in North America, but only half of these have been formally described. In Australia, there are 413 described species of Hydracarina in 89 genera, representing 22 families (Harvey, 1998).

**Class Entognatha (Order Collembola)**

Habitat: Collembols or springtails are primarily terrestrial, soil and litter dwelling, preferring however wet or damp surroundings (Hopkin, 1997). The majority of species associated with aquatic habitats are accidentals, often as temporary inhabitants of the water surface. However, virtually all collembolans have an affinity for areas marginal to aquatic habitats because of their requirement of high humidity. A few species are restricted to aquatic habitats and exhibit a high degree of specialisation for an aquatic existence (Heckman, 2001).

Diversity: There are ca 9000 described species world wide (Resh & Carde, 2003). Thirty species (4 families) are associated with European waters (Gisin, 1978 in Ward, 1992), and 50 aquatic species are found in North America (Waltz & McCafferty, 1979 in Ward, 1992).

**Class Insecta**

Habitat: Insects are mainly terrestrial but some groups are denominated as 'aquatic insects' because they spend at least part of their lives in aquatic environments. These 'aquatic insects' most likely evolved as terrestrial organisms and later on adapted to freshwater; they are thus secondary aquatic organisms. They occur in all freshwater environments, sometimes in brackish waters, but they almost never colonised marine systems.

Diversity: More than one million insect species have been described, that is over 50% of all known organisms. Only 2% of all insect species exhibit aquatic stages representing a total of about 50 000 species (Table 6).

*Order Ephemeroptera.* Habitat: Mayflies are hemimetabolous insects; the nymphs are aquatic and the adults are terrestrial. Nymphs are found in virtually all types of freshwaters throughout the world. (Williams & Feltmate, 1992). The most diverse fauna occurs in warm lotic habitats.

Table 6. Estimates of the number of aquatic insects in the world and for continents or large biogeographic areas. (adapted and completed from Hutchinson 1993)

	Afrotropic	Nearctic	Palaearctic oriental	Europe	Neotropic	Oriental	Australian	World
Ephemeroptera	295 <sup>1</sup>	670 <sup>6</sup>		350 <sup>6</sup>			84 <sup>4</sup>	>3000
Odonata	699 <sup>1</sup>	> 650 <sup>5</sup>		150 <sup>7</sup>			302 <sup>4</sup>	5500
Plecoptera	49 <sup>1</sup>	578 <sup>4</sup>		423 <sup>7</sup>			196 <sup>4</sup>	2000
Megaloptera	8 <sup>1</sup>	43 <sup>4</sup>		6 <sup>4</sup>	63 <sup>3</sup>		26 <sup>4</sup>	300
Trichoptera	>1000 <sup>1</sup>	1524 <sup>1</sup>	1228 <sup>1</sup>	1724 <sup>1</sup>	2196 <sup>2</sup>	3522 <sup>1</sup>	1116 <sup>1</sup>	>10000
Hemiptera		404 <sup>4</sup>		129 <sup>4</sup>			236 <sup>4</sup>	3300
Coleoptera		1655 <sup>4</sup>		1077 <sup>4</sup>			730 <sup>4</sup>	>6000
Diptera		5547 <sup>4</sup>		4050 <sup>4</sup>			1300 <sup>4</sup>	>20000
Orthoptera		ca 20		0				ca 20
Neuroptera		6 <sup>4</sup>		9 <sup>4</sup>			58 <sup>4</sup>	ca 100
Lepidoptera		782 <sup>8</sup>		5 <sup>4</sup>				ca 1000
Hymenoptera		55 <sup>4</sup>		74 <sup>4</sup>				>129

<sup>1</sup> Elouard & Gibon (2001).

<sup>2</sup> Flint et al. (1999).

<sup>3</sup> Contreras-Ramos (1999).

<sup>4</sup> Hutchinson (1993).

<sup>5</sup> Ward (1992).

<sup>6</sup> Resh (2003).

<sup>7</sup> Limonofauna Europaea (2003).

<sup>8</sup> Lange (1996).

**Diversity:** The Ephemeroptera either comprise a little over 2100 described species (Williams & Feltmate, 1992) or more likely 3000 species in 375 genera (Resh & Carde, 2003).

**Distribution and endemism:** A high diversity of Ephemeroptera is found at northern latitudes and especially in North America (McCafferty, 1996). The rate of endemism is high (99%) for the 111–172 known ephemeropteran species from Madagascar, because ephemeropterans are poor flyers and do not disperse easily (Elouard & Gibon, 2001). The most diverse ephemeropteran fauna occurs in warm lotic habitats (Wiggins & Mackay, 1978; Ward & Berner, 1980). The mayfly faunas of Australia, New Zealand and temperate South America are similar, suggesting a Gondwanean origin for most Australian families: Leptophlebiidae, Siphonuridae, Oniscigastridae, Ameletopsidae, and Coloburiscidae (Peters & Campbell, 1991).

**Order Odonata.** **Habitat:** Also Odonata are hemimetabolous insects with aquatic nymphs and terrestrial adults. There are a few truly marine species, several that live in brackish water, and

many that survive in arid regions where the larvae can develop quickly in the warm waters of temporary ponds before they dry up.

**Diversity:** Extant Odonata species belong to three suborders: Anisozygoptera containing only two species, Zygoptera or damselflies, and Anisoptera or true dragonflies. A total of around 5500 species has been described in the world (Ward, 1992; Williams & Feltmate, 1992). According to Corbet (1999), there are about 2500 species of Zygoptera and considerably more than 2500 described species of Anisoptera.

**Distribution and endemism:** Odonates are distributed from the tropics to the tree line in polar regions. In Australia, there are 314 known species of dragonflies, half of these are endemic and appear to be Gondwanean relics (Watson et al., 1991). The two species of Anisozygoptera are restricted to Japan and the Himalayas (Tsuda, 2000). Endemism at species level is high in Madagascar for Zygoptera (94.4%) but lower for Anisoptera, which are the better fliers (52%; Elouard & Gibon, 2001). The level of endemism is also high for Australian odonates in cold water genera present

in Tasmania and southwest Australia (Peters & Campbell, 1991).

*Order Plecoptera.* Habitat: Stoneflies are hemimetabolous insects. The nymphs are aquatic and usually occur in cool or cold running waters typically below 25 °C and with a high oxygen content.

Diversity and Endemicity: Some 2000 species have been described world wide (Williams & Feltmate, 1992; Ward, 1992).

Distribution: Stoneflies are adapted to low temperatures so they are mostly restricted to higher latitudes and altitudes. Most extant families of plecopterans are confined to the temperate zones of either the Southern or the Northern Hemispheres (Illies, 1965; Zwick, 1980). Consequently the highest number of plecopteran species are encountered in North America (478 sp.) and in Europe (423 sp.).

*Order Hemiptera – Heteroptera.* Habitat: Heteroptera are hemimetabolous insects. Most species of Hemiptera or true bugs are terrestrial. All species of the sub-order Homoptera are terrestrial with a few semi-aquatic species associated with vegetation on the intertidal zone or freshwater margins (Foster & Treherne, 1976; Polhemus, 1984). Within the suborder Heteroptera, which is primarily terrestrial, there are several truly aquatic or semi-aquatic families. According to Hutchinson (1993) two separate groups of Heteroptera are associated closely with water in two different ways: one group consists of the Gerromorpha, which live primarily on the water surface and floating vegetation though, at least, a few can dive; the other group consists of the Nepomorpha that spend most of their life under water (water bugs).

Diversity: The world fauna of aquatic and semi-aquatic heteropterans comprises over 3300 species in 16 families (Ward, 1992). Williams & Feltmate (1992) mentioned 3200 hydrophilic species of Heteroptera.

*Order Orthoptera.* Habitat: The grasshoppers, locusts and crickets constitute an almost exclusively terrestrial order. Orthopterans are hemimetabolous insects. They are not usually thought of as being aquatic, nor even semi-aquatic, but several species live in association with water

(hydrophilous species). Semi-aquatic species frequent wet margins of freshwater bodies or are found on emergent littoral vegetation (Ward, 1992).

Diversity: There are 20 described semi-aquatic species of Orthoptera world wide (Hutchinson, 1993).

*Order Trichoptera.* Habitat: The caddisflies are holometabolous insects: the larvae and pupae live in most types of water bodies including both cold and warm springs, temporary waters, etc. (Williams & Feltmate, 1992).

Diversity: About 10 000 described species of caddisflies are known world wide (Williams & Feltmate, 1992). Flint et al. (1999) suggested that the real number of trichopteran species is around 50 000.

Distribution and endemicity: Trichopteran species are distributed over most of the globe, except Antarctica. However, while some families occur world wide, others are restricted to either the northern or southern hemisphere (Ward, 1992; Williams & Feltmate, 1992). Africa has the lowest diversity in Trichoptera (Elouard & Gibon, 2001). The trichopteran diversity is higher in the tropical regions, but many trichoptera species can also be found in high elevation areas of temperate regions (Elouard & Gibon, 2001). In Australia, most trichopteran species are endemic with hotspots located in Tasmania and in the Southwest of Australia (Peters & Campbell, 1991).

*Order Megaloptera.* Habitat: The Megaloptera is a small order of holometabolous insects: all species are aquatic as larvae and terrestrial as eggs, pupae and adults.

Diversity and Endemicity: About 250–300 species of Megalopterans are described world wide (Ward, 1992; Williams & Feltmate, 1992).

Distribution: All living species belong to one of the two super-families. the Corydalidae are widely distributed throughout temperate regions but they are absent from Europe with a few species in the tropics; the Sialidae are confined to temperate latitudes (Ward, 1992; Williams & Feltmate, 1992).

*Order Coleoptera.* Habitat: Coleoptera is a holometabolous order with primarily terrestrial species, but about 10% of the coleopteran families have



aquatic or semi-aquatic species. Aquatic beetles inhabit freshwater, brackish-water and some marine environments. The most diverse and abundant fauna occurs in well-vegetated freshwater habitats (Williams & Feltmate, 1992). Unlike many of the preceding groups, in aquatic beetles both larvae and adults can be aquatic.

**Diversity:** The Coleoptera are one of the most diverse groups of living organisms with over 500 000 estimated species. The world fauna contains about 6000 aquatic and semi-aquatic beetles (Hutchinson, 1993; Williams & Feltmate, 1992). The most important families of aquatic beetles are the Dysticidae (4000 species), the Gyrinidae (700 species) and the Noteridae (150 species; Hutchinson, 1993). Revenga & Kura (2002) suggested much higher estimates for aquatic beetles, at approximately 10% of all Coleoptera, which would account for 35 000 aquatic species of Coleoptera.

**Distribution:** Most aquatic beetles are thought to be cosmopolitan (Dysticidae & Gyrinidae), or widespread (Noteridae; Hutchinson, 1993).

*Order Diptera.* **Habitat:** Although most species are terrestrial, those with aquatic larvae may be predominant insects in many freshwater habitats. Dipterans are holometabolous and are found in every conceivable aquatic environment and are often the only insects in freshwater habitats with extreme environmental conditions. At least 30 families have aquatic or semi-aquatic representatives (Williams & Feltmate, 1992; Hutchinson, 1993).

**Diversity:** Over half of all known aquatic insects are dipterans. The order contains an estimated 200 000 species world wide, although only just over half have been described (Hutchinson, 1993). The number of dipteran species breeding in water is estimated to be >20 000 (Resh, pers. com.).

Lane & Crosskey (1993) estimated the number of species in groups of medical importance: Tipulidae, 14 000 sp.; Culicidae, 3450 sp.; Anophelidae, 420 sp.; Simuliidae, 1570 sp.; Ceratopogonidae, 5000 sp.; Tabanidae, 4000 sp.

**Distribution:** The Tipulidae are distributed world wide, although their greatest diversity is in the humid tropics. Stone et al. (1965) recorded 1458 species in America north of Mexico. The Simuliidae or black flies occur on all the major land-masses, apart from Antarctica. The Tabanidae or Horse flies are distributed throughout the world.

The Chironomidae are non-biting midges whose distribution extends to both the northern and southern limits of land, and they are the dominant group in the Arctic.

*Order Lepidoptera.* **Habitat:** The butterflies and moths are traditionally considered a terrestrial group, but there are nevertheless some aquatic or semi-aquatic species. Lepidoptera are holometabolous insects. With few exceptions, aquatic and semi-aquatic Lepidoptera are intimately associated with aquatic vascular plants, and thus most species occur in ponds and the littoral of lakes. Most of the truly aquatic species occur in the family Pyralidae. All pre-imaginal stages of aquatic pyralids occur in the water while adults are terrestrial.

**Diversity and distribution:** The total number of aquatic and semi-aquatic described species of Lepidoptera has not been compiled. However, over 782 species of Lepidoptera with aquatic and semi-aquatic stages are found in North America (Lange, 1996). There are 148 pyralids in North America and 1670 pyralids in Australia (Lange, 1996; Nielsen, 1999).

*Order Neuroptera.* **Habitat:** Neuropterans (also called planiplenns) are holometabolous insects with mostly terrestrial species. Three families contain truly aquatic members: Sisyridae or spongillaflyies, Osmylidae, and Neurorthidae, whose larvae are semi-aquatic and live in wet margins along freshwater bodies (Williams & Feltmate, 1992). The species of Sisyridae are associated to freshwater sponges. This constitutes a rare example of a single family of an otherwise terrestrial insect group depending for its existence on a small freshwater family (Spongillidae) of an otherwise exclusively marine phylum (Ward, 1992).

**Diversity:** There are some 4300 species of Neuroptera world wide, of which ca. 100 species are considered as aquatic or semi-aquatic (Hutchinson, 1993). There are 45 species of spongillaflyies distributed throughout the world. (Ward, 1992).

**Distribution and endemism:** Most of the known aquatic species of Neuroptera are found in Australia (58 sp.) while the diversity is much lower in Europe (9 sp.) or North America (6 sp). We cannot report comprehensive data on neuropteran endemism.

*Order Hymenoptera.* Habitat: Hymenoptera is a holometabolous order with a few aquatic or semi-aquatic species. Some species are only marginally aquatic while others might spend most of their life stages under water (Ward, 1992). Several families contain species that are, in some way, associated with water such as the parasitic wasps depending on aquatic hosts. The adult enters the water to attack the hosts, usually the aquatic stage of other insects, except Collembola, Ephemeroptera and Plecoptera. The specific habitat of aquatic Hymenoptera is dictated by the habitat of the hosts that can occur in both running and standing freshwaters (Williams & Feltham, 1992; Ward, 1992).

Diversity and distribution: There is currently a total of ca. 100 parasitic wasps with aquatic hosts world wide. There are 10 North American wasp families and 55 species of parasitic wasps are considered aquatic (Hagen, 1996 in Merritt & Cummins, 1996).

#### PHYLUM CHORDATA (SUBPHYLUM VERTEBRATE)

##### Class Teleostomi – Subclass Actinopterygii (Fish)

Habitat: Fish are well represented in both marine and freshwater habitats. Some species also migrate between salt and freshwater (diadromous species)

Diversity: An estimated 24 600 valid fish species have been described world wide. Nelson's (1994) estimate of a total of 28 500 fish (marine and freshwater) is probably reasonable. Although fish are among the best-known freshwater groups, the rate of discovery of new species was on an average of 309 species a year for the period 1976–1994, indicating that many species are still to be discovered. Presently, ca. 10 000 species of fish live principally in freshwaters, and an additional 500 are diadromous.

Endemicity: Hot-spots of endemicity of freshwater fishes occur in tropical freshwaters, which are currently the least investigated areas but also the most threatened biota. According to our present knowledge, there are 'flocks' of several hundreds of cichlid species in the largest East African Lakes (Victoria, Malawi, Tanganyika) (Lévêque, 1997; Lévêque & Paugy, 1999). In Lake Tanganyika evolution has led to the occurrence of species flocks within a few families : seven Mastacembelid

species, six species of the Bagrid *Chrysichthys*, seven species *Synodontis* and four species of the Centropomi. The remarkable diversity of the large barbs (genus *Barbus*) in Lake Tana (Ethiopia) constitutes a potential species flock (Nagelkerke et al., 1994). A totally endemic fish flock, comprising 29 species (11 genera) of sculpins (Cottoidei) occurs in Lake Baikal (Asia) (Timoshkin, 1997). In lake Titicaca (South America) 24 endemic *Orestias* species (Cyprinodontidae) are presently recognised (Lauzanne, 1982). These species-flocks are sometimes considered to be a world heritage which is endangered and has to be preserved from destruction by human activities such as over fishing or introductions of aquatic species.

While the high fish species endemicity in lakes has promoted a considerable interest among biologists, the endemicity in river systems is less known.

Distribution: The ichthyofaunas of Europe west of the Ural mountains (ca. 360 sp.), of North America (ca. 1050 sp.) and Australia-New Guinea (ca.500 sp.) are the most thoroughly documented to date (Lundberg et al., 2000). The current estimate for Africa is ca. 3000 species (Lévêque, 1997) but the number of some families such as Cichlidae is likely to be greatly underestimated. The neotropical ichthyofauna (Central and South America) is estimated to include from 3500 species (Stiassny, 1999) to more than 5000 species (Lundberg et al., 2000). For tropical Asia,

Table 7. Distribution of fish species diversity at continental scale

Zones	Species number	FAO areas fishbase
Europe + (USSR)	360 <sup>1</sup>	393 + 448
Africa	3000 <sup>2</sup>	3042
North America	1050 <sup>1</sup>	1542
South America	5000 + <sup>1</sup>	3731
Asia	3500 + <sup>3</sup>	3443
Australia–New Guinea	500 <sup>1</sup>	
Australasia		616
Total	13 400	13 215

<sup>1</sup> Lundberg et al. (2000).

<sup>2</sup> Lévêque (1997).

<sup>3</sup> Kottelat & Whitten (1996).

extending from the Indus basin eastward to South China, an estimate of 3000 species is proposed by Lundberg et al. (2000). Kottelat & Witten (1996) gave a figure of more than 3500 species for Asia. In China, about 900 freshwater fishes are recorded (He & Chen, 1996) (Table 7).

### **Class Amphibia**

**Habitat:** Amphibians are strictly freshwater animals and do not tolerate salt water. The great majority of amphibian species have aquatic larval stages and therefore depend on inland waters for implementing their life cycle and for continued survival of populations. However, relatively few species are fully aquatic.

**Diversity:** A total of 5504 amphibian species have currently been recorded world wide (World Database 'Amphibian species of the world'), including 4837 Anura (frogs and toads), 502 Caudata (newts and salamanders) and 165 Gymnophiona (caecilians).

**Distribution and endemism:** Corbett (1999) reported a total of 74 amphibians known in Europe, but Gasc et al. (1997) listed only 62 species of European amphibians. Approximately 230 species of amphibians occur in the continental United States. In Japan a total of 56 amphibians have been described to date, many of which are salamanders. Most endemic species in the western US are widely dispersed while endemics in the eastern and southeastern US tend to be clustered in centres of endemism.

### **Class Reptilia**

The class Reptilia includes turtles, crocodiles, lizards, and snakes. All crocodylians and many turtles inhabit freshwaters but nest on land. Many lizards and snakes occur along water margins; a few snakes are entirely aquatic.

**Subclass Parareptilia (Turtles).** **Habitat:** There are two suborders of living turtles: the Pleurodira or side-necked turtles which are found in the southern hemisphere and are semi-aquatic turtles; the Cryptodira, or hidden-necked turtles including all turtles of the world, marine, freshwater and terrestrial.

**Diversity:** There are around 200 species of freshwater turtles throughout the warm temperate and tropical regions of the world (IUCN/ SSC Tortoise and Freshwater Turtle Specialist group 1991).

**Distribution:** The side-necked turtles include two families, the Chelidae with 36 species distributed in Australia, New Guinea, and South America and the Pelomedusidae with 23 species, found in Africa and South America (Ernst & Barbour, 1989).

The freshwater and semi-aquatic hidden-necked turtles include three species of Chelydridae (snapping turtles) found in North America and China; 22 species of Trionychidae (soft-shelled turtles) distributed in Africa, Asia, Indonesia, Australia and North America; 22 species of Kinosternidae (mud and musk turtles) exclusively on the American continent; 91 species of Emydidae (pond, box or water turtles) represented in all parts of the world except for Australia and Antarctica.

### **Subclass Diapsida**

#### *Lepidosauromorph*

#### *Crocodylians*

**Diversity and Distribution:** There are 23 living crocodylian species widespread throughout tropical and subtropical countries. Alligators and caimans (family Alligatoridae) are found almost exclusively in North, Central and South America. The sole exception is the Chinese alligator, which occurs in Eastern China. A few species of the family Crocodylidae (true crocodiles) is present on the American continent, but most Crocodylidae are found throughout Africa, India and Asia. The single member of the family Gavialidae (Indian gaviel) is found in India and adjacent countries.

#### *Fresh water snakes*

**Habitat:** Two species belonging to the family Acrochordidae are strictly adapted to freshwater habitats: the file snake (*Acrochordus arafurae*) and the Javan wart snake (*A. javanicus*). In addition, there are a few species of semi-aquatic snakes, such as the green anaconda (*Eunectes murinus*), one of the largest snakes in the world.

**Diversity and distribution:** The file snake and the Javan wart snake are both found in the Indo-Pacific region. Revenga & Kura (2002) reported an estimate of seven species of semi-aquatic snakes. Kottelat & Whitten (1996) mentioned 24 species of freshwater semi-aquatic snakes in Asia.

### Saurishia – Class Aves (Birds)

Habitat: No birds are entirely aquatic, because avian eggs cannot survive a prolonged immersion in water. It is impossible to clearly separate inland water species from primarily terrestrial ones. Aquatic birds may be defined as wading, swimming and diving birds of either fresh or salt water. However, many birds are closely associated with wetlands and water margins; relatively few including divers, grebes and ducks are restricted to river and lake systems. There are also a number of non-wading birds that feed largely on fish and other aquatic animals and are adapted to diving and surface-snatching. Among them are kingfishers families, the fish owls, fish eagles and a few other raptors.

Diversity and distribution: Among the 420 North American breeding birds, Sauer et al. (1997) identified a wetland-open water group including 86 species, that is about 1/5 of the breeding species. There are 253 European bird species affiliated to freshwaters including all the charadriiform wading birds (Roselaar, pers. com.). So for Europe, about 27% out of a total of 700 European bird species depend on inland waters. Using a conservative value of 20% for the 9000 species of birds currently known in the world, there might be about 1800 bird species world wide that are more or less dependant on freshwaters.

### Class Therapsida – Mammalia

Many mammals live in close proximity to freshwater ecosystems on which they depend for their survival. However, only a small number of representatives of several mammal orders are considered to be aquatic or semi-aquatic spending most of their life in slow-flowing rivers (Revenga & Kura, 2002). The best known representatives are the beavers, otters, hippopotamus, and river dolphins.

The beaver is found in northern boreal regions with two species, one in Europe, and one in North America. There are also rice rats, swamp rats, muskrats and water voles in North and South America. However the best known aquatic rodents in south America are the capybara. (*Hydrochaeris hydrochaeris*) and the myocastor (*Myocastor coypus*). In Africa there are several species of water

rats and creek rats (Kingdon, 1997). Four species of beaver rats occur in Oceania.

There are four species of otters in Africa (Nel & Somers, 2002), one in North America, one in Europe, three in South and Central America, and four in Asia. There are four water dependent water shrews (genus *Sorex*) in North America (Whitaker, 1991) and ten species in Europe and Asia (Stone, 1995). In Africa, three species of otter shrews (Potamogale) occur in the Congo basin, and a few species of Tenrecs in Madagascar. (Kingdon, 1997).

The hippopotamus (*Hippopotamus amphibius*) only occurs in Africa as well as the pigmy hippopotamus (*Hexaprotodon liberiensis*). In addition, several semi-aquatic ungulates are known from Africa (the sitatunga, *Tragelaphus spekei*), South America (the marsh deer, *Blastocerus dichotomus*), Asia (water buffalo, *Bubalus bubalis*, and two deer species).

Five species of river dolphins and one of freshwater porpoises live in large rivers in South America and South Asia. In Asia there are also five species of cetaceans, among which the Yangtze River dolphin or baiji (*Lipotes vexillifer*) and the Gange River dolphin (*Orcaella brevirostris*) (Reeves et al., 2003).

Other representatives are:

- the duck-billed platypus (*Ornithorhynchus anatinus*) from Australia (Nowak, 1991),
- the water opossum (*Chironectes minimus*) from South America,
- the mink (*Mustela vison*) in North America,
- two species of seal in Europe and Siberia (Reijnders et al., 1993),
- three species of manatees (*Trichechus*),
- three species of desmans present in Europe (Nowak, 1991),
- the otter civet (*Cynogale bennettii*) in Asia,
- the aquatic genet (*Osbornictis piscivora*) in Africa.

### Discussion and conclusion

#### *Importance of freshwater habitats for animal groups*

It is commonly recognised that the first life forms originated in the sea and have later colonised

freshwater and terrestrial habitats (Barnes & Mann, 1991). The adaptation to terrestrial life occurred independently in various lineages of aquatic animals, and some terrestrial lineages re-adapted secondarily to freshwaters (i.e. insects). Hence, two main groups of freshwater animals can be identified (Banarescu, 1990):

A group of marine origin (primary aquatic animals with no terrestrial ancestors) that invaded freshwaters directly from the sea: lower metazoans, branchiate molluscs (mussels and prosobranchiates), crustaceans, lampreys and fishes. Among these groups, some species live indifferently in saline, brackish and freshwater, others live almost exclusively in brackish waters. Numerous fish and prawn species are diadromous with a life cycle including both marine and freshwater stages. Marine biodiversity has remained higher at higher taxonomic levels than freshwater biodiversity because many important marine invertebrate groups such as Echinodermata, Ctenophora, or Chaetognatha, have failed to colonise freshwater habitats. The osmotic challenge of life in freshwaters probably prevented colonisation by several marine invertebrate groups.

A group of terrestrial origin (secondary aquatic taxa) that probably underwent major co-evolution on land and subsequently invaded freshwaters. For example, many pulmonate snails with a primitive kind of lung are thought to have first colonised the land, and secondarily returned to freshwater where they can still breathe air (Barnes & Mann, 1991). The origin of terrestrial insects is speculative, but most likely they had their main adaptive radiation on open land at the same time as flowering plants.

However, a significant proportion of present-day insects spend part of their life history in freshwater. No equivalent re-invasion of marine habitats could be observed, maybe because insects failed to compete with the abundant crustaceans found in the fringing marine habitats and occupying similar niches to those occupied by insects in freshwaters.

The different origins of freshwater species may explain why the group of 'freshwater dependant species' occupies a wide range of habitats (Table 8): some species may be in the on-going process of adapting to freshwater, while others are

only colonising the ecotones, while they are physiologically or biologically unable to live in freshwater.

#### *Global assessment of freshwater animal diversity*

This paper is an attempt to provide a quantitative evaluation of the global animal freshwater species diversity with regard to data availability (Table 9). The overall order of magnitude of presently described freshwater species is 100 000, half of which are represented by the very speciose class of Insecta. However, the true number is definitely much higher than this.

Even doubling the present number of described species, the order of magnitude remains low compared to the species diversity of coral reefs or tropical rainforests. It is assumed that tropical forests contain more than half of the world's species estimated around 10 million (1.4 million named species; Revenga & Kura, 2002). For instance, it is expected that as many as 30 million arthropod species may exist in tropical forests (Revenga & Kura, 2002). However, it should be stressed that some 20 000 species of vertebrates (35–40% of the known vertebrates) are true or water dependant freshwater species while inland water habitats occupy around 1% of the planet's surface not submerged in seas and oceans.

The present preliminary study highlighted gaps in the basic knowledge of freshwater species richness:

- as expected, most information is available from North America and Europe. The tropical areas are still poorly investigated while their species richness is widely recognised to be higher than in temperate zones. South America and Asia are especially lacking global comprehensive estimates of species richness for many groups, even the usually well-known ones such as molluscs or insects.
- Some animal groups have been less studied than others, and data on their diversity and distribution is scarce. The vertebrates are the best known groups, whereas in many cases knowledge on invertebrates that are not useful or posing threats to humans (e.g. disease vectors) is still very poor.

Table 8. Relationships of the 'true freshwater' and the 'freshwater dependent' taxa (phyla and classes) to marine, freshwater and terrestrial habitats (adapted from Smith 2001)

Phyla	Classes	M/FW <sup>-</sup>	M/FW <sup>+</sup>	M = FW	FW/M <sup>-</sup>	P	FW/LC	T/FW
Porifera		X						
Cnidaria								
	Hydrozoa	X						
Nemertea		X						
Platyhelminthes								
	Turbellaria			X				
	Cestoda					X		
	Trematoda					X		
Gastrotricha				X				
Rotifera					X			
Nematoda				X				
Annelida								
	Polychaeta	X						
	Oligochaeta				X			
	Hirudinae				X			
Bryozoa		X						
Tardigrada				X			X	
Mollusca								
	Bivalvia		X					
	Gastropoda		X					
Amphipoda								
Branchiopoda	Cladocera				X			
	Anostraca				X			
	Notostraca				X			
	Conchostraca				X			
	Haplopoda				X			
Ostracoda				X				
Copepoda				X				
Malacostraca								
	Mysidacea	X						
	Cumacea							
	Tanaidacea	X						
	Isopoda							
	Amphipoda		X					
	Decapoda		X					
Arachnida								X
Entognatha	Collembola							X
Insecta							X	
Vertebrata								
	Teleostimi				X			
	Amphibia						X	
	Reptilia							X
	Aves							X
	Mammalia	X						X

M/FW<sup>-</sup> = mostly marine with few freshwater species; M/FW<sup>+</sup> = Mostly marine with many freshwater species; FW/M<sup>-</sup> = Mostly freshwater with few marine species; P = parasites; FW/LC = complete part of their life cycle in freshwater; T/FW = Terrestrial but need fresh water for food & habitat.

Table 9. Global species richness of freshwater animal groups: Current state of knowledge

Phyla	Classes/orders	Species numbers
Porifera		197
Cnidaria		30
	Hydrozoa	ca. 20
Nemertea		12
Plathelminthes		ca. 500
Gastrotricha		ca. 250
Rotifera		1817
Nematoda		3000
Annelida		
	Polychaeta	?
	Oligochaeta	700
	Hirudinae	ca. 300
Bryozoa		70–75
Tardigrada		
Mollusca	Bivalvia	ca. 1000
	Gastropoda	ca. 4000
Arthropoda		
Crustacea		
Branchiopoda		
	Cladocera	>400
	Anostraca	273
	Notostraca	9
	Conchostraca	130
	Haplopoda	1
Amphipoda		
Ostracoda		3000
Copepoda		2085
Malacostraca		
	Mysidacea	43
	Cumacea	20
	Tanaidacea	2
	Isopoda	ca. 700
	Amphipoda	1700
	Decapoda	1700
Arachnida		5000
Entognatha	Collembola	
Insecta		
	Ephemeroptera	>3000
	Odonata	5500
	Plecoptera	2000
	Megaloptera	300
	Trichoptera	>10 000
	Hemiptera	3300
	Coleoptera	>6000
	Diptera	>20 000

Table 9. (Continued)

Phyla	Classes/orders	Species numbers
	Orthoptera	ca. 20
	Neuroptera	ca. 100
	Lepidoptera	ca. 100
	Hymenoptera	ca. 100
Vertebrata		
	Teleostomi	13 400
	Amphibia	5504
	Reptilia	ca. 250
	Aves	ca. 1800
	Mammalia	ca. 100

*Assessment of freshwater biodiversity and the Global Freshwater System*

The attempt to address freshwater biodiversity at a global scale is related to the development of a new global approach integrating data and knowledge from local over regional to global scales. This global perspective is motivated by the global scale reached by freshwater biodiversity changes and drivers of change.

*Freshwater biodiversity changes occur at global scale*

Due to a general lack of data, it is difficult to assess the status of the inland water biodiversity. However, evidence of biological impoverishment is pervasive in aquatic systems and when available the data are very disturbing. For example in USA, where the status of aquatic biodiversity is relatively well-documented compared to other areas, 34% of fish, 65% of crayfishes and 75% of unionid mussels are classed rare to extinct (Master, 1990). Of 214 stocks of Pacific salmon, 74% have a high or moderate risk of extinction (Nehlsen et al., 1991). As a whole, the native fishes of North America are in serious decline and currently 364 taxa are listed by the American Fisheries Society as endangered, threatened or of special concern (Williams et al., 1991). In California, M $\ddot{o}$ yle et al. (1995) reported a rising trend of extinction and endangerment in the region's native fishes from 24% in 1988 to 43% in 1992. Nearly half of Mexico is arid or semiarid with scarce waters. At least 92 springs and 2500 km of

river have dried in this area. This has affected nearly 200 species of freshwater fishes, 120 under some threat 15 extinct through human impact. As of 1985, an average of 68% of species was eradicated in local fish faunas (Contreras & Lozano, 1994).

#### *Freshwater biodiversity and global drivers of change*

The magnitude of the response of freshwater systems to global change will depend on a complex array of physical and biological factors. These changes are likely to directly affect the survival, reproduction and growth of organisms, as well as the distribution, persistence and diversity of species. Global change may affect principally the climate through temperature and precipitation regime (amount, annual distribution, etc.). Bot may have consequences on the overall distribution of freshwater biota (Tonn, 1990), as well as on the physiology and biology of individual species (Regier et al., 1990).

Several anthropogenic factors are also responsible for the erosion of freshwater biodiversity. Until recently, these factors had impacts at local or regional scales. However, some of them are spreading throughout the world and can now be considered as global trends:

- Habitat alteration is a major cause of aquatic biodiversity loss, and degradation or destruction of habitats is particularly threatening in rivers. Flow regulation occurs on almost all large river and alters the natural flood regime in fresh waters. Man-made lakes associated with hydroelectric dams or built for irrigation purposes prevent fish migrations, and alter the flow pattern downstream. Catchments are affected by large-scale land-use practices often associated with deforestation. These practices generate rapid headwater erosion and increase of sediment load in river waters, as do mining-related activities.
- Human activities generate excessive inputs of nutrients (nitrogen and/or phosphorus) from point or non-point sources resulting in river and lake eutrophication. The eutrophication process leads to changes in pelagic communities and benthic invertebrate biodiversity, mostly through depletion of available oxygen, and abundance can be modified as well.
- Introduction of alien species into aquatic systems has been frequent. Welcomme (1988) listed

237 inland animal species that have been introduced into 140 countries world wide, but the total number is now much higher. One of the major problems of freshwater species introductions is its irreversibility, at least at the human lifetime scale. Once introduced and established, it is impossible, given current technology, to eradicate a fish, mollusc or plant species from a large natural water body. As a consequence, we are likely to see a continued impoverishment of native aquatic biodiversity and an increased homogenisation of the world's freshwater biota.

We need to develop tools and methodology to address the problem of scale. In climate and hydrologic studies, data and processes are commonly integrated from local to global scale. In ecology, studies still address biodiversity changes usually at a local scale. The challenge is also to provide a global assessment of freshwater biodiversity that could be related to global data on climate and water cycle. Such a global assessment is also critical for decision makers to address issues related to the global water system including the biological component. Meantime, the efforts to provide a global assessment would also open the path for a macro-ecological approach of freshwater biodiversity.

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