

Biodiversity and biogeography of Antarctic copepods

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Abstract: A census of pelagic copepods identifies 346 species from 38 families (i.e. 16.7% of all copepods). Among them, 289 species are considered "cosmopolitan" and 57 "endemic". Most of the species were described in the late 19th or early 20th century. However, due to a resurgence of interest in biological diversity, a large number of exhaustive revisions at various taxonomic levels have recently been initiated. One hundred and thirteen documents covering the census and distribution of copepod species are analysed. The distribution of species in the South Seas is given for 24 sectors chosen in relation to the geographical coordinates of the South Atlantic, South Pacific and Southern Indian oceans and their location with respect to the Antarctic Convergence or the continental shelf. The respective roles of Lagrangian displacement, of the hydrological features characterising the Southern Ocean and of the general ocean currents are emphasised to explain the scattered distributions of the species. Twenty-one species are catalogued as bipolar, 46 species as specifically sub-Antarctic and 222 cosmopolitan ones are probably from sub-tropical/temperate regions.

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Introduction

Interest in biological diversity is reviving, but as pointed out by Williamson (1998) marine biodiversity remains poorly investigated, with the number of marine studies representing only a small proportion (*c.* 5%) of terrestrial studies. While the diversity of benthic Antarctic fauna may be considered from an evolutionary point of view thanks to paleogeographical studies (Crame 1994), it is still not possible to carry out a census of the zoobenthos. Likewise, the planktonic faunal communities are at the first step in the perception of biodiversity: the numeration of species, with an attempt to localise both their precise distribution around the Southern Ocean and, if possible, their geographical origin.

The role of spatial heterogeneity in regulating diversity in the sea may be highlighted with the pelagic communities of copepods. Their locations remain a problem, in relation to their Lagrangian displacement, as the circulation patterns control the dynamics of all zooplankton populations in the Southern Ocean (Huntley & Niiler 1995). Moreover, our knowledge of pelagic biodiversity is gleaned from sampling during oceanographic surveys, which makes it discontinuous and dependent on available sampling gear. There is also the absence of quantitative data concerning the numerical abundance of the species. Indeed, the 113 documents used for the evaluation of biodiversity in Antarctic copepods are qualitative and many are devoted to systematics. In contrast, only the more numerous species are considered for studies focussing on ecology, physiology or the energy balance.

A short review of hydrological features

No biogeographical distribution of pelagic communities around the Antarctic can be understood without reference to the three

main hydrological traits of the Southern Ocean – circumpolar currents, hydrological fronts and gyres – and to their link with shelf seas, the ice-shelf and island topography. These unusual features may possibly provide biotope-refuges for neritic species.

Water-mass circulation is governed by a complex system of hydrological fronts: the sub-tropical front (STF; 45°S), the sub-Antarctic Front (SAF), the Polar Front or Antarctic Convergence (PF or AC; 50°S) and the Antarctic divergence (AD; 65°S). Between the Polar Front and the Antarctic Divergence, waters are displaced eastwards by the Antarctic Circumpolar Current (ACC) at a mean speed of 0.5 knots, while south of the AD, a counter-current drifts westwards (Fig. 1). These fronts correspond to clear-cut frontier zones between well-identified water bodies, at least in the upper few hundred metres. Indeed, at different bathymetric levels, several physical and chemical properties characterize waters originating from different places (Fig. 2).

In Polar Front zones the water bodies flow in parallel, slightly meandering currents, facilitating cross-frontal interleaving and advective mixing processes, such as internal storm-generated waves and eddies that are a dynamic factor in the shearing and injection of waters (Park & Gamberoni 1997).

The occurrence of gyres is another characteristic of Antarctic circulation (Fig. 1). The largest is the Weddell–Scotia Sea gyre, with a 1700 km circumference, moving slowly eastwards and then vertically downwards in a movement associated with the westward-flowing counter-current along the continental slope, entering Drake Passage and the South Pacific Basin.

In the Ross Sea the water masses, hampered by the southward invasion of warm-water components of the circumpolar deep water, do not extend northwards from under the ice shelf (Fontaine 1988).

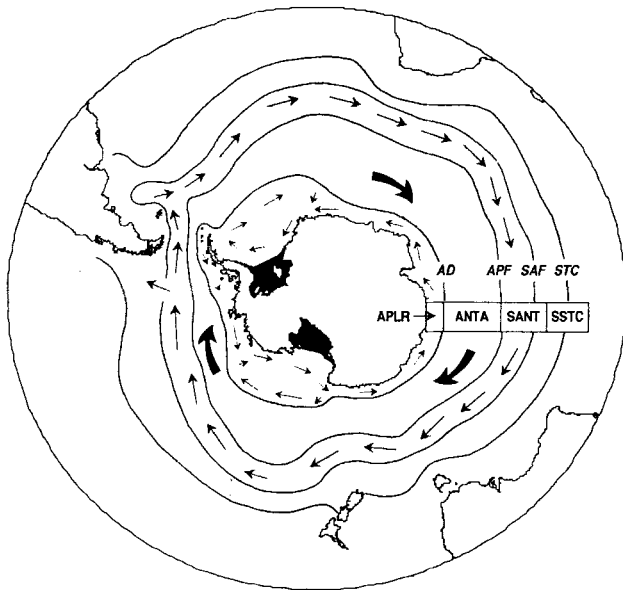


Fig. 1. Diagram of oceanography in the Southern Ocean (from Longhurst 1988, p. 341; reproduced with the permission of Academic Press).

So pelagic copepods have to cope with current trajectories, the mixing of waters and vertical transition waters of different origin (Ansorge *et al.* 1999).

Census of copepods

According to Van der Spoel & Heyman (1983), radiation of the sub-Antarctic and Antarctic species may well have occurred during the Miocene. The ecological radiation schemes proposed in the last ten years have hypothesized a marine, epibenthic origin followed by the colonization of the open pelagic environment. At the Family level, several phylogenies have been proposed, all grounded on morphological or anatomical characters such as cuticular pore signatures (Mauchline 1988, Fleminger & Hülsemann 1987) or the structure of the spermatheca (Cuoc *et al.* 1997, Barthélémy *et al.* 1998). Molecular genetics is now being used to confirm speciation within certain genera (Bucklin *et al.* 1995).

The number of species

It is useful to remind ecologists that when publishing the names of species they should be followed by the naming authorities. This is often lacking in ecological papers, which can lead to misinterpretation of geographical distribution.

The most recent world-wide census of copepods reports 2075 species (Razouls & De Bovée). Of these, 346 species (i.e. 16.7% of all species) are considered to be Antarctic; 83.7% of them (289 species) are cosmopolitan and 16.5% (57 species) are endemic, either to the whole Southern Ocean or to certain restricted zones.

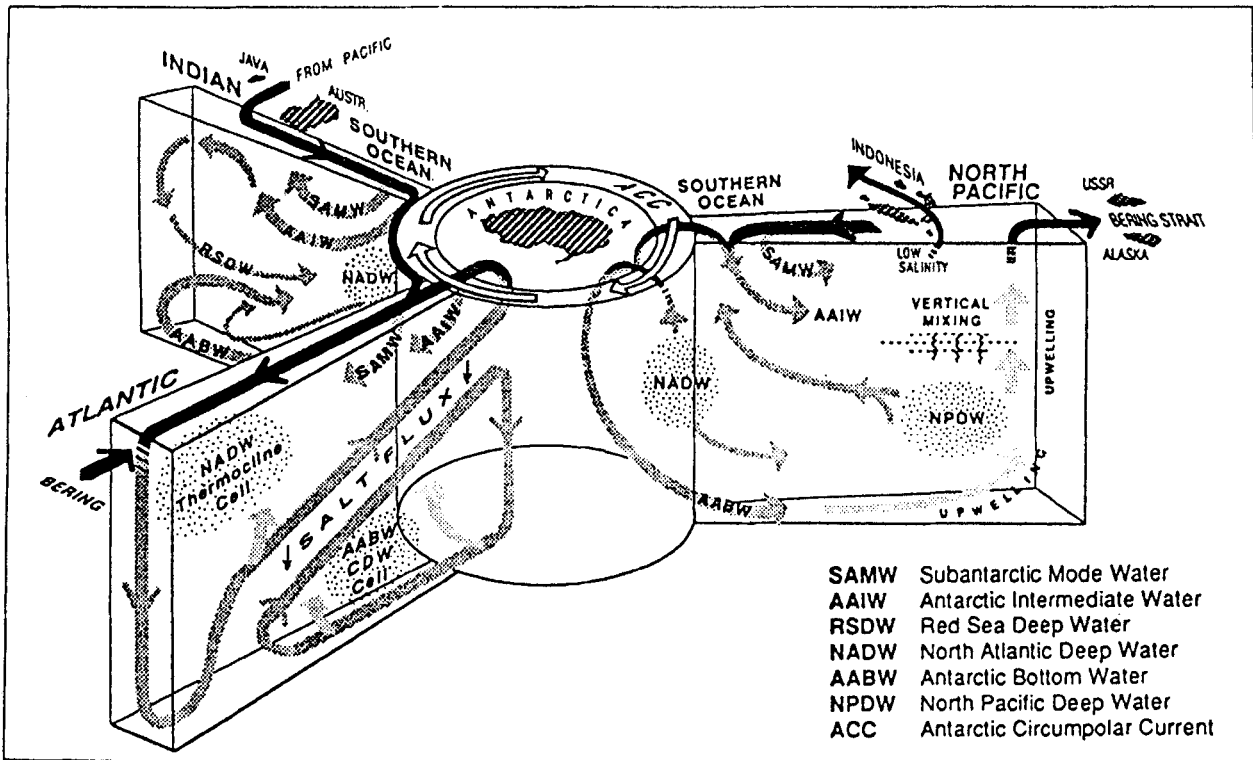


Fig. 2. Map of the global thermohaline circulation (from Gordon 1992 in Jean-Baptiste 1994; reproduced with permission of the Editor of *Oceanus*).

All species sampled in the Southern Ocean *sensu lato* (from 45°S latitude (STF) to ice-edge) are considered to be Antarctic. Copepods belong to 38 families: 26 Calanoida, 1 Cyclopoida, 4 Poecilostomatoida (Appendix). Antarctic copepods constitute about 66% of the carbon biomass in the Antarctic Polar Biome (Longhurst 1998), but in some sub-Antarctic fjords, a single species of copepod may represent 90–100% of the meso-zooplankton (Razouls *et al.* 1997). However, the likelihood of finding a given species in a particular part of the Antarctic Ocean is highly variable, as shown in Table I.

A large number of families, genera and species have been revised since the initial descriptions. Most of the descriptions and localities were published in the late 19th or early 20th century: 189 species from 1843 to 1909, 85 between 1910 and 1969, 72 in the last thirty years (Fig. 3)

Up to 1939, oceanographic expeditions provided the bulk of the new species described.

Since the 1970s, the biodiversity of Antarctic copepods in collections has been under reappraisal, initially by the revision of systematics at each taxonomic level: Heron (1977) revised the Oncaeidae; T. Park (1978–93) investigated several families (Aetideidae, Euchaetidae, Phaennidae) or genera and Markhasaeva (1996) the Aetideidae family.

In 1996 Schulz (Schulz 1996a, 1996b) described two new pelagic Antarctic copepod species: *Mospicalanus schielae*, which is bathypelagic and *Frigocalanus rauscherti*, which is hyperbenthic.

Some species included in the Antarctic list are still under review in relation to the complexity of the nomenclature, the definition of endemism for pelagic communities and the population concept, due to the difficulty in defining their distribution.

Population concept in zooplankton assemblages

Any individual is presumed to be a member of its own population, defined as individuals living together and able to interbreed. But, due to physical effects or biological behaviour, members of a population may drift away and be removed for the population. Conversely new migrants may be integrated into a local population. As a result of previous temperature conditions or development, animals from different water

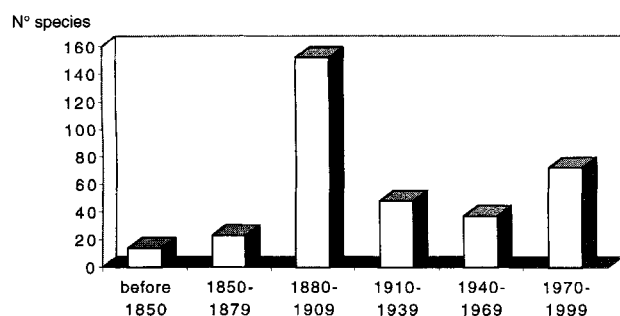


Fig. 3. Number of copepod species described from earliest times to 1999.

Table I. Number of species in the 24 zones defined in this paper.

No of species	No of zones containing all these species
11	20–24
38	11–19
53	6–10
138	2–5
106	1

masses may be identified by differences in individual size and reproductive state, resulting in distinct cohorts of different ages (Ottestad 1932).

A population may also be permanently modified by transport in water masses, facilitating gene flow. Such disruptive individual distribution may lead to the occurrence of species over widespread biogeographical regions.

Definition of endemism for pelagic copepods

Fifty seven species are recognised as endemic (Table II), but they do not all have the same status in terms of endemism:

Four are known only north of the AC: *Euaugaptilus brevirostratus* (PSE, ISE), *Calocalanus antarcticus* and *Calocalanus fiolentus* (ISW), *Amallothrix pseudopropinqua* (PSW, PSE, ISE).

Fourteen are found in the vicinity of the AC (north or south) *Calanoides acutus*, *Drepanopus pectinatus*, *Onchocalanus trigoniceps*, *Onchocalanus wolfendeni*, *Amallothrix hadrosoma*, *Amallothrix parafalcifer*, *Mixtocalanus vervoorti*, *Scaphocalanus antarcticus*, *Scaphocalanus parantarcticus*, *Scaphocalanus vervoorti*, *Scolecithricella cenotelis*, *Scolecithricella schizosoma*, *Oncaea illgi*, *Oncaea macilenta*.

Thirty-nine others have been recorded only south of the AC.

Some of them are clearly associated with particular ecosystems, e.g.

a) the water layer under the ice, and the ice-shelf environment (23 endemic species, Table V). Some have been sampled all around the Antarctic continent, others have been described from only one zone: *Frigocalanus rauscherti* Schulz (South Shetland Islands), *Xanthocalanus harpagatus* Bradford and Wells, *Tharybis magna* Bradford and Wells (Ross Sea),

b) the brackish waters of Antarctic lakes (*Drepanopus bispinosus* Bayly),

c) the neritic-coastal waters around sub-Antarctic islands and fjords. *Drepanopus forcipatus* Giesbrecht inhabits the South Atlantic (Falkland Islands, South Orkney Islands and South Georgia) and SW Pacific. According to Hülsemann (1985a), the Polar Front zone represents an effective barrier to mixing of the two populations of this

Table II. Endemic species in the Pacific, Atlantic and Indian sectors of the Southern Ocean.

Species common to several Antarctic sectors	Species localized in one sector of the Southern Ocean		
	Pacific	Atlantic	Indian
<i>Paralabidocera antarctica</i>	*	*	*
	<i>Paralabidocera grandispina</i>		<i>Paralabidocera separabilis</i>
<i>Aetideopsis antarctica</i>	*		*
	<i>Chiridiella megadactyla</i>		<i>Batheuchaeta antarctica</i> <i>Batheuchaeta pubescens</i>
<i>Euaugaptilus austrimus</i>	*	*	<i>Pseudochirella formosa</i>
<i>Euaugaptilus brevirostratus</i>	*		*
	<i>Euaugaptilus hadrocephalus</i>		
<i>Calanoides acutus</i>	*	*	*
			<i>Drepanopus bispinosus</i>
<i>Drepanopus pectinatus</i>	*		*
<i>Paraeuchaeta austrina</i>	*	*	*
	<i>Paraeuchata erebi</i>		
<i>Paraeuchaeta similis</i>	*	*	*
	<i>Paraeuchaeta tycodesma</i>		
<i>Metridia andraeana</i>	*		<i>Heterorhabdus nigrotinctus</i>
			*
			<i>Metridia trispinosa</i> <i>Calocalanus antarcticus</i> <i>Calocalanus violentus</i>
<i>Onchocalanus paratrigoniceps</i>	*		*
<i>Onchocalanus wolfendeni</i>	*	*	*
	<i>Xanthocalanus antarcticus</i>		
<i>Xanthocalanus gracilis</i>	*	*	*
	<i>Xanthocalanus harpagatus</i>		
			<i>Xanthocalanus tenuiserratus</i>
<i>Amalothrix hadrosoma</i>	*	*	
<i>Amalothrix parafalcifer</i>	*	*	*
<i>Amalothrix pseudopropinqua</i>	*		*
<i>Landrumius antarcticus</i>	*	*	
<i>Mixtocalanus vervoorti</i>	*		*
<i>Scaphocalanus antarcticus</i>	*	*	*
<i>Scaphocalanus parantarcticus</i>	*	*	*
<i>Scaphocalanus vervoorti</i>	*	*	*
<i>Scolecithricella cenotelis</i>	*	*	*
<i>Scolecithricella schizosoma</i>	*		*
	<i>Scolecithrix incisa</i>		
	<i>Mospicalanus schielae</i>		
<i>Stephos antarcticus</i>	*		*
			<i>Temora kerguelensis</i>
		<i>Neoscolecithrix antarctica</i>	
	<i>Tharybis magna</i>		
	<i>Conaea hispida</i>		
	<i>Conaea succurva</i>		
	<i>Oncaea bowmani</i>		
	<i>Oncaea brocha</i>		
	<i>Oncaea convexa</i>		
	<i>Oncaea damkaeri</i>		
	<i>Oncaea illgi</i>		
	<i>Oncaea macilenta</i>		
	<i>Oncaea olsoni</i>		
	<i>Oncaea petila</i>		
	<i>Oncaea walleni</i>		
	<i>Frigocalanus rauscherti</i>		
<i>n</i> = 23	<i>n</i> = 22	<i>n</i> = 1	<i>n</i> = 11

Table III. Localization of the sub-Antarctic species in the Pacific, Atlantic and Indian sectors of the Southern Ocean as a function of their situation with respect to the Antarctic Convergence.

Common species	Pacific sector	Atlantic sector	Indian sector
<i>Aetideus australis</i>	*	*	*
	<i>Acartia ensifera</i> N		
	<i>Aetideus pseudarmatus</i> N		
	<i>Aetideopsis tumorosa</i>		
<i>Euchirella latirostris</i> N	*		*
<i>Euchirella rostromagna</i>	*	*	*
<i>Euchirella similis</i> N	*		*
<i>Pseudochirella hirsuta</i>	*	*	*
<i>Pseudochirella mawsoni</i>	*	*	*
		<i>Euaugaptilus aliquantus</i> S	
<i>Euaugaptilus brevirostratus</i> N	*		*
	<i>Euaugaptilus perasetosus</i> S		
<i>Haloptilus ocellatus</i>	*	*	*
	<i>Calanoides macrocarinatus</i> N		
	<i>Calanoides patagoniensis</i> N		
<i>Calanus propinquus</i>	*	*	*
<i>Calanus simillimus</i>	*	*	*
<i>Candacia cheirura</i> N	*		*
<i>Candacia maxima</i>	*	*	*
<i>Clausocalanus brevipes</i>	*	*	*
	<i>Clausocalanus ingens</i> N		
<i>Clausocalanus laticeps</i>	*	*	*
<i>Ctenocalanus citer</i>	*	*	
<i>Drepanopus forcipatus</i>	*	*	
<i>Drepanopus pectinatus</i>	*		*
<i>Subeucalanus longiceps</i>	*		*
<i>Paraeuchaeta antarctica</i>	*	*	*
<i>Paraeuchaeta biloba</i>	*	*	*
	<i>Paraeuchaeta dactylifera</i>		
<i>Paraeuchaeta eltaninae</i> S	*	*	*
<i>Paraeuchaeta parvula</i>	*	*	*
<i>Paraeuchaeta rasa</i>	*	*	*
<i>Paraeuchaeta regalis</i>	*	*	*
<i>Heterorhabdus austrinus</i>	*	*	*
<i>Heterorhabdus farrani</i>	*	*	*
<i>Heterorhabdus pustulifer</i>	*	*	*
	<i>Lucicutia rara</i> N		
		<i>Bathycalanus eltaninae</i> S	
<i>Bathycalanus inflatus</i>	*	*	
		<i>Bradycalanus pseudotypicus</i> S	
<i>Metridia gerlachei</i>	*	*	*
			<i>Calocalanus antarcticus</i> N
			<i>Calocalanus fiolenti</i> N
			<i>Calocalanus longispinus</i> N
<i>Cornucalanus robustus</i>	*	*	*
<i>Amallothrix dentipes</i>	*	*	
<i>Amallothrix pseudopropinqua</i> N	*		*
<i>Stephos longipes</i> S	*	*	*
<i>Oithona frigida</i>	*	*	*
<i>Oncaea antarctica</i>	*	*	*
<i>Oncaea curvata</i>	*	*	*

Total species = 51

Endemic species (in bold) = 5

N = North AC, S = South AC, without N or S = North and South AC

Table IV. Geographical distribution of bipolar species.

	Pacific Ocean			Arctic Ocean	Atlantic Ocean			Indian Ocean Antarctic
	Antarctic	South Chile	North		North	South Brazil	Antarctic	
<i>Aetideopsis minor</i>	*			*		*	*	*
<i>Batheuchaeta peculiaris</i>	*		*					
<i>Chiridius polaris</i>	*		*			*		*
<i>Gaetanus paracurvicornis</i>		*	*		*			*
<i>Pseudochirella batillipa</i>	*		*	*		*		*
<i>Pseudochirella spectabilis</i>	*	*	*	*	*	*		*
<i>Augaptilus cornutus</i>			*		*			*
<i>Candacia falcifera</i>	*					*		*
<i>Epicalymma schmitti</i>	*		*	*	*			
<i>Epicalymma umbonata</i>	*		*	*	*			
<i>Lubbockia carinata</i>	*		*					
<i>Lubbockia flemingeri</i>	*		*					
<i>Lubbockia forcipula</i>	*		*					
<i>Lubbockia wilsonae</i>	*		*					*
<i>Oncaea lacinia</i>	*			*	*			
<i>Oncaea parila</i>	*		*	*	*			*
<i>Oncaea prolata</i>	*		*				*	
<i>Oncaea compacta</i>	*			*				
<i>Oncaea pumilis</i>	*			*				
<i>Spinocalanus horridus</i>	*		*	*	*		*	
<i>Spinocalanus antarcticus</i>				*			*	

species. Statistically significant differences found between populations from the coasts of Patagonia and South Georgia may indicate that these two populations are morphologically the same but genetically distinct. In contrast, *D. pectinatus* Brady is found only on the continental shelf of the South Indian Ocean (Crozet, Kerguelen, Heard islands). Its absence from Prince Edward and Marion islands supports the supposition that these islands constitute a separate province (Briggs 1974).

Cosmopolitan species

Among the 289 cosmopolitan species, the most typically sub-antarctic or amphiboreal ones were classified using the matrix of the world-wide distribution of copepods (Razouls & de Bovée in press):

- 46 species are characteristic of the sub-Antarctic sector: 10 species occur only in the NAC area, 6 only in the SAC and 30 are found throughout the AC (Table III). The criterion for decision to identify species as sub-Antarctic is founded on their wide distribution and where they are thought to originate: the South Atlantic areas (South Africa E & W, central South Atlantic, off Brazil-Argentina), the South Indian Ocean or the South Pacific zones (Eastern Australia, Chile–Juan Fernandez cluster).
- 21 species are amphiboreal. These copepods, restricted to northern parts in the Northern Hemisphere (Arctic Ocean, northern part of Atlantic and Pacific oceans), seem also to inhabit great depths in the Antarctic region. Among them, only one, *Spinocalanus antarcticus* Wolfenden is bipolar, dwelling exclusively in the northern

Arctic Basin and in the Antarctic (SE Indian Ocean and SE ice edge, Weddell Sea). Yamanaka (1976) suggests that the bipolar distribution of species may be due to a remnant community from deep water, or even from bottom water, flowing to the South from the Atlantic and Indian Oceans (Table IV).

c) 91 species live occasionally in an ice environment (Table V).

Indistinct geographic distribution

The distribution of cosmopolitan copepods (289 species) inhabiting the Southern Ocean, is shown on the map (Fig. 4). With the exception of the endemic species (57), the amphiboreal species (21) and the sub-Antarctic species (46) the 222 remaining species may well be from sub-tropical and/or temperate zones (Razouls & de Bovée in press).

Classifying copepods by their hydro-geographical zone

The distributions of the various Antarctic copepod species have been identified in terms of 24 arbitrarily-defined geographical zones in the Southern Ocean, defined on the basis of two criteria: a) the geographical provinces - eastern, southern, western - of the Atlantic, Indian, and Pacific oceans, and b) the areas around the Antarctic continent Longhurst (1998):

- the sub-Antarctic area, or sub-Antarctic water ring province, north of the Antarctic Convergence area (NAC) is only characterized by gradients of temperature and salinities and is the most imprecise to localize (Saint-

Table V. Localisation of copepods sampled in an ice-environment.

	Ross Sea	McMurdo area	Weddell ice	Indian cont		Ross Sea	McMurdo area	Weddell ice	Indian cont
<i>Paralabidocera antarctica</i>	*	*	*	*	<i>Bathycalanus princeps</i>				*
<i>Paralabidocera grandispina</i>	*	*			<i>Bathycalanus richardi</i>			*	
<i>Aetideopsis antarctica</i>	*	*		*	<i>Megacalanus princeps</i>				*
<i>Aetideopsis minor</i>	*	*	*	*	<i>Metridia curticauda</i>	*		*	*
<i>Aetideopsis rostrata</i>			*		<i>Metridia gerlachei</i>	*	*	*	*
<i>Bradyidius armatus</i>				*	<i>Metridia lucens</i>				*
<i>Chiridiella megadactyla</i>	*				<i>Metridia princeps</i>	*	*		*
<i>Chiridius polaris</i>				*	<i>Pleuromamma gracilis</i>	*			
<i>Euchirella rostromagna</i>			*	*	<i>Cephalophanes frigidus</i>				*
<i>Gaetanus antarcticus</i>		*	*	*	<i>Cornucalanus chelifer</i>				*
<i>Gaetanus intermedius</i>			*		<i>Onchocalanus magnus</i>	*			*
<i>Gaidius brevispinus</i>				*	<i>Onchocalanus trigoniceps</i>			*	
<i>Gaidius pungens</i>			*		<i>Onchocalanus wolfendeni</i>	*	*	*	*
<i>Gaidius tenuispinus</i>	*	*	*	*	<i>Xanthocalanus antarcticus</i>		*		
<i>Pseudochirella hirsuta</i>				*	<i>Xanthocalanus gracilis</i>				*
<i>Pseudochirella spectabilis</i>				*	<i>Xanthocalanus harpagatus</i>	*			
<i>Augaptilus cornutus</i>				*	<i>Xanthocalanus tenuiserratus</i>				*
<i>Augaptilus glacialis</i>			*		<i>Labidocera acutifrons</i>				*
<i>Euauaptilus laticeps</i>			*		<i>Amalothrix dentipes</i>	*			
<i>Euauaptilus placitus</i>				*	<i>Amalothrix emarginata</i>				*
<i>Haloptilus acutifrons</i>			*		<i>Amalothrix parafalcifer</i>			*	
<i>Haloptilus longicornis</i>				*	<i>Racovitzanus antarcticus</i>	*	*	*	*
<i>Haloptilus ocellatus</i>	*	*	*	*	<i>Scaphocalanus affinis</i>			*	
<i>Haloptilus oxycephalus</i>	*		*		<i>Scaphocalanus antarcticus</i>			*	
<i>Pseudaugaptilus longiremis</i>			*		<i>Scaphocalanus farrani</i>	*		*	*
<i>Temorites brevis</i>			*	*	<i>Scaphocalanus impar</i>				*
<i>Calanoides acutus</i>	*	*	*	*	<i>Scaphocalanus magnus</i>			*	*
<i>Calanus propinquus</i>	*	*	*	*	<i>Scaphocalanus subbrevicornis</i>			*	*
<i>Calanus simillimus</i>		*		*	<i>Scaphocalanus verwoorti</i>		*	*	
<i>Neocalanus tonsus</i>		*			<i>Scolecithricella cenotelis</i>			*	
<i>Candacia maxima</i>	*				<i>Scolecithricella minor (= glacialis)</i>	*	*	*	*
<i>Clausocalanus brevipes</i>			*		<i>Scolecithrix incisa</i>	*			
<i>Clausocalanus laticeps</i>			*		<i>Mimocalanus cultrifer</i>			*	
<i>Ctenocalanus citer</i>		*	*	*	<i>Spinocalanus abyssalis</i>	*		*	*
<i>Ctenocalanus vanus</i>	*	*	*	*	<i>Spinocalanus antarcticus</i>			*	*
<i>Drepanopus bispinosus</i>				*	<i>Spinocalanus magnus</i>	*		*	*
<i>Farrania frigida</i>	*		*	*	<i>Teneriforma naso</i>			*	
<i>Microcalanus pusillus</i>		*		*	<i>Stephos antarcticus</i>		*		*
<i>Microcalanus pygmaeus</i>	*	*	*	*	<i>Stephos longipes</i>	*	*	*	*
<i>Rhincalanus gigas</i>	*	*	*	*	<i>Tharybis magna</i>	*			
<i>Paraeuchaeta antarctica</i>	*	*	*	*	<i>Mormonilla phasma</i>			*	
<i>Paraeuchaeta austrina</i>	*	*		*	<i>Oithona frigida</i>	*	*	*	*
<i>Paraeuchaeta biloba</i>	*				<i>Oithona similis</i>	*	*	*	*
<i>Paraeuchaeta erebi</i>	*	*			<i>Corycaeus (Agetus) flaccus</i>	*			
<i>Paraeuchaeta rasa</i>			*		<i>Corycaeus (Urocorycaeus) furcifer</i>	*			
<i>Paraeuchaeta similis</i>	*	*		*	<i>Farranula gracilis</i>	*			
<i>Paraeuchaeta tycodesma</i>	*	*			<i>Epicalymma schmitti</i>			*	
<i>Heterorhabdus austrinus</i>	*		*	*	<i>Lubbockia aculeata</i>			*	
<i>Heterorhabdus farrani</i>	*		*	*	<i>Oncaea antarctica</i>		*	*	
<i>Heterorhabdus pustulifer</i>	*				<i>Oncaea confiera</i>	*		*	*
<i>Heterostylites longicornis</i>		*		*	<i>Oncaea convexa</i>			*	
<i>Heterostylites major</i>	*			*	<i>Oncaea curvata</i>	*	*	*	*
<i>Lucicutia macrocera</i>	*		*		<i>Oncaea englishi</i>			*	
<i>Lucicutia magna</i>				*	<i>Oncaea parila</i>			*	
<i>Lucicutia ovalis</i>	*		*	*	<i>Oncaea prolata</i>			*	
<i>Lucicutia wolfendeni</i>			*	*	<i>Oncaea venusta</i>			*	*
<i>Bathycalanus bradyi</i>				*	<i>Sapphirina metallina</i>				*

endemic species in bold

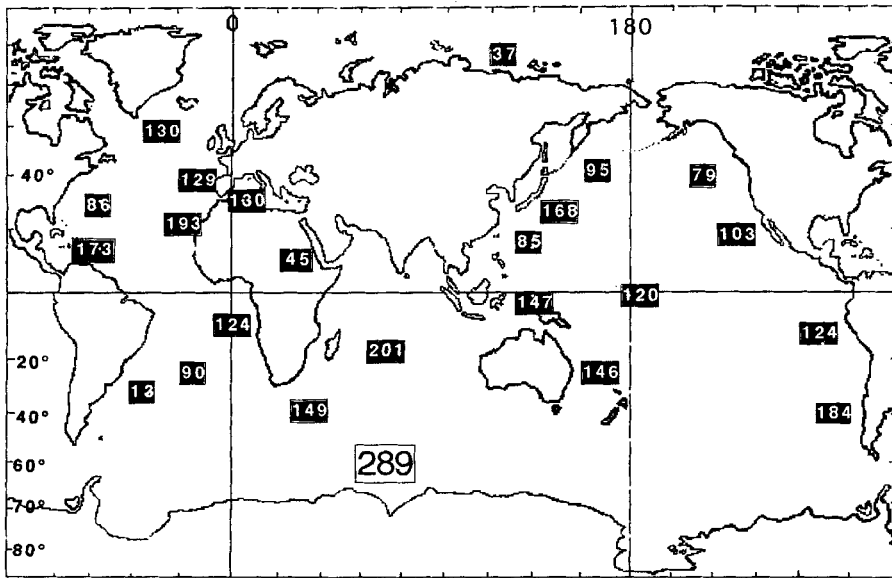


Fig. 4. Map of the origins of the 289 cosmopolitan copepod species found in the Southern Ocean. The labels give the number of species recorded both in the Southern Ocean and in others oceanic areas. The labels display the numbers of species common to the Southern Ocean and the other oceanic zones where they have been recorded. Except for the Antarctic, the common species have been numbered in each of their areas, independently from how many areas they belong to.

Gaily 1991). Its northern limit has been fixed here at 45°S, to take into account both the communities extending into the Polar Front and those spreading north to the sub-Antarctic Front (SAF) and on to the sub-tropical Front (STF), or the reverse, as seen for Coccolithophores in the Weddell Sea transported from sub-tropical waters (Winter *et al.* 1999).

- ii) the Antarctic Province, south of the Antarctic Convergence area (SAC), in the whole zone of the ACC. Whenever possible, precise localizations have been taken into account: the Antarctic Peninsula and Drake Passage, Ross and Weddell seas.
- iii) the Continental Ice border, represented by areas of the continental ice-shelf or ice-seawater (McMurdo, south and south-western shelves of Indian Ocean).

The number of recorded species is far from uniform in the different sectors, and records are lacking in three NAC sectors (southern and south-eastern Atlantic, South Pacific) (Table VI).

Factorial Correspondence Analysis (Fig. 5) was applied to the presence-absence matrix built from the 346 planktonic copepod species encountered in the 24 zones of the Antarctic Province identified above. The figure shows the plane defined by the second and third axes of the analysis.

The first axis is not represented because it separates the ISWN area (North Convergence part of the south-west Indian Ocean) from all the other areas on the basis of the high diversity of *Calocalanus* spp. - 13 species were studied by Shmeleva (1978) in these areas alone. Consequently it supplies little information on the biogeographical distribution of copepod species.

The axis-2/axis-3 plane clearly indicates a distribution of areas from the southern part of all the oceans (Pacific (PSS),

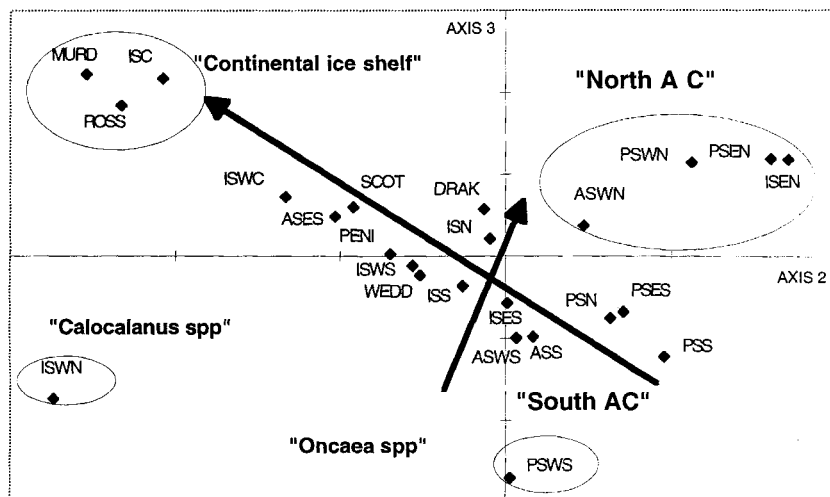


Fig. 5. Factorial correspondence analysis between species and the 24 identified areas. WEDD = Weddell Sea, ROSS = Ross Sea, MURD = McMurdo area, SCOT = Scotia Sea, PENI = Peninsula, DRAK = Drake Passage, A = Atlantic, P = Pacific, I = Indian. The next letter indicates the oceanic sector: SW, S, SE, NW, N, NE. The last letter (N, S, C) indicates the position: north, south (of the Antarctic Convergence) or continental (close to/under the continental ice shelf).

Atlantic (ASS); Indian (ISES). The plane is separated in two directions: the first north of the Antarctic Convergence of all the oceans (PSEN, ISEN, ASWN), and the second indicating a continental gradient to the Weddell and Scotia Seas, Peninsula or the nearest part of the ocean to the Antarctic continent (ISC and ISWC). *Calocalanus* spp. was found once again (ISWN) and in the southern part *Oncaea* spp (PSWS) was identified thanks to the expertise of Heron (1977) on the *Eltanin* cruises. This indicates the bias occurring in biodiversity studies due to the preponderance of the best-known genus and to the lack of quantitative data on their abundance or densities.

If we accept the Polar Front as the southern limit of the sub-Antarctic sector, some ambiguities arise:

- a) As shown by the list of the sub-Antarctic copepods originating in subtropical areas, a species may be found on both sides of the Polar Front (AC). One example is *Drepanopus pectinatus*, which is endemic to the continental shelf of Crozet, Heard and Kerguelen islands and is found both north and south of the AC, but always in fjords, in the neritic sector. It is considered a sub-Antarctic species.
- b) In the western South Pacific, *Acartia ensifera* or *Centropages aucklandicus*, known to be endemic and neritic in New Zealand, are believed to follow the West Wind Drift circulation because of the northern displacement of the sub-tropical convergence. They have been counted among the sub-Antarctic species, although their core records are sub-tropical.
- c) In contrast, the species of *Euaugaptilus* and *Bathycalanus* from sub-tropical origin, are found only in the bathypelagic zone south of the AC.

The distribution patterns of copepods reflect the discontinuity in space and time of the sampling effort and of the patchy sampling area. Relevant information about the geographical distribution of pelagic copepods should also include the sampling methods used. Sampling is usually done by vertical or oblique hauls, which means that the optimum depth, if any, for copepod species is rarely identifiable (Appendix). Depth preferences have to be treated with caution for several reasons. Some are biological and due either to diel vertical migration, or to seasonal and ontogenic features. Some of the most numerous species (*Calanoides acutus*, *Rhincalanus gigas*, *Calanus propinquus*), termed interzonal by Zmijewska (1987), make such excursions, preferring deeper water in winter and surface water in summer. Other reasons are linked to hydrological facts, as pointed out by Huntley & Nüller (1995): "the circulation of the ocean may act either as a dispersive or cohesive force on the population" and more recently by Angel (1998) who highlights the role of physical control on zooplanktonic communities.

Table VI. Number of species localised in each of the 24 defined oceanic sectors.

NAC		SAC	
General	Particular	General	Particular
Pacific SW: 103		127	Ross Sea: 50 McMurdo: 35
Pacific S: 4		60	
Pacific SE: 153		96	
	Drake: 53		Peninsula: 79 Scotia: 35 Weddell: 81
Atlantic SW: 55		108	
Atlantic S: -		64	
Atlantic SE: -		19	
Indian SW: 50		68	Ice shelf: 18
Indian S: 75		104	Ice shelf: 68
Indian SE: 115		93	

NAC / SAC = North / South of the Antarctic Convergence

Biological/physiological constraints

Due to the physiological stress generated by low temperatures and the episodic scarcity of their algal food supply, it is likely that cosmopolitan species introduced into the Antarctic environment do not accomplish their entire life cycle there. Because they are out of their core region, and in borderline conditions, they can survive but not reproduce. Of the 289 cosmopolitan species found in the southern oceans, only 14 are common in the Antarctic.

The most relevant features are their life-span and life cycle. The highly seasonal changes in their hydrological and feeding environments affect the life-span and reproductive effort of species, particularly of those living in ice-covered water.

Most of the zooplankton in the Weddell Sea probably complete their life cycle within the gyre (Hopkins & Torres 1988). Spawning generally takes place in spring and summer. The development of young stages, depending on temperature, last several months. They either reach adulthood in the same year, e.g. *Paralabidocera antarctica* (Tanimura *et al.* 1996) and *Stephos longipes* (Kurbjeweit *et al.* 1993), or they enter diapause during the winter period, often migrating to deep water. In this case, they achieve their last moult and reach adulthood during the following summer, as in *Rhincalanus gigas* or *Calanoides acutus* (Atkinson 1998). Other ways for copepods to adapt to a cold environment include the production of lipid reserves (Hagen *et al.* 1993) and change from strictly herbivorous feeding habits to opportunistic omnivory (Hopkins *et al.* 1993).

Conclusions

The aim of this paper was to review current understanding of the Antarctic copepod biodiversity. This synthesis shows that we probably do not know all the species of pelagic copepods dwelling in peculiar ecosystems such as very deep waters or the epi-benthos.

The ecological affinities and the relative abundances of

small species as defined in Atkinson's synthesis (1999) for the Scotia Sea highlight the specific distribution in relation to mesoscale hydrologic conditions. But for many other species of the Southern Ocean we have only few data, if any. An intensive collection and compilation of data from an extensive literature survey is needed.

The biodiversity and biogeography of pelagic Antarctic copepods is linked to movements of water masses at different scales of time and space. Knowledge of the biodiversity of Antarctic mesozooplankton needs improvement of the taxonomic knowledge of copepods using conventional as well as new biomolecular tools.

Gene flow in populations is probably ensured by the permanent circulation of currents (West Wind Drift and East Wind Currents), associated with the circulation of deep water masses, and the mixing zones born from meanders and gyres in the frontal zones. Zooplankton experience these different water masses during their specific vertical migrations (nycthemeral, seasonal or ontogenic) and may be trapped inside them and transported away from their core regions.

The deep or intermediate currents, as well as the Antarctic wind drifts, seem the most probable agents of distribution of Antarctic copepods. Indeed, the distribution of Antarctic copepods is probably related to the opening of the Drake Passage (about 90 m.y.a.) and to circumpolar oceanic circulation.

The next step in the study of copepods must be the detailed investigation of certain target species with regard to:

- a) speciation, comparing the genetic structure of true populations clearly geographically distinct, but belonging to the same genus, *Drepanopus bungei* (Arctic, Barentz Sea), *D. bispinosus* (brackish Antarctic lakes), *D. forcipatus* (Atlantic sub-Antarctic areas, Falkland Islands, southern Chile?), *D. pectinatus* (Indian neritic sector, Crozet, Heard and Kerguelen Plateau),
- b) the genetic structure of common species with a circum-Antarctic distribution, such as *Calanoides acutus*, *Calanus propinquus*, *Calanus simillimus*, *Metridia gerlachei*, *Rhincalanus gigas*, and
- c) research in upwelling areas of certain species, indicators of deep-water layers that may be allied to bipolar species.

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Appendix. Taxonomic list of Antarctic copepod species. (For references see end of Appendix)

Families	Sampling depth (m)	References
CALANOIDA		
Acartiidae		
<i>Acartia ensifera</i> Brady, 1899	0–200	19/20
<i>Paralabidocera antarctica</i> (Thompson, 1898)	0–100	13,22,27,28,29,33,44,49,50,56,84,91/92,93,94,95,97,98,105,111,113
<i>Paralabidocera grandispina</i> Waghorn, 1979	70	48,103
<i>Paralabidocera separabilis</i> Brodsky & Zvereva, 1976	cote-glacé	22
Aetideidae		
<i>Aetideopsis antarctica</i> (Wolfenden, 1908)	0–600–1000	14,27,40,41,104,106
<i>Aetideopsis minor</i> (Wolfenden 1908)	0–200–1000	13,16,23,27,40,42,43,53,61,64,89,97,98,103,105
<i>Aetideopsis multiserrata</i> (Wolfenden, 1904)	0–1000–3000	8,26,53,64
<i>Aetideopsis rostrata</i> Sars, 1903	0–300	11,53,64
<i>Aetideopsis tumorosa</i> Bradford, 1969	0–1000	53,64
<i>Aetideus arcuatus</i> (Vervoort, 1949)	0–1000	55,64,112
<i>Aetideus armatus</i> (Boeck, 1872)	0–600; 100–1000	8,19/20,24,25,26,27,36,37,74,75,83,86,98
<i>Aetideus australis</i> (Vervoort, 1957)	0–3000	3,16,55,62,64,90,98,103
<i>Aetideus bradyi</i> A.Scott, 1909	0–100	8
<i>Aetideus pseudarmatus</i> Bradford, 1971	0–200	16
<i>Batheuchaeta antarctica</i> Markhaseva, 1986	0–4000	53
<i>Batheuchaeta lamellata</i> Brodsky, 1950	0–3000	53
<i>Batheuchaeta peculiaris</i> Markhaseva, 1983	300	53
<i>Batheuchaeta pubescens</i> Markhaseva, 1986	0–4000	53
<i>Bradyidius armatus</i> Giesbrecht, 1897	3000	106
<i>Chiridiella megadactyla</i> Bradford, 1971	0–1000	13
<i>Chiridiella subaequalis</i> Grice & Hülsemann, 1965	600–1000	42,53
<i>Chiridius gracilis</i> Farran, 1908	0–1000	51,53,55,64,98
<i>Chiridius molestus</i> Tanaka, 1957	0–1000	55
<i>Chiridius polaris</i> Wolfenden, 1911	0–1000	27,53,64,98,106
<i>Chirundina streetsii</i> Giesbrecht, 1895	0–1000	53,64
<i>Euchirella latirostris</i> Farran, 1929	0–750	16,27,98
<i>Euchirella maxima</i> Wolfenden, 1905	0–300	64
<i>Euchirella rostrata</i> (Claus, 1866)	0–1000	8,16,27,37,64,51,62,74,86,89,98,100,106
<i>Euchirella rostromagna</i> Wolfenden, 1911	100–500–2000	8,11,16,27,40,42,43,49,50,61,64,80,89,90,97,98,103,109,111
<i>Euchirella similis</i> Wolfenden, 1911	400–2000	8,64,98
<i>Gaetanus antarcticus</i> Brady, 1918	600–1000+	8,19/20,27,37,40,42,53,64,98,105,106
<i>Gaetanus kruppi</i> Giesbrecht, 1903	0–800–2000	8,64
<i>Gaetanus latifrons</i> Sars, 1905	0–750	8,16,53,98
<i>Gaetanus minor</i> Farran, 1905	0–1000	64,98
<i>Gaetanus paracurvicornis</i> Brodsky, 1950	3000–5000	53
<i>Gaetanus pileatus</i> Farran, 1903	0–1000	8,53,64
<i>Gaetanus intermedius</i> Campbell, 1930/Wolfenden, 1905?	500–1000+	40,42,64
<i>Gaidius brevispinus</i> (Sars, 1901)	0–600; 100–1000	8,16,26,27,37,53,86,97,98,106,112
<i>Gaidius pungens</i> Giesbrecht, 1895	0–500	3,8,13,16,19/20,24,25,27,37,40,42,43,53,61,62,64,79,86,89,97,98,100,103,106
<i>Gaidius tenuispinus</i> (Sars, 1901)	100–1000+	112,111
<i>Pseudeuchaeta brevicauda</i> Sars, 1905	1000–2000	9,53,64,98,110
<i>Pseudochirella batillipa</i> Park, 1978	> 2000	53,64
<i>Pseudochirella dubia</i> (Sars, 1905)	7000	53
<i>Pseudochirella formosa</i> Markhaseva, 1989	0–3000	53
<i>Pseudochirella hirsuta</i> (Wolfenden, 1905)	500–1000+4000	8,27,37,40,42,53,64,98,106,110
<i>Pseudochirella mawsoni</i> Vervoort, 1957	–0–1000+	8,16,40,53,64,89,98
<i>Pseudochirella notacantha</i> (Sars, 1905)	0–750–1000+	27,37,53,98
<i>Pseudochirella obtusa</i> (Sars, 1905)	0–1000+	8,42,53,64
<i>Pseudochirella pustulifera</i> (Sars, 1905)	300–1000–5000	8,37,53,64
<i>Pseudochirella spectabilis</i> (Sars, 1900)	0–1000–5000	53,64,98,106
<i>Pseudochirella spinosa</i> (Wolfenden, 1905)	750–1000	37
<i>Undeuchaeta incisa</i> Esterly, 1911	0–1000+	64
<i>Undeuchaeta major</i> Giesbrecht, 1888	50–750–2000	8,27,37,98,110
<i>Undeuchaeta plumosa</i> (Lubbock, 1856)	750–0	8,16,27,83,98
<i>Valdiviella brevicornis</i> Sars, 1905	0–1000–4000	64,110
<i>Valdiviella insignis</i> Farran, 1908	1000–2000+4000	8,62,64,98,110
<i>Valdiviella minor</i> Wolfenden, 1911	0–2000	64

<i>Valdiviella oligarthra</i> Steuer, 1904	0–2000	64
Arietellidae		
<i>Arietellus simplex</i> Sars, 1905	300–600–1000	40,42,98
Augaptilidae		
<i>Augaptilus cornutus</i> Wolfenden, 1911	3000	106
<i>Augaptilus glacialis</i> Sars, 1900	500–1000	42,55,97,98
<i>Centraugaptilus rattrayi</i> (T.Scott, 1894)	250–750	8,37,40
<i>Euaugaptilus aliquantus</i> Park, 1993	0–2000	70
<i>Euaugaptilus angustus</i> (Sars, 1905)	0–1000	70
<i>Euaugaptilus austrinus</i> Park, 1993	0–1000–3000	70
<i>Euaugaptilus brevisrostratus</i> Park, 1993	0–1000–2000	70
<i>Euaugaptilus bullifer</i> (Giesbrecht, 1889)	0–2000	70
<i>Euaugaptilus gibbus</i> (Sars, 1905)	0–1000	70
<i>Euaugaptilus hadrocephalus</i> Park, 1993	0–1000	70
<i>Euaugaptilus laticeps</i> (Sars, 1905)	500–1000+	27,40,42,70,98
<i>Euaugaptilus magnus</i> (Wolfenden, 1904)	1500	8,70,98
<i>Euaugaptilus maxillaris</i> Sars, 1920	0–2000	70
<i>Euaugaptilus nodifrons</i> (Sars, 1905)	0–1000–3000	8,70
<i>Euaugaptilus oblongus</i> Sars, 1905	0–1200	70
<i>Euaugaptilus perasetosus</i> Park, 1993	0–3000	70
<i>Euaugaptilus placitus</i> (A. Scott, 1909)	1000–2000	106
<i>Haloptilus acutifrons</i> (Giesbrecht, 1892)	250–100	55,81/82,98,100
<i>Haloptilus fons</i> Farran, 1908	100–600	37,69
<i>Haloptilus longicirrus</i> Brodsky, 1950	0–600	69
<i>Haloptilus longicornis</i> (Claus, 1863)	2000	106
<i>Haloptilus ocellatus</i> Wolfenden, 1905	50–1000	11,13,19/20,27,37,40,42,45,49,50,61,62,69,79,83,89,90,91/92,97,98,105,106,109,111,112
<i>Haloptilus oxycephalus</i> (Giesbrecht, 1889)	0–1000	3,8,11,13,23,24,25,26,27,36,37,40,42,49,1,62,69,74,79,97,98,99,103,109,111,112
<i>Pachyptilus eurygnathus</i> Sars, 1920	500–900	8,42,98
<i>Pontoptilus ovalis</i> Sars, 1907	750–500	98
<i>Pseudaugaptilus longiremis</i> Sars, 1907	200–1000	42,98
Bathypontiidae		
<i>Temorites brevis</i> Sars, 1900	200–1000	40,42,98,106
Calanidae		
<i>Calanoides acutus</i> (Giesbrecht, 1902)	0–1000	2,3,6,8,11,13,15,23,24,26,27,29,32,34,36,37,40,41,42,43,45,48,49,50,52,57,60,61,68,71,75,81,83,84,86,89,90,91,97,98,99,103,105,106,107,108,109,111,112,113
<i>Calanoides carinatus</i> (Kröyer, 1848)	50	74,90,91/92,98
<i>Calanoides macrocarinatus</i> Brodsky, 1972	0–500	15
<i>Calanoides patagoniensis</i> Brady, 1883	0–200	1,19/20,51,55
<i>Calanus australis</i> Brodsky, 1959	0–1000	8,15,27,51,55,74
<i>Calanus propinquus</i> Brady, 1883	0–1000	3,6,8,11,13,19/20,23,24,26,27,29,34,36,37,40,41,42,43,45,48,49,50,52,57,60,61,62,69,71,73,74,75,82,83,86,89,90,92,93,95,97,98,99,103,104,105,106,108,109,111,112,113
<i>Calanus simillimus</i> Giesbrecht, 1902	0–600	2,3,8,10,15,24,26,27,37,43,49,50,51,55,57,60,62,72,76,83,86,90,91/92,97,98,103,105,106,108,109,111,112
<i>Mesocalanus tenuicornis</i> (Dana, 1849)	0–50	8,15,27
<i>Nannocalanus minor</i> (Claus, 1863)	0–600	8,19/20,51,85,91/92
<i>Neocalanus gracilis</i> (Dana, 1849)	100–750	27,98
<i>Neocalanus tonsus</i> (Brady, 1883)	0–500	8,15,19/20,27,51,55,83,90,91/92,98,105
Candaciidae		
<i>Candacia cheirura</i> Cleve, 1904	0–100	8,27,51,55,98
<i>Candacia falcifera</i> Farran, 1929	300–1000	27,37,40,42,89,97,98
<i>Candacia maxima</i> Vervoort, 1957	300–600	13,26,27,40,50,62,86,89,98,103,112
<i>Paracandacia simplex</i> (Giesbrecht, 1889)	0–1000	8
Centropagidae		
<i>Centropages aucklandicus</i> Krämer, 1895	0–10	27,91/92
<i>Centropages brachiatus</i> (Dana, 1849)	0–200	1,8,19/20,51,55,74,91/92
<i>Centropages bradyi</i> Wheeler, 1901	0–100	51,55,83,98
<i>Centropages furcatus</i> (Dana, 1849)	0–1200	8,27
Clausocalanidae		
<i>Clausocalanus brevipes</i> Frost & Fleminger, 1968	0–600	11,15,25,26,36,51,55,72,74,86
<i>Clausocalanus ingens</i> Frost & Fleminger, 1968	0–500	8,15,51,55
<i>Clausocalanus laticeps</i> T. Scott, 1864	500–700	3,8,11,15,24,25,26,27,36,37,50,51,55,62,74,75,83,84,86,90,91/92,98,103,108,109,111

<i>Clausocalanus pergens</i> Farran, 1926	250–100	83,98
<i>Ctenocalanus citer</i> Heron & Bowman, 1971	0–1000	11,25,26,31,32,40,42,48,50,55,56,95/96
<i>Ctenocalanus vanus</i> Giesbrecht, 1888	0–200	13,15,24,27,29,34,36,37,40,43,44,49,51,62,74,75,83,86,90,91/92,93,98, 104,105,106,107,109,111,112,113
<i>Drepanopus bispinosus</i> Bayly, 1882	(lake 0–10)	5,95/96,102,
<i>Drepanopus forcipatus</i> Giesbrecht, 1888	(neritic) 0–250	4,5,8,23,37,46,50,51,55,60,74,82,103
<i>Drepanopus pectinatus</i> Brady, 1883	(neritic) 0–250	5,15,19/20,25,26,46,76,77,86,98
<i>Farrania frigida</i> (Wolfenden, 1911)	500–1000	13,27,37,40,42,97,98,106,112
<i>Microcalanus pusillus</i> Sars, 1903	0–350	105,106
<i>Microcalanus pygmaeus</i> (Sars, 1900)	0–1000	10,13,15,25,26,27,34,37,40,42,43,48,55,56,57,61,72,83,89,91/92,93,98, 103,109, 111,112,113
Eucalanidae		
<i>Eucalanus hyalinus</i> (Claus, 1866)	100–2500	8,15,37,55,74,85,98,106
<i>Rhincalanus gigas</i> Brady, 1883	0–100–1000–4000	2,3,6,8,11,13,15,19/20,23,24,25/26,27,32,34,36,37,40,42,43,45,49,50,52, 57,60,61,62,71,72,74,75,81/82,86,89,90,91/92,97,98,103,105,106,107,108, 109,110,111,112,113
<i>Rhincalanus nasutus</i> Giesbrecht, 1888	0–500–4000	1,8,10,15,37,51,55,74,98,110
<i>Subeucalanus longiceps</i> (Matthews, 1925)	0–600	3,8,15,24,25,26,27,37,51,54,55,60,72,74,84,85,90,98,103,112
<i>Subeucalanus mucronatus</i> (Giesbrecht, 1888)	100	98
Euchaetidae		
<i>Euchaeta acuta</i> Giesbrecht, 1892	0–1000	98
<i>Paraeuchaeta aequatorialis</i> Tanaka, 1958	500–1000–3000	64,110
<i>Paraeuchaeta abbreviata</i> Park, 1978	0–1000+	64
<i>Paraeuchaeta antarctica</i> (Giesbrecht, 1902)	0–1000+4000	3,11,13,14,18,19/20,24,26,27,28,29,34,37,40,42,43,45,49,50,51,55,61,64, 71,73,75,77,83,86,89,90,97,98,103,105,106,108,109,110,111,113
<i>Paraeuchaeta austrina</i> (Giesbrecht, 1902)	500–700	14,28,34,42,84,98,106
<i>Paraeuchaeta barbata</i> (Brady, 1883)	0–700–1000+4000	18,27,37,40,42,64,98,110
<i>Paraeuchaeta biloba</i> Farran, 1929	0–500–1000+4000	18,26,27,28,37,40,55,64,86,89,98,103,110,111
<i>Paraeuchaeta calva</i> Tanaka, 1958	2000–3000	110
<i>Paraeuchaeta comosa</i> Tanaka, 1958	0–1000+	64
<i>Paraeuchaeta confusa</i> Tanaka, 1958	2000–3000	110
<i>Paraeuchaeta dactylifera</i> (Park, 1978)	0–1200+	18,64
<i>Paraeuchaeta eltaninae</i> (Park, 1978)	0–1000	18,64
<i>Paraeuchaeta erebi</i> Farran, 1929	0–800	14,27,28,40
<i>Paraeuchaeta exigua</i> (Wolfenden, 1911)	0–3000	25,26,49,62,64,98
<i>Paraeuchaeta hanseni</i> (With, 1915)	0–2000	64
<i>Paraeuchaeta kurilensis</i> Hepner, 1971	0–1000+	18,64
<i>Paraeuchaeta malayensis</i> Sewell, 1929	600–1000–4000	110
<i>Paraeuchaeta parvula</i> (Park, 1978)	0–1000+	18,64,89
<i>Paraeuchaeta pseudotonsa</i> (Fontaine, 1967)	0–2000–4000	18,64,110
<i>Paraeuchaeta rasa</i> Farran, 1929	0–600–4000	18,26,40,42,64,89,98,110
<i>Paraeuchaeta regalis</i> (Grice & Hülsemann, 1968)	0–1000+	18,64
<i>Paraeuchaeta sarsi</i> (Farran, 1908)	0–600–4000	18,64,110
<i>Paraeuchaeta scotti</i> (Farran, 1908)	0–600–4000	37,64,110
<i>Paraeuchaeta similis</i> (Wolfenden, 1908)	700–2000	13,14,27,28,40,64,98,105,106,110
<i>Paraeuchaeta tumidula</i> (Sars, 1905)	0–2000	18,64
<i>Paraeuchaeta tycodesma</i> (Park, 1978)	0–2000	14,28,64
Heterorhabdidae		
<i>Disseta palumboi</i> Giesbrecht, 1889	500–1000	37
<i>Heterorhabdus abyssalis</i> (Giesbrecht, 1889)	500–250	98
<i>Heterorhabdus austrinus</i> Giesbrecht, 1902	0–100–1000	8,13,19/20,24,26,27,34,36,37,40,42,43,50,49,61,74,79,81/82,86,89,97,98, 103,104,109,111,112,113
<i>Heterorhabdus clausi</i> (Giesbrecht, 1889)	750–0	98
<i>Heterorhabdus compactus</i> (Sars, 1900)	250–1000	27,37,40
<i>Heterorhabdus farrani</i> Brady, 1918	200–1000	8,13,19/20,26,27,40,42,43,61,62,83,86,90,91/92,97,98,106,112,111
<i>Heterorhabdus nigrotinctus</i> Brady, 1918	0–200	19/20
<i>Heterorhabdus papilliger</i> (Claus, 1863)	0–300	8,89
<i>Heterorhabdus pustulifer</i> Farran, 1929	0–600	8,13,27,86,97,98,112
<i>Heterorhabdus spinifrons</i> (Claus, 1863)	0–600	1,8,19/20,55
<i>Heterostylites longicornis</i> (Giesbrecht, 1889)	1000	98,105
<i>Heterostylites major</i> (F.Dahl, 1894)	200–600	13,27,40,42,97,98,106,112
Lucicutiidae		
<i>Lucicutia clausi</i> (Giesbrecht, 1889)	700–800	40,55
<i>Lucicutia curta</i> Farran, 1905	500–1000	27,40,42,98,112
<i>Lucicutia flavicornis</i> (Claus, 1863)	0–300	19/20,89
<i>Lucicutia macrocera</i> Sars, 1920	500–1000	13,40,42,86,98

<i>Lucicutia magna</i> Wolfenden, 1903	500–1000	27,37,106
<i>Lucicutia ovalis</i> (Giesbrecht, 1889)	500–1000–2000	3,13,37,40,42,98,106,112
<i>Lucicutia rara</i> Hülsemann, 1966	0–1000	8
<i>Lucicutia wolfendeni</i> Sewell, 1932	500–1000–3000	8,27,40,42,86,89,98,106
Mecynoceridae		
<i>Mecynocera clausi</i> I.C.Thomson, 1888	0–600	15,83,90,98
Megacalanidae		
<i>Bathycalanus bradyi</i> (Wolfenden, 1905)	0–1000	8,40,42,98,106
<i>Bathycalanus eltaninae</i> Björnberg, 1968	1000–2000	7,8
<i>Bathycalanus inflatus</i> Björnberg, 1968	1000–2000	7,8
<i>Bathycalanus princeps</i> (Brady, 1883)	3000	8,59
<i>Bathycalanus richardi</i> Sars, 1905	1000–2000	59
<i>Bradycalanus gigas</i> Sewell, 1947	1000–2000	59
<i>Bradycalanus pseudotypicus</i> Björnberg, 1968	1000–2000	7,8
<i>Bradycalanus typicus</i> A.Scott, 1909	1000–2000	59
<i>Bradycalanus sarsi</i> (Farran, 1939)	1000–2000	59
<i>Megacalanus princeps</i> Wolfenden, 1904	2000	15,59,98,106
Metridinidae		
<i>Gaussia princeps</i> (T.Scott, 1894)	0–1200	9
<i>Metridia andraeana</i> Brady, 1918	0–200	19/20
<i>Metridia brevicauda</i> Giesbrecht, 1889	500–1000	8,37,98
<i>Metridia curticauda</i> Giesbrecht, 1889	200–1000	3,8,13,23,26,27,40,43,61,89,97,98,106,111,112
<i>Metridia gerlachei</i> Giesbrecht, 1902	0–1000	3,6,8,11,13,19/20,23,24,26,27,29,32,34,37,40,42,43,45,48,49,50,57,61,62,71,72,73,81/82,83,89,90,91/92,93,95/96,97,98,99,103,104,105,107,108,109,111,112,113
<i>Metridia longa</i> (Lubbock, 1854)	0–200	23
<i>Metridia lucens</i> Boeck, 1864	0–1000	3,8,23,25,26,27,37,43,50,51,55,57,74,83,86,89,98,103,108,109,111,112,113
<i>Metridia macrura</i> Sars, 1905	0–100	86
<i>Metridia princeps</i> Giesbrecht, 1889	0–1000	8,27,37,42,98,104,105,106
<i>Metridia trispinosa</i> Brady, 1918	0–200	19/20
<i>Metridia venusta</i> Giesbrecht, 1889	500–750	98
<i>Pleuromamma abdominalis</i> (Lubbock, 1856)	0–100	8,19/20,27,36,37,98
<i>Pleuromamma borealis</i> (F.Dahl, 1893)	0–600	8,27
<i>Pleuromamma gracilis</i> (Claus, 1863)	0–600	27,37,74,104
<i>Pleuromamma piseki</i> Farran, 1929	250–100	8,98
<i>Pleuromamma quadrungulata</i> (F.Dahl, 1893)	750–0	8,98
<i>Pleuromamma robusta</i> (F.Dahl, 1893)	200–1000	3,24,25,26,27,37,43,50,55,62,74,86,89,97,98,103,112,111
<i>Pleuromamma xiphias</i> (Giesbrecht, 1889)	0–50–750	8,37,98
Paracalanidae		
<i>Calocalanus antarcticus</i> Shmeleva, 1978	0–100	88
<i>Calocalanus contractus</i> Farran, 1926	0–100	88
<i>Calocalanus elegans</i> Shmeleva, 1965	0–100	88
<i>Calocalanus elongatus</i> Shmeleva, 1968	0–100	88
<i>Calocalanus fiolentus</i> Shmeleva, 1978	0–100	88
<i>Calocalanus gracilis</i> Tanaka, 1956	0–600	26,88
<i>Calocalanus gresei</i> Shmeleva, 1973	0–100	88
<i>Calocalanus longisetosus</i> Shmeleva, 1965	0–100	88
<i>Calocalanus longispinus</i> Shmeleva, 1978	0–100	88
<i>Calocalanus ovalis</i> Shmeleva, 1965	0–100	88
<i>Calocalanus pavo</i> (Dana, 1849)	0–100	83,88
<i>Calocalanus pavoninus</i> Farran, 1936	0–50	59
<i>Calocalanus plumatus</i> Shmeleva, 1965	0–100	88
<i>Calocalanus plumulosus</i> (Claus, 1863)	0–150	85,88
<i>Calocalanus styliremis</i> Giesbrecht, 1888	0–50	8,37,85,88
<i>Paracalanus aculeatus</i> Giesbrecht, 1888	100	85,98
<i>Paracalanus indicus</i> Wolfenden, 1905	150	8
<i>Paracalanus parvus</i> (Claus, 1863)	100	19/20,55,74,85,98
Phaennidae		
<i>Cephalophanes frigidus</i> Wolfenden, 1911	500–2000	40,68,27,37,42,98,86,106
<i>Cornucalanus chelififer</i> (Thompson, 1903)	0–2000	8,37,68,106
<i>Cornucalanus robustus</i> Vervoort, 1957	500–1000	8,22,40,42,68,97
<i>Cornucalanus simplex</i> Wolfenden, 1905	0–2000	68,98
<i>Onchocalanus cristatus</i> (Wolfenden, 1904)	0–2000	37,68
<i>Onchocalanus hirtipes</i> Sars, 1905	0–1000	68
<i>Onchocalanus magnus</i> (Wolfenden, 1906)	0–2000	13,37,40,42,68,97,98,106

<i>Onchocalanus paratrigoniceps</i> Park, 1983	0–2000	68
<i>Onchocalanus trigoniceps</i> Sars, 1905	0–2000	8,68,100
<i>Onchocalanus wolfendeni</i> Vervoort, 1950	200–1000	13,40,42,68,97,105,106
<i>Phaenna spinifera</i> Claus, 1863	250	55
<i>Talacalamus greeni</i> (Farran, 1905)	0–2000	8,68
<i>Xanthocalanus antarcticus</i> Wolfenden, 1908	surface	105
<i>Xanthocalanus gracilis</i> Wolfenden, 1911	100–1000–2000	37,40?,106
<i>Xanthocalanus harpagatus</i> Bradford & Wells, 1983	seafloor–ice	17
<i>Xanthocalanus tenuiserratus</i> Wolfenden, 1911	0–400	106
Phyllopodidae		
<i>Phyllopus bidentatus</i> Brady, 1883	500–750	37,98
Pontellidae		
<i>Labidocera acutifrons</i> (Dana, 1849)	2000	8,106
Pseudocyclopiidae		
<i>Frigocalanus rauscherti</i> Schulz, 1996	hyperbenthic	80
Scolecithricidae		
<i>Amalothora obtusifrons</i> Sars, 1905	0–2500	67
<i>Amalothrix dentipes</i> (Vervoort, 1951)	0–200–1000	8,13,18,23,26,40,42,67,83,97,98,112
<i>Amalothrix emarginata</i> (Farran, 1905)	500–1000	18,27,37,40,42,67,86,98,106
<i>Amalothrix hadrosoma</i> (Park, 1980)	1000	42,67
<i>Amalothrix parafalcifer</i> (Park, 1980)	0–2500	18,67,100
<i>Amalothrix pseudopropinqua</i> (Park, 1980)	0–2000	18,67
<i>Amalothrix robusta</i> (T.Scott, 1894)	500–200	8,27,86,98
<i>Archescocleithrix auropecten</i> (Giesbrecht, 1892)	1000	97,112
<i>Landrumius antarcticus</i> Park, 1983	0–3000	67
<i>Landrumius gigas</i> (A.Scott, 1909)	0–2500	67
<i>Lophothrix frontalis</i> Giesbrecht, 1895	0–2000	67
<i>Mixtocalanus alter</i> (Farran, 1929)	100–1000	27?40,67,98
<i>Mixtocalanus vervoortii</i> (Park, 1980)	0–600	26,67
<i>Racovitzanus antarcticus</i> Giesbrecht, 1902	0–800	3,8,11,13,18,19/20,23,25,26,27,34,37,40,42,43,48,49,50,61,62,67,81/82,83,90,91/92,97,98,106,108,109,112,111,113
<i>Scaphocalanus affinis</i> (Sars, 1905)	500–2000	8,18,27,37,86,98,100
<i>Scaphocalanus antarcticus</i> Park 1882	500–1000	40,42,66
<i>Scaphocalanus curtus</i> (Farran, 1926)	100–500	55
<i>Scaphocalanus echinatus</i> (Farran, 1905)	100–1000	18,27,37,66
<i>Scaphocalanus elongatus</i> A.Scott, 1909	0–3000	66
<i>Scaphocalanus farrani</i> Park, 1982	200–1000	8,13,25,26,27,37,40,42,55,66,91/92,97,98,106,112,113
<i>Scaphocalanus impar</i> (Wolfenden, 1911)	1200	106
<i>Scaphocalanus magnus</i> (T. Scott, 1894)	700–1000	8,10,18,86,98,100
<i>Scaphocalanus major</i> (T. Scott, 1894)	0–1000–3000	66
<i>Scaphocalanus medius</i> (Sars, 1907)	0–2000	66
<i>Scaphocalanus parantarcticus</i> Park, 1982	0–1000	40,42,66,89
<i>Scaphocalanus subbrevicornis</i> (Wolfenden, 1911)	0–1000	18,27,66,84,97,98,100,106
<i>Scaphocalanus vervoortii</i> Park, 1982	0–100–1000	11,18,25,26,40,42,43,49,66,100,
<i>Scolecithricella cenotelis</i> Park, 1980	500–1000	40,42,43,65
<i>Scolecithricella dentata</i> (Giesbrecht, 1892)	0–2500	55,65,100
<i>Scolecithricella minor</i> (Brady, 1883)	ubiq	3,8,11,13,18,19/20,23,24,25,26,27,34,36,37,40,42,43,49,50,55,61,62,65,75,81/82,83,86,90,91/92,93,97,98,103,106,108,109,112,111,113,
<i>Scolecithricella ovata</i> (Farran, 1905)	250–1000	18,26,27,37,42,65,97,98
<i>Scolecithricella profunda</i> (Giesbrecht, 1892)	0–500	65
<i>Scolecithricella schizosoma</i> Park, 1980	0–1200	18,65
<i>Scolecithricella vittata</i> (Giesbrecht, 1892)	0–1200	65
<i>Scolecithrix danae</i> (Lubbock, 1856)	0–1000	19/20,75
<i>Scolecithrix incisa</i> Farran, 1929	0–100	27
<i>Scolecithrix valida</i> Farran, 1908	500–2000	18,27,37,67,86,98
<i>Scottocalanus securifrons</i> (T.Scott, 1894)	bathy	18,67
<i>Scottocalanus thori</i> With, 1915	0–1200	67
Spinocalanidae		
<i>Mimocalanus cultrifer</i> Farran, 1908	0–1000	40,98,100
<i>Mospicalanus schielae</i> Schulz, 1996	1000–3000	79
<i>Spinocalanus abyssalis</i> Giesbrecht, 1888	300–1000–2000	8,13,26,27,37,40,42,43,91/92,98,106
<i>Spinocalanus antarcticus</i> Wolfenden, 1906	1200	100,106
<i>Spinocalanus brevicaudatus</i> Brodsky, 1950	500–4000	55
<i>Spinocalanus horridus</i> Wolfenden, 1911	2000–1000	27,37
<i>Spinocalanus longicornis</i> Sars, 1900	0–1000	15,40
<i>Spinocalanus magnus</i> Wolfenden, 1904	400–1000	8,13,27,37,40,42,97,98,106

<i>Spinocalanus terranovae</i> Damkaer, 1975	0–1700	27,55,97,98
<i>Teneriforma naso</i> Farran, 1936	500–1000	42
Stephidae		
<i>Stephos antarcticus</i> Wolfenden, 1908	100	95/96,105,106
<i>Stephos longipes</i> Giesbrecht, 1902	0–1000	11,27,29,34,40,42,48,49,56,61,83,93,113,91/92,95/96,105,106,112,111,113
Temoridae		
<i>Temora kerguelensis</i> Wolfenden, 1911	0–200	106
<i>Temora turbinata</i> (Dana, 1849)	0–50	27
Tharybidae		
<i>Neoscolecithrix antarctica</i> Hülsemann, 1985	200–1000	47
<i>Tharybis magna</i> Bradford & Wells, 1983	sea floor–ice	17
<i>Undinella brevipes</i> Farran, 1908	300–1000	8,26,40,42,98
MORMONILLOIDA		
Mormonollidae		
<i>Mormonilla phasma</i> Giesbrecht, 1891	100–1000	37,42
CYCLOPOIDA		
Oithonidae		
<i>Oithona atlantica</i> Farran, 1908	0–1000	8,24,51,55,63,74,78
<i>Oithona fallax</i> Farran, 1913	0–1000	78
<i>Oithona frigida</i> Giesbrecht, 1902	0–1000	13,19/20,23,25,26,27,32,34,36,37,40,42,43,44,58,35,56,57,60,77,78,83,91/92,93,97,98,105,106,109,111,112,113
<i>Oithona plumifera</i> Baird, 1843	0–1000	24,27,78,83,86
<i>Oithona similis</i> Claus, 1866	0–1000	8,13,23,24,25,26,27,29,31,32,34,35,36,40,42,43,44,48,55,56,57,58,63,77,78,81/82,83, 86, 91/92,93,95,104,105,106,108,109,111,112,113
<i>Oithona simplex</i> Farran, 1913		78
POECILOSTOMATOIDA		
Corycaeidae		
<i>Corycaeus (Onychocorycaeus) pacificus</i> F. Dahl, 1894	0–1000	85
<i>Corycaeus (Agetis) flaccus</i> Giesbrecht, 1891	0–1000	27
<i>Corycaeus (Urocorycaeus) furcifer</i> Claus, 1863	0–1000	27
<i>Farranula gracilis</i> (Dana, 1849)	0–450	27
Lubbockiidae		
<i>Lubbockia aculeata</i> Giesbrecht, 1891	100–1000	42,55,97,98,111
<i>Lubbockia carinata</i> Heron & Damkaer, 1978	1000–2000	39
<i>Lubbockia flemingeri</i> Heron & Damkaer, 1978	1000–2000	39
<i>Lubbockia forcipula</i> Heron & Damkaer, 1978	1000–2000	39
<i>Lubbockia minuta</i> Wolfenden, 1905	500	55
<i>Lubbockia wilsonae</i> Heron & Damkaer, 1969	1000–2000	39,98
Oncaeidae		
<i>Conaea succurva</i> Heron, 1977	1000–2000	38
<i>Conaea hispida</i> Heron, 1977	1000–2000	38
<i>Conaea rapax</i> Giesbrecht, 1891	0–600; 750–2000	37,38,42
<i>Epicalymma schmitti</i> Heron, 1977	500–1000–2000	38,42
<i>Epicalymma umbonata</i> Heron, 1977	1000–2000	38
<i>Oncaea antarctica</i> Heron, 1977	0–1000–2000	3,25,26,32,38,40,42,43,91/92
<i>Oncaea bowmani</i> Heron, 1977	1000–2000	38
<i>Oncaea brocha</i> Heron, 1977	1000–2000	38
<i>Oncaea compacta</i> Heron, 1977	1000–2000	38
<i>Oncaea confifera</i> Giesbrecht, 1891	0–1000	8,13,19/20,24,27,34,35,37,51,55,56,57,83,90,97,98,100,104,106,111,112,113
<i>Oncaea convexa</i> Heron, 1977	200–1000–2000	38,42
<i>Oncaea curvata</i> Giesbrecht, 1902	0–1000	13,25,26,27,29,31,34,37,38,40,42,43,44,48,55,56,57,58,60,85,90,91/92,93,95,97,98,104,105,106,111,112,113
<i>Oncaea damkaeri</i> Heron, 1977	1000–2000	38
<i>Oncaea englishi</i> Heron, 1977	0–1000–2000	38,42,43,55,58
<i>Oncaea illgi</i> Heron, 1977	0–1000–2000	38
<i>Oncaea inflexa</i> Heron, 1977	0–500–1000	26,38
<i>Oncaea lacinia</i> Heron, English & Damkaer, 1984	0–125	38
<i>Oncaea macilenta</i> Heron, 1977	0–1000–2000	38
<i>Oncaea mediterranea</i> (Claus, 1863)	0–1000	27,38,98
<i>Oncaea olsoni</i> Heron, 1977	1000–2000	38

<i>Oncaea parila</i> Heron, 1977	0–400–1000–2000	38,58,91/92
<i>Oncaea petila</i> Heron, 1977	1000–2000	38
<i>Oncaea prolata</i> Heron, 1977	0–1000–2000	38,42,43
<i>Oncaea pumilis</i> Heron, 1977	1000–2000	38
<i>Oncaea rotunda</i> Heron, 1977	0–600–1000–2000	26,38
<i>Oncaea setosa</i> Heron, 1977	1000–2000	38
<i>Oncaea similis</i> Sars, 1918	0–500–1000	38
<i>Oncaea venusta</i> Philippi, 1843	400	19/20,36,85,91/92,100,106
<i>Oncaea walleni</i> Heron, 1977	1000–2000	38
Sapphirinidae		
<i>Sapphirina angusta</i> Dana, 1849	1000?	doubtful record
<i>Sapphirina metallina</i> Dana, 1849	1200	106
SIPHONOSTOMATOIDA		
Rataniidae		
<i>Ratania atlantica</i> Farran, 1926	600–900	27,42,98
HARPACTICOIDA		
Aegisthidae		
<i>Aegisthus mucronatus</i> Giesbrecht, 1891	500–750	98
Clytemnestridae		
<i>Clytemnestra rostrata</i> (Brady, 1883)	50–250	37,83
Ectinosomatidae		
<i>Microsetella norvegica</i> (Boeck, 1864)	0–600	19/20,25,26,27,34,60,84
<i>Microsetella rosea</i> (Dana, 1848)	0–250–500	36,83,85,91/92,98
Miracidae		
<i>Macrosetella gracilis</i> (Dana, 1848)	400–3000	106
<i>Oculosetella gracilis</i> (Dana, 1852)	0–600	26,98
MONSTRILLOIDA		
Monstrilloidae		
<i>Monstrilla conjunctiva</i> Giesbrecht, 1902	0–500	34

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