

# Global diversity of copepods (Crustacea: Copepoda) in freshwater

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**Abstract** The zoogeographic distributions of the 2,814 species of copepods reported from freshwater are analysed. Faunal diversity is compared between zoogeographic regions: the Palaearctic region has more than double the species richness of the next most diverse region, the Neotropical. Historical factors affecting levels of diversity are identified. More than 90% of all freshwater copepods are endemic to a single-zoogeographic region and endemic genera occur in all regions except Antarctica. Species that are not endemic to a single region include the highly vagile and cosmopolitan species occurring in four or more regions. The greatest faunal connectivity, as identified by Sørensen's Index, is between Palaearctic and Nearctic regions, and identifies the Holarctic taxa. Key human-related issues, such as the role of copepods as vectors for human parasites and the losses caused by parasitic copepods in commercial aquaculture, are mentioned.

**Keywords** Zoogeography · Copepods · Freshwater · Endemism · Species richness

## Introduction

Copepods occur in almost all freshwater habitats from the largest ancient lakes to subterranean waters, from pools of glacial meltwater to hot springs, and from hypersaline lakes to phytotelmata. They are extremely abundant in freshwater and comprise a major component of most planktonic, benthic and groundwater communities, including semi-terrestrial situations such as damp moss and leaf litter in humid forests. With an estimated 13,000 morphospecies known, the greatest diversity of copepods is found in the marine environment, but approximately 2,814 species inhabit freshwater. Copepods originated in the marine environment: Huys & Boxshall (1991) hypothesized that all ten orders of Copepoda recognized at that time had their origins in the marine hyperbenthic community. Boxshall & Jaume (2000) recognized a minimum of 22 lineages as having independently colonized freshwater, but several other predominantly coastal marine and estuarine taxa have made incursions into freshwater, due to their basic euryhalinity (cf. Lee, 1999). The greatest difficulty in the analysis of global diversity of copepods in freshwater is defining the salinity limits for inclusion. In nature, habitats exhibit a continuum of salinity regimes from fresh to fully marine. Drawing a line

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through the “brackish” water is a somewhat arbitrary process especially since precise salinity data are often not available for records from estuaries or coastal lagoons. Saline and hypersaline inland continental waters tend to be populated by representatives of typically freshwater higher taxa and are, therefore, included in this analysis.

Most freshwater copepods are free-living, but they have adopted parasitism in numerous independent lineages. About 330 species of copepods in freshwater are parasitic, most commonly on fish hosts, but also on molluscs. Copepods also live as commensal epibionts on freshwater invertebrates, such as crayfishes, medusae and sponges.

It is important to set estimates of regional species richness in their historical context. Nineteenth century species concepts were largely established by and applied by European natural historians who tended to record European-like species from around the world under classical European names. In the second half of the 20th century revisionary studies generated more fine-scale taxonomic resolution and the recognition of numerous species complexes replacing so-called cosmopolitan species. The pioneering work on chydorid cladocerans by Frey (summarised in Frey, 1986) was soon mirrored for copepods, such as *Mesocyclops leuckarti*, but in many copepod taxa such fine-scale resolution has yet to be achieved for morphospecies. In addition, the advent of molecular methodology has not yet fully impacted on species-identity concepts in freshwater copepods. Studies of the genetics of the invasive temorid *Eurytemora affinis* have revealed discordant rates of morphological differentiation, molecular evolution and reproductive isolation, resulting in speciation events that are not accompanied by morphological differentiation in the secondary sexual characters traditionally employed for species discrimination. Instead of being a cosmopolitan euryhaline Holarctic species, *E. affinis* is now recognised as a species complex of genetically divergent and physiologically distinct populations with habitat transitions, such as the invasion of freshwater, entailing rapid evolutionary events (Lee, 1999, 2000).

### Species diversity

Copepods from five orders occur in freshwater (Table 1) and this diversity is reflected in the enormous

range of life styles adopted, from small-particle feeding to predation and parasitism (Boxshall & Halsey, 2004). In the Calanoida, the Diaptomidae is the dominant family in inland waters in Europe, Asia, North America, Africa and northern low-altitude South America. It does not occur in New Zealand and New Caledonia, and only two species (*Tropodiaptomus australis* and *Eodiaptomus lumholtzi*) have been found in Australia. The family comprises about 440 species in four subfamilies: the two largest comprising 24 species (Paradiaptominae) and about 410 species (Diaptominae). Diaptomids in general are small-particle feeders (Fig. 1A) but the biology, diversity and evolutionary histories of these two subfamilies differ markedly. The Diaptominae is extremely widely distributed and most are planktonic, inhabiting the water column. The Paradiaptominae is restricted to Africa, with outliers in southern Europe and south-western Asia. They are often restricted to extreme habitats, such as temporary pools. The other two subfamilies comprise small-sized species inhabiting subterranean waters.

The Centropagidae contains marine, brackish, freshwater and athalassic saline water species. They are the most important calanoids in continental waters in Australasia. Species of the *Boeckella*-group (comprising at least those approximately 70 species referred to *Boeckella*, *Hemiboeckella* and *Calamocia*) occur in fresh and athalassic saline waters in Australia, New Zealand, southern and high-altitude South America and New Caledonia (Bayly, 1995; Defaye, 1998; Dussart & Defaye, 2002). A single species, *B. triarticulata* (Fig. 1D), occurs in Mongolia (see records in Dussart & Defaye, 2002) and an introduced population of this species has been reported from Italy. Three centropagid genera, *Limnocalanus*, *Osphranticum* and *Sinocalanus*, are present in continental waters in the Northern Hemisphere. The sole species of *Osphranticum* occurs in freshwater in North America, as far south as Guatemala. *Limnocalanus* species occur in freshwater lakes and in the Caspian Sea. *Sinocalanus* comprises five species found primarily in estuarine waters.

The Temoridae also comprises a mix of coastal marine, estuarine and freshwater taxa. According to Dussart & Defaye (2002), 30 species in three genera, *Epischura*, *Eurytemora* and *Heterocope* Sars, inhabit continental waters in the northern Hemisphere. Most of the *Eurytemora* species are brackish water forms, although *E. velox* and *E. lacustris* are freshwater

**Table 1** Number of freshwater species recorded per zoogeographic region

Taxon	PA region	NA region	NT region	AT region	OL region	AU region	PAC	ANT region	World species number
Calanoida									
Diaptomidae	144	77	82	72	92	2	–	–	441
Centropagidae	7	4	22	–	4	47	2	7	79
Temoridae	22	18	–	–	–	–	–	–	30
Aetideidae ( <i>Senecella</i> )	2	2	–	–	–	–	–	–	2
Harpacticoida									
Canthocamptidae	325	59	109	46	58	51	3	4	627
Parastenocarididae	108	8	65	34	16	2	1	–	249
Ameiridae	97	9	17	9	10	15	6	–	149
Miraciidae	27	–	6	13	3	8	1	–	53
(Diosaccidae)									
Ectinosomatidae	11	1	–	–	1	–	–	–	13
Phyllognathopodidae	3	2	3	3	3	3	–	1	10
Harpacticidae	4	–	–	–	1	–	–	–	4
Chappuisiidae	2	–	–	–	–	–	–	–	2
Huntemanniidae	3	1	1	1	–	–	–	–	6
Laophontidae	2	3	1	2	2	3	–	–	7
Cletodidae	1	–	–	–	3	–	–	–	3
Darcythompsoniidae	1	–	–	–	–	–	–	–	1
Cyclopoida									
Cyclopidae	337	114	174	167	115	64	16	5	800
Oithonidae	–	2	6	–	2	–	–	–	7
Ozmanidae	–	–	2	–	–	–	–	–	2
Lernaeidae	17	8	10	39	47	2	–	–	114
Ergasilidae	56	26	63	19	23	8	–	–	173
Gelyelloida									
Gelyellidae	2	–	–	–	–	–	–	–	2
Siphonostomatoida									
Lernaeopodidae	31	12	–	–	1	–	–	–	38
Caligidae	1	–	–	–	–	–	–	–	1
Dichelesthiidae	1	1	–	–	–	–	–	–	1
Total	1,204	347	561	405	381	205	29	17	2,814

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

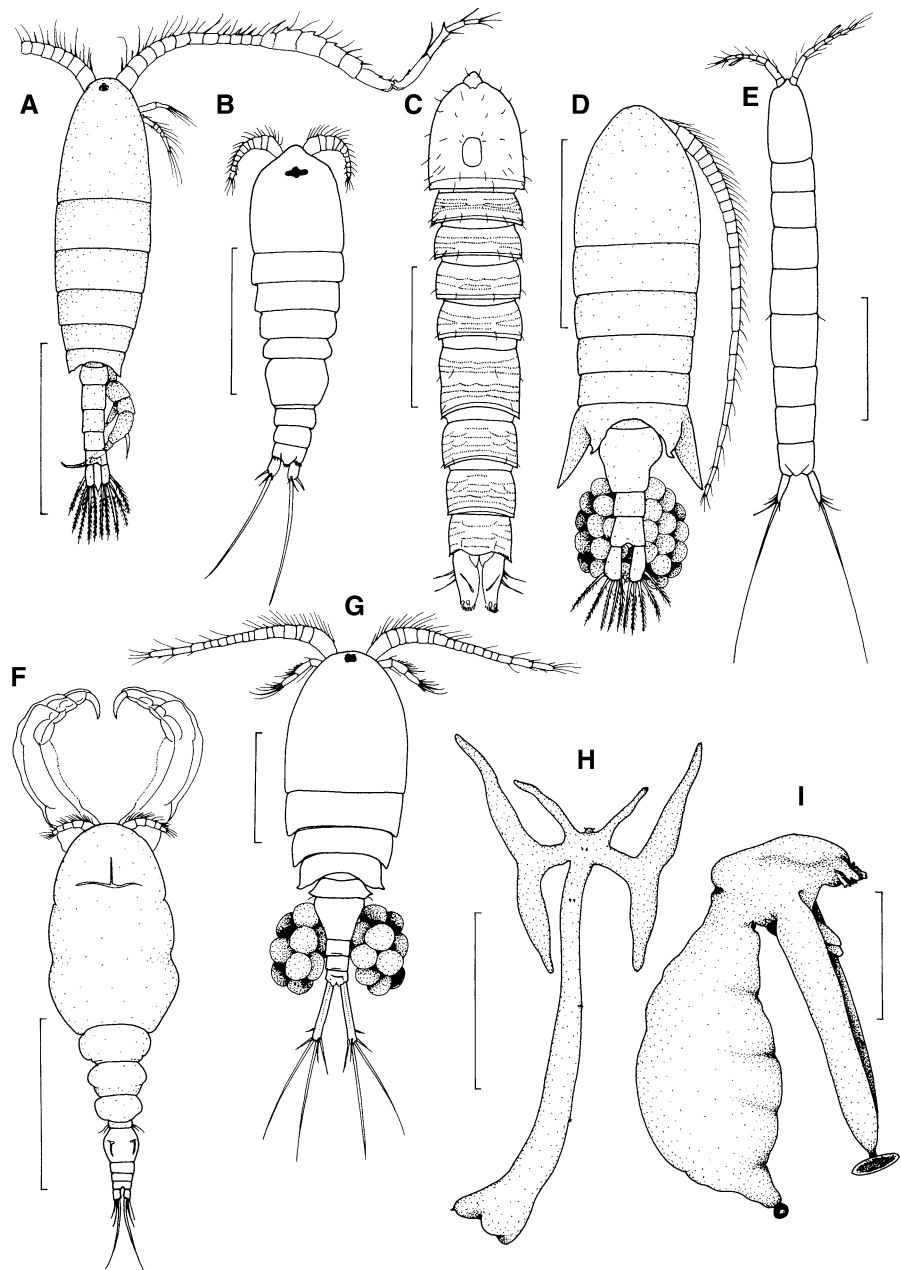
species. All are restricted to the higher latitudes of the Northern Hemisphere.

Currently placed in the Aetideidae (Boxshall & Halsey, 2004), *Senecella* comprises two species, *S. calanoides* and *S. siberica*, distributed in high latitude North America and northern Siberia, around the shores of the Kara and Laptev Seas. Both occur in brackish coastal waters, as well as in freshwater. The Pseudodiaptomidae and Acartiidae comprise

primarily coastal and estuarine species. A few species occur in fresh, brackish and continental waters (Dussart & Defaye, 2002) but neither family is considered further.

The Canthocamptidae is the largest family in the Harpacticoida, comprising about 627 species. It is predominantly freshwater in distribution, but contains fully marine taxa and specialist estuarine forms, such as *Mesochra*. *Cletocamptus* is of uncertain taxonomic

**Fig. 1** The diversity of copepods in fresh water. (A) Diaptomidae (*Eudiaptomus gracilis*, male); (B) Cyclopidae (*Graeteriella unisetigera*, female); (C) Canthocamptidae (*Moraria baikalomoraria* *brevicauda*, female); (D) Centropagidae (*Boeckella triarticulata* female); (E) Parastenocarididae (*Parastenocaris roettgeri*, female); (F) Ergasilidae (*Acusicola mazatlanensis*, female); (G) Cyclopidae (*Cyclops abyssorum*, female); (H) Lernaecidae (*Lernaea cyprinacea*, female); (I) Lernaepodidae (*Achtheres percarum*, female). Scale bars: A, G = 0.5 mm, B, C = 0.2 mm, D, I = 1 mm, E = 0.1 mm, F = 0.4 mm, H = 5 mm



affinity and its species occur throughout the salinity range but a few species occur in full freshwater, such as in Lake Titicaca. Virtually all species of Parastenocarididae are found in freshwater, mainly in interstitial habitats. Freshwater Canthocamptidae (Fig. 1C) and the Parastenocarididae (Fig. 1E) both have cosmopolitan distributions, except for the latter's absence from New Zealand (Dussart & Defaye, 1990). The difference in species richness

may partly be an artifact, due to incomplete sampling of the groundwater habitats favoured by parastenocaridids. Two smaller families, the Chappuisiidae (two species) and the Phyllognathopodidae (about 10 species) occur exclusively in freshwater but the former is found only in Northern Europe, whereas the latter is extremely widely distributed.

The Ameiridae contains almost 150 freshwater species and is especially diverse in subterranean

waters (Rouch, 1986; Galassi, 2001). Freshwater species are found widely across Europe, Asia, North America and Africa, especially northern Africa (Dussart & Defaye, 1990), although this may represent sampling bias. It is one of the more speciose families in freshwater and is dominated by the group of genera related to *Nitokra* and *Nitocrella*. These genera inhabit karstic habitats, calcrete formations and other subterranean waters. Some ameirids have entered into symbiotic relationships with freshwater invertebrates.

The Ectinosomatidae is overwhelmingly marine but contains a few estuarine and freshwater species. The latter belong in six genera: *Pseudectinosoma*, *Halectinosoma*, *Pseudobradya*, *Ectinosoma*, *Rangabradya* and *Arenosetella*. Available information on phylogenetic relationships indicates that there have been several independent colonizations of freshwater within the family, such as that within *Pseudectinosoma* (e.g. Galassi et al., 1999). The Harpacticidae is similar, mainly marine with a few freshwater forms. It contains genera such as *Tigriopus*, which typically live in coastal splash zone pools and are tolerant of extreme variations in salinity, and *Harpacticus* which is common in coastal lagoons. These forms are not treated here as freshwater. The true freshwater clade consists only of *Harpacticella* species, which are found in the Palaearctic and Oriental Regions.

The Miraciidae (=formerly the Diosaccidae) is another predominantly marine family, but contains numerous freshwater forms, especially in the *Schizopera*-group of genera. These freshwater forms are found in Western Eurasia, Australia and Africa, especially in the Rift Valley lakes, where an evolutionary radiation has taken place. There are 10 species of the *Schizopera*-group described from Lake Tanganyika (Coulter, 1991). The speciose marine family Laophontidae contains a small number of brackish and freshwater species: some *Laophonte* species occur in coastal lagoons, and *Troglo-laophonte* occurs in a brackish cave. These brackish forms are excluded from the analysis. True freshwater laophontids include the cosmopolitan *Onychocamptus mohammed* and some species of *Heterolaophonte* (e.g. *H. quinquespinosa* and *H. stromi*) that occur in inland saline lakes in southeastern Australia and in high Arctic lakes. The Cletodidae is primarily marine but contains a few euryhaline (brackish to freshwater) taxa, such as

*Limnocolletes*. The Huntemaniidae is similar—predominantly marine with a few freshwater and estuarine species. *Nannopus palustris*, for example, inhabits the fresher zones of estuaries across the Holarctic, the Caspian Sea and Lake Kinneret, and *N. perplexus* was described from Lake Tanganyika. The darcythompsoniid *Leptocaris brevicornis* occurs in Lake Kinneret and a lake in El Salvador.

The largest copepod family is the Cyclopidae which comprises over 800 species (Dussart & Defaye, 2006), the great majority belonging to two freshwater subfamilies, Eucyclopininae and Cyclopininae. The Euryteinae contains marine and estuarine species only, and the Halicyclopininae consists predominantly of brackish forms belonging to *Halicyclops* and related genera, with a few freshwater species. The Euryteinae is excluded from subsequent consideration. The Cyclopidae (Fig. 1G) is cosmopolitan in freshwaters and its members exploit a huge variety of habitats, from subterranean waters (Fig. 1B) to ancient lakes, and life styles from small-particle feeders, to predators or even parasites of gastropod molluscs (Boxshall & Strong, 2006).

The Oithonidae contains primarily marine planktonic forms but several species are found in brackish habitats, such as mangrove swamps, and a few occur in freshwater. Some species occur exclusively in freshwater: there is, for example, a small cluster of *Oithona* species in east coast drainages of South America (Rocha, 1986). *Limnoithona* is a brackish-water specialist.

The Ergasilidae has a unique life cycle within the copepods: its developmental stages from nauplius to adult, occurring in the plankton, only after mating do fertilized adult females seek out and infest hosts for the final, parasitic phase of their life cycle. Most ergasilids are known only from their parasitic females and these typically utilize fishes as hosts, with a few on bivalve mollusks, attaching by claw-like antennae (Fig. 1F). Ergasilids are found on and around the coastal margins of all continents excluding Antarctica, and occur in all salinity regimes although the majority can be regarded as freshwater. Estuarine ergasilids commonly utilize hosts, which move freely between salinity regimes.

The Lernaecidae comprises 114 species, all parasites of freshwater fishes, classified in two monophyletic lineages, the subfamilies Lernaecinae and Lamproglenninae (Ho, 1998). All Lamproglenninae

are found in the Palaearctic, Oriental and Afrotropical regions. The Lernaenae is more widely distributed, occurring in all regions except Antarctica, although the Australian fauna comprises only two species. The Ozmanidae consists of two endoparasitic species in freshwater gastropod molluscs in South America.

The only members of the order Siphonostomatoida found in freshwater are parasites of fishes. The *Salmincola*-clade (Fig. 1I) within the Lernaepodidae comprises 38 species in seven genera, which utilize a wide range of fish hosts (Kabata, 1979). The Caligidae contains over 400 marine species but just a single freshwater species, *Caligus lacustris*, which also occurs in brackish waters and the Black Sea. *Dichylesthium oblongum* parasitises sturgeons and was regarded by Kabata (1979) as a marine species carried into freshwater by the migrations of its host.

Finally, the order Gelyelloida comprises a single family, the Gelyellidae, one genus and two species currently reported only from groundwater habitats of south-western Europe.

### Present distribution and main areas of endemism

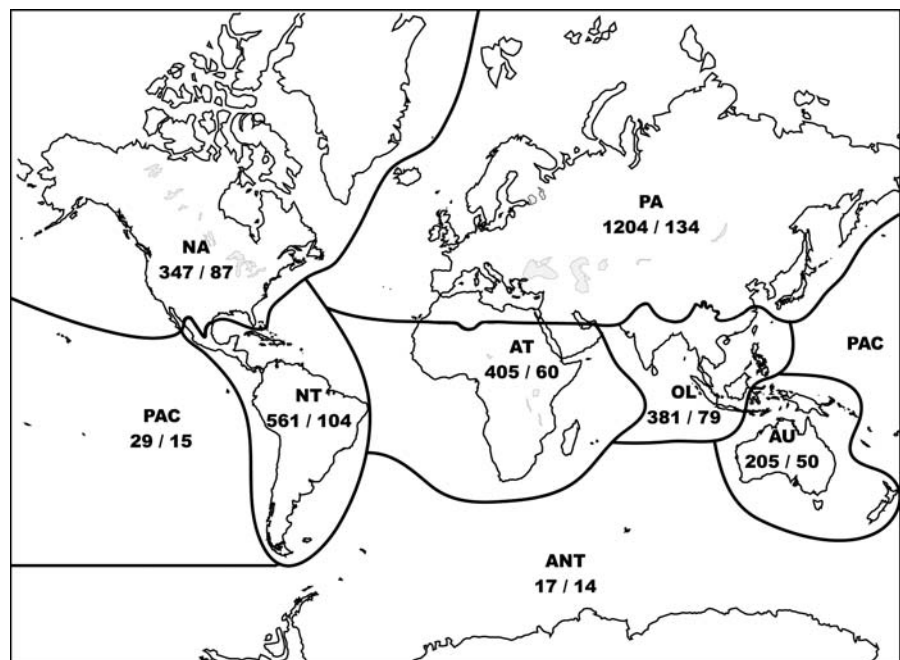
Cosmopolitan taxa occurring in freshwater in all zoogeographic regions except the Antarctic include

the families Ameiridae, Canthocamptidae, Cyclopidae, Diaptomidae, Ergasilidae, Harpacticidae, Laophontidae, Lernaenidae, Parastenocarididae and Phyllognathopodidae, although the distribution of the Diaptomidae and the Parastenocarididae within the Australasian region is limited. Almost as widely distributed are the Centropagidae, which occur in all regions except the Afrotropical. For these taxa, presence/absence data at the family level are too coarse to reveal distribution patterns and quantitative data, such as species richness per region, and qualitative data at a finer-taxonomic resolution, such as genus or subgenus level, must be considered. The large, cosmopolitan canthocamptid genus *Attheyella* is an excellent example. It has been divided into six subgenera: of these, two (*Attheyella* and *Mrazekiella*) are predominantly Palaearctic in distribution, two (*Chappuisiella* and *Delachauxiella*) are predominantly Neotropical, and one (*Canthosella*) occurs in both Oriental and Neotropical regions (Fig. 2).

### Palaearctic region

The Palaearctic region has 1,204 recorded species—more than double the number recorded for any other region (Table 1). The major contributors are the Cyclopidae (28%), especially *Diacyclops*, *Eucyclops*,

**Fig. 2** Geographical distribution of species and genera of freshwater copepods (Species number/Genus number), coded according to the main zoogeographic regions. PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic





*Acanthocyclops* and *Speocyclops*, the Canthocamptidae (27%) especially *Elaphoidella*, *Moraria*, *Bryocamptus* and *Attheyella* (*Attheyella*) and *Attheyella* (*Mrazekiella*), and the Diaptomidae (12%), especially *Arctodiaptomus*, *Diaptomus*, *Eudiaptomus* and *Hemidiaptomus*. Parasites comprise less than 9% of the total but the Palaearctic also has the greatest species richness, as well as the greatest family-level diversity of fish parasites.

Several small lineages including the freshwater Temoridae, *Senecella*-species, the *Harpacticella*-group and the *Salmincola*-lineage, occur only in the more northerly part of the Northern Hemisphere. The restriction of these relatively small lineages to the northern part of the Holarctic region suggests that the Pleistocene glaciations may have had a profound effect on their distributions. All may be postglacial invasions.

#### Nearctic region

The Nearctic, with 347 recorded species, exhibits less than one-third of the richness of the Palaearctic (Table 1), and a significant proportion of species is shared between these two regions, i.e. are Holarctic in distribution. At the genus level, there are few Nearctic endemics, since most are Holarctic. The major contributors to the species richness are the Cyclopidae (33%), especially *Diacyclops* and *Acanthocyclops*, the Diaptomidae (22%) especially *Aglaodiaptomus*, *Hesperodiaptomus* and *Leptodiaptomus*, and the Canthocamptidae (17%), especially *Elaphoidella*. The dominant parasitic families are the Ergasilidae (7%) and Lernaepodidae (3%).

#### Afrotropical region

Sub-Saharan Africa has a copepod fauna of 405 species (Table 1). The major contributors are the Cyclopidae (41%), especially *Eucyclops* and *Thermocyclops*, and the Diaptomidae (18%) especially *Tropodiaptomus*, followed by the Lernaecidae (10%). The benthic families Canthocamptidae, particularly *Elaphoidella* and *Echinocamptus*, and Parastenocarididae contribute only 11% and 8% to the total, respectively. Centropagids are absent from African inland waters and it has been inferred that Africa was probably never colonized by centropagids (Bayly, 1995; Boxshall & Jaume, 2000). Boxshall & Jaume

(2000) also speculated that the ancestors of the subfamily Paradiaptominae were the first calanoids to colonize freshwater on the African plate and that the diaptomines invaded the African continental waters initially from the North, and spread southwards, diversifying and largely displacing the paradiaptomines, except in more extreme habitats.

#### Neotropical region

The Neotropical region has the second-highest richness, with 561-recorded species (Table 1), although this number is expected to rise with increasing study. The major contributors are the Cyclopidae (31%), especially *Eucyclops*, *Metacyclops* and *Mesocyclops*, the Canthocamptidae (19%), especially *Elaphoidella*, *Attheyella* (*Chappuisiella*) and *A. (Delachauxiella)*, the Diaptomidae (15%), and Parastenocarididae (12%). Within the Diaptomidae, the most speciose genera are *Notodiaptomus* and *Argyrodaptomus*, both endemic to the region. Boxshall & Jaume (2000) postulated that the presence of diaptomids at low altitudes in the northern and central parts of South America resulted from a late invasion from North America, occurring after closure of the Panama gap in the Pliocene about 3 mya. After invading from the North, the diaptomids would have spread rapidly, through the highly interconnected, lowland river systems that make South America unique. Boxshall & Jaume speculated that the diaptomids replaced the existing calanoid fauna of *Boeckella*-group centropagids except at high altitudes (i.e. the Andean cordillera) and at high latitudes (e.g. Patagonian), where they are still dominant today. Bayly (1995) argued that the *Boeckella*-group first invaded southern inland continental waters at a time when Australia, New Zealand and South America were still linked but Africa, Madagascar and India had already drifted northwards. Bayly estimated this colonization as occurring between 120 mya and 80 mya.

A small cluster of *Oithona* species has been recorded in Amazonia (Rocha, 1986). The extensive brackish interface between marine and freshwater habitats in the Amazon may have provided the route by which *Oithona* has colonized neotropical freshwaters, but Boxshall & Jaume (2000) noted the possibility that *Oithona* might have arrived during a marine incursion into the Upper Amazon (cf. Lovejoy et al., 1998).

The Ergasilidae comprises 11% of the total richness but Thatcher (1998) calculated that only a tiny proportion of the possible ergasilid fauna of Amazonia is currently known: our knowledge of the Ergasilidae is incomplete. El-Rashidy (1999) showed that most Neotropical freshwater ergasilids probably belong to a single monophyletic lineage which has diversified spectacularly in Amazonia and now encompasses 13 endemic genera. The genus *Acusicola* has subsequently spread northwards through Central America and a single species has penetrated the Nearctic, as far as Texas. This is further evidence that the closure of the Panama gap in the Pliocene permitted an intense period of North/South faunal exchange in both directions (cf. Suárez-Morales et al., 2004).

#### Oriental region

The diversity of the Oriental region is relatively low, with only 16 families represented by 381 species (Table 1). The major contributors are the Cyclopidae (30%), especially *Mesocyclops* and *Thermocyclops*, the Diaptomidae (24%), especially *Tropodiaptomus* and *Heliodiaptomus*, the Canthocamptidae (15%), especially *Elaphoidella*, and the Lernaecidae (12%). The species richness may be expected to rise substantially since the benthic fauna has been only patchily sampled.

The Oriental region is home to seven genera of Lernaecidae, three of which (*Indopeniculus*, *Pillainus*, and *Indolernaea*) are endemic (Table 2). However, the bulk of the species richness is contributed by *Lamproglena* (22 species) and *Lernaea* (15 species). The former also occurs in the Afrotropical and Palaearctic regions, whereas the latter is cosmopolitan. Approximately 45% of lernaecids occur in the Oriental region and another 35% is reported from the Afrotropical region. According to Ho (1998), this pattern, with 80% of species confined to Asia and Africa, resulted from an explosive cladogenesis on the “Indian Raft”, which took place after the ancestral lernaecids colonized the Cyprinidae as hosts.

#### Australasian region

The Australasian fauna exhibits the lowest richness (205 species) of all regions except the Pacific islands and Antarctica (Table 1). However, despite the

aridity of large areas of the Australian continent, which might explain the apparent paucity of species, recent research into the subterranean fauna of arid Western Australia (Karanovic, 2004) has revealed an unexpectedly high diversity and degree of endemism. The major contributors to the overall species richness are the Cyclopidae (31%), especially *Mesocyclops* and *Eucyclops*, the Canthocamptidae (25%) especially *Canthocamptus*, and the Centropagidae (23%). The centropagids have been the focus for much biogeographical research. Bayly (1995) inferred that Australia was inhabited by numerous *Boeckella* species prior to its separation from Antarctica, and contrasted it with *Calamoecia*, which almost certainly evolved after separation.

Australian athalassic saline waters are inhabited by a specialized fauna comprising centropagids (such as *Calamoecia clitellata* and *C. salina*), canthocamptids (such as *Mesochra baylyi*), and cyclopids (such as *Merideicyclops baylyi*). They are likely derived from freshwater ancestors, according to Bayly (1993), who suggested that these halobiont species probably evolved after the mid-Miocene (16 mya) and that their successful colonization was related to the evolution of exceptional cellular tolerance or cellular osmoregulation.

#### Pacific island region

The Pacific island fauna is low in diversity with only 29 species recorded (Table 1). Calanoids are rare: two centropagids are described from New Caledonia and no diaptomids are known. One brackish ergasilid is reported but no freshwater copepod parasites are known, although a little research has been done on the larger islands. Benthic copepods comprise the bulk of the fauna, but several are vagile species with widespread distributions, such as *Nitokra lacustris*, *Phyllognathopus viguieri*, *Paracyclops chiltoni*, *Mesocyclops aspericornis* and *Tropocyclops prasinus*. The proportion of regional endemics is relatively small.

#### Antarctic region

Most of the 17 reported species occur on the Subantarctic islands. Pugh et al. (2002) hypothesized that all continental and maritime Antarctic Crustacea represent Holocene immigrants. More specifically, they interpreted the population of the centropagid



**Table 2** Number of freshwater genera recorded per zoogeographic region; number in parentheses indicates number of genera that are endemic to the region

Taxon	PA region	NA region	NT region	AT region	OL region	AU region	PAC	ANT region	Total genera number
Calanoida									
Diaptomidae	25 (9)	14 (4)	18 (14)	7 (3)	22 (10)	2 (0)	–	–	60 (40)
Centropagidae	3 (0)	3 (0)	3 (3)	–	2 (0)	7 (2)	2 (1)	3 (0)	8 (5)
Temoridae	3 (0)	3 (0)	–	–	–	–	–	–	4 (0)
Aetideidae ( <i>Senecella</i> )	1 (0)	1 (0)	–	–	–	–	–	–	1 (0)
Harpacticoida									
Canthocamptidae	23 (11)	9 (1)	12 (3)	6 (1)	9 (2)	8 (2)	1 (0)	3 (0)	38 (21)
Parastenocarididae	2 (1)	1 (0)	6 (5)	1 (0)	1 (0)	1 (0)	1 (0)	–	6 (4)
Ameiridae	6 (1)	5 (0)	4 (0)	3 (0)	3 (0)	6 (2)	1 (0)	1 (0)	9 (4)
Miraciidae (Diosaccidae)	2 (0)	–	1 (0)	1 (0)	2 (1)	1 (0)	1 (0)	–	2 (1)
Ectinosomatidae	5 (1)	1 (0)	–	–	1 (1)	–	–	–	6 (2)
Phyllognathopodidae	1 (0)	1 (0)	2 (1)	1 (0)	2 (1)	1 (0)	–	1 (0)	3 (2)
Harpacticidae	1 (0)	–	–	–	1 (0)	–	–	–	1 (1)
Chappuisiidae	1 (1)	–	–	–	–	–	–	–	1 (1)
Huntemanniidae	2 (0)	2 (0)	1 (0)	1 (0)	1 (0)	–	–	–	2 (0)
Laophontidae	4 (0)	3 (0)	2 (0)	2 (0)	2 (0)	3 (0)	–	1 (0)	6 (0)
Cletodidae	1 (0)	–	–	–	1 (0)	–	–	–	1 (0)
Darcythompsoniidae	1 (0)	–	–	–	–	–	–	–	1 (0)
Cyclopoida									
Cyclopidae	32 (6)	23 (1)	30 (11)	25 (2)	19 (1)	19 (3)	9 (0)	5 (0)	55 (24)
Oithonidae	–	1 (0)	2 (0)	–	1 (0)	–	–	–	2 (0)
Ozmanidae	–	–	1 (1)	–	–	–	–	–	1 (1)
Lernaeidae	4 (0)	1 (0)	6 (5)	7 (3)	7 (3)	1 (0)	–	–	16 (11)
Ergasilidae	8 (1)	5 (0)	16 (13)	6 (1)	5 (0)	3 (1)	–	–	24 (16)
Gelyelloida									
Gelyellidae	1 (1)	–	–	–	–	–	–	–	1(1)
Siphonostomatoida									
Lernaeopodidae	6 (3)	3 (1)	–	–	–	–	–	–	7 (4)
Caligidae	1 (0)	–	–	–	–	–	–	–	1 (0)
Dichelesthidae	1 (0)	1 (0)	–	–	–	–	–	–	1 (0)
Total	134 (35)	87 (8)	104 (54)	60 (12)	79 (19)	50 (10)	15 (1)	14 (0)	257 (138)

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

*Boeckella poppei* inhabiting freshwater lakes in East Antarctica, as a recent anthropogenic introduction, and that of the endemic *Gladioferens antarcticus* as a ‘marine interloper’. These interpretations were challenged by Bayly et al. (2003) who presented robust evidence that *B. poppei* has been present in isolated populations in East Antarctica for significant time periods, possibly pre-dating the current interglacial,

and that *G. antarcticus* is a true Antarctic endemic whose ancestors have been present in the region, since before Australia separated from Antarctica.

#### Hotspots

The concept of biodiversity hotspots as areas of exceptional biotic richness set against a background

of relatively low diversity has been widely adopted, as a method of identifying priority areas for conservation. Most analyses have identified ancient lakes as hotspots for freshwater biodiversity. For copepods, Lake Baikal with over 120 species, the majority of which are endemic (Boxshall & Evstigneeva, 1994), and Lake Tanganyika with 69 species, of which 34 (49%) are endemic (Coulter, 1991; Boxshall & Strong, 2006), constitute prime hotspots. In both the copepod fauna comprises several species flocks, defined as monophyletic clades endemic to the lake and presumed to have originated via intralacustrine speciation. The age of the lake (i.e. the time available for speciation to have taken place), the heterogeneity of habitats at all scales within the lake, and their biotic complexity are all potential factors affecting the generation and maintenance of high levels of biodiversity in ancient lakes. Boxshall & Evstigneeva (1994) suggested that trophic specialisation was a key driver in the adaptive radiation of the cyclopids in Lake Baikal in contrast to the canthocamptids where they considered differentiation in mating behaviour to be a key driver.

In recent decades, awareness of the diversity of groundwater faunas has increased. Sket (1999) for example, noted that 70% of the 245 harpacticoid copepods and 60% of the 145 cyclopoids recorded in the *Limnofauna Europaea* compendium were stygobites. Culver & Sket (2000) recommended that cave systems inhabited by at least 20 stygobitic species should be designated biodiversity hotspots. Worldwide only 20 karstic systems and two sites in porous aquifers meet this criterion (Culver & Sket, 2000; Danielopol & Pospisil, 2002). The species richness of the Lobau wetland in the Danube flood plain led Danielopol & Pospisil (2002) to refer to it as a biodiversity hotspot. In a sampled area of 0.8 km<sup>2</sup> they discovered 30 copepod species of which 10 were hypogean. The situation is not unique: Karanovic (2004) discovered a subterranean fauna of 31 species (24 new) in the arid Murchison region of western Australia, and Stoch (1995) reported 70 species from the Venezia Giulia (N.E. Italy and southeastern Slovenia) of which 33 (47%) were stygobionts. Galassi (2001) reviewed the patterns of diversity of groundwater copepods, noting that stygobiont copepods inhabit all kinds of aquifers (karstic, fissured and porous). She

identified local heterogeneity, patchiness in geomorphological and hydrological characteristics, as well as biotic interactions as causal factors affecting diversity patterns over a range of spatial and temporal scales.

### Endemism

The level of endemism in freshwater copepods seems remarkable. The great majority (2,558 out of 2,814 species, or 90.9%) of species occur in a single region. The Neotropical, Afrotropical, Palaearctic and Australasian Regions each display in excess of 80% endemism (Table 3). Nearctic and Oriental Regions display intermediate levels (65–75%) and the Pacific islands and Antarctica both display between 45% and 50%. Species that are not endemic to a single region include highly vagile and cosmopolitan species that occur in four or more regions.

Endemic genera occur in all regions except Antarctica (Table 2), in all orders and across all life styles. The Neotropical is home to the greatest number of endemic genera (Table 2). There is evidence that in the Ergasilidae most of the endemic genera represent a single monophyletic lineage (El-Rashidy, 1999). Similarly, Boxshall & Halsey (2004) recognized the possibility that the cluster of five lernaeid genera endemic to the Neotropics may be closely related (i.e. form a monophyletic group). No phylogeny exists for the Diaptomidae but, building on the speculation (Boxshall & Jaume, 2000) that diaptomines only invaded South America after the closure of the Panama gap, it is possible that the cluster of 14 endemic genera might also form a monophyletic lineage.

### Faunal links

Pair-wise analysis of the occurrence of species that inhabit more than one zoogeographic region (Table 4) provides a relative measure of the faunal connectivity between regions. The dominant links as estimated by Sørensen's index (SI) are those between the Palaearctic and Nearctic, between the Nearctic and Neotropical, and between the Oriental and Australasian regions. The Palaearctic to Nearctic link identifies Holarctic taxa and these typically belong to lineages, the distributions of which have been profoundly affected by the Pleistocene glaciations. The Nearctic to Neotropical link in part testifies to the strength of

**Table 3** Number of endemic species recorded from each zoogeographic region

Taxon	PA region	NA region	NT region	AT region	OL region	AU region	PAC	ANT region	Total endemic species number
Calanoida									
Diaptomidae	121	65	77	71	81	2	–	–	417
Centropagidae	3	1	14	–	1	45	2	1	67
Temoridae	11	8	–	–	–	–	–	–	19
Aetideidae ( <i>Senecella</i> )	–	–	–	–	–	–	–	–	
Harpacticoida									
Canthocamptidae	285	46	114	37	40	51	1	1	575
Parastenocarididae	117	9	69	36	16	1	1	–	249
Ameiridae	94	6	11	9	4	9	3	3	139
Miraciidae	25	–	5	11	1	6	1	–	49
(Diosaccidae)									
Ectinosomatidae	11	–	–	–	1	–	–	–	12
Phyllognathopodidae	1	–	2	2	1	1	–	1	8
Harpacticidae	3	–	–	–	–	–	–	–	3
Chappuisiidae	2	–	–	–	–	–	–	–	2
Huntemanniidae	1	1	–	1	1	–	–	–	4
Laophontidae	2	–	–	–	–	1	–	–	3
Cletodidae	–	–	–	–	2	–	–	–	2
Darcythompsoniidae	1	–	–	–	–	–	–	–	1
Cyclopoida									
Cyclopidae	254	56	130	123	68	43	4	2	680
Oithonidae	–	–	5	–	–	–	–	–	5
Ozmanidae	–	–	2	–	–	–	–	–	2
Lernaeidae	11	7	10	37	42	1	–	–	108
Ergasilidae	50	21	63	17	20	7	1	–	179
Gelyelloida									
Gelyellidae	2	–	–	–	–	–	–	–	2
Siphonostomatoida									
Lernaeopodidae	25	5	–	–	1	–	–	–	31
Caligidae	1	–	–	–	–	–	–	–	1
Dichelethiidae	–	–	–	–	–	–	–	–	
Total endemic species	1,020	225	502	344	279	167	13	8	2,558
Total species (Table 1)	1,204	347	561	405	381	205	29	17	2,814
Proportion of endemics	84.7%	64.8%	89.5%	84.9%	73.2%	81.5%	44.8%	47.1%	90.9

PA: Palaearctic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

the faunal exchange that took place between North and South America after the closure of the Panama gap. The Oriental to Australasian link may indicate the main dispersal route of the freshwater colonists of Australia. There is also a relatively strong link between Palaearctic and Oriental regions, which may reflect the weakness of the barrier separating

these regions, particularly in central and eastern China. The link between Antarctic and Neotropical regions is strong—10 out of the 17 species present in the Antarctic are shared with the Neotropics. These are mainly centropagids and cyclopids that are distributed from the Falklands to the circum-Antarctic islands. This faunal link is not identified by

**Table 4** Faunal links between zoogeographic regions estimated using Sørensen's index, based on species-level data: values exceeding 0.1000 shown in bold

	PA	NA	AT	NT	OL	AU	PAC
NA	<b>0.1251</b>						
AT	0.0646	0.0771					
NT	0.0453	<b>0.1101</b>	0.0621				
OL	0.0984	0.0769	0.0941	0.0679			
AU	0.0397	0.0507	0.0623	0.0574	<b>0.1058</b>		
PAC	0.0162	0.0319	0.0461	0.0407	0.0585	0.0684	
ANT	0.0066	0.0275	0.0190	0.0346	0.0101	0.0270	0.0435

Sørensen's Index, given the paucity of the Antarctic fauna relative to the Neotropical.

### Introduced species

There are numerous examples of introduced species from all life styles, planktonic to parasitic. In free-living copepods, at least 18 species have been involved in intercontinental introduction (Reid & Pinto-Coelho, 1994). The translocation of fish stocks for aquaculture has been implicated in the introduction of parasites such as *Paraergasilus longidigitus*, *Neoergasilus japonicus* and *Lernaea cyprinacea* (Fig. 1H) Introductions have also been associated with the transportation of tropical plants for horticulture and agriculture. For example, the presence of the Asiatic centropagid *Boeckella triarticulata* in Italy was attributed to movement of Chinese carp, the introduction of *Mesocyclops ogunnus* to the Cayman Islands and Brazil may have resulted from transportation of organisms for aquaculture, and it has been suggested that *M. pepheiensis* (as *M. ruttneri*), an East-Asian species, was introduced to the southern USA by rice culture. The uncontrolled exchange of ballast water has been implicated in the introduction of estuarine taxa, including *Limnoithona*, *Sinocalanus*, *Pseudodiaptomus* and *Acartia*.

### Human related issues

Copepods act as intermediate hosts for a variety of parasites. Species of *Mesocyclops* and *Thermocyclops* are intermediate hosts for guineaworm (*Dracunculus medinensis*), a debilitating nematode parasite.

Guineaworm larvae are consumed by copepods and remain in the body cavity until ingested by drinking unfiltered water. Guineaworm is less prevalent than in the past but remains a human health problem, particularly in West Africa and India. Other parasites of man that utilize copepods as intermediate hosts include the fish tapeworm, *Diphyllobothrium latum*.

Parasitic copepods such as *Lernaea cyprinacea* and *Ergasilus sieboldi* can be serious pests, causing mass mortality and significant commercial losses in freshwater aquaculture. They are often found in inconspicuous microhabitats on the host and may be overlooked in fish quarantine checks. Translocation of fish stocks, without sufficient checks, is responsible for the widespread introduction of these pests outside of their natural ranges.

Free-living copepods can be voracious predators and this functional role has been exploited in the use of *Mesocyclops* species as biological control agents against mosquitoes. The spread of diseases such as malaria and dengue fever involves mosquito vectors and *Mesocyclops* have been experimentally trialled as a biocontrol agent for mosquito larvae. The success of these trials has been variable, but in Viet Nam for example, *Mesocyclops* has been used effectively in controlling mosquito larvae at local levels.

Desertification and the overexploitation of ground water are major conservation issues for copepods. Groundwater copepods, especially those with narrow geographical distributions, are at risk from intrusion of saline waters as the groundwater table is lowered.

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