Antarctic Science 24(2), 131–138 (2012) © Antarctic Science Ltd 2011 doi:10.1017/S095410201100071X

High zooplankton diversity in the extreme environments of the McMurdo Dry Valley lakes, Antarctica

LARS-ANDERS HANSSON[1], SAMUEL HYLANDER[1], HERBERT J.G. DARTNALL[2], SVEN LIDSTRÖM[3] and JAN-ERIK SVENSSON[4]

[1]*Institute of Biology/Aquatic Ecology, Ecology Building, Lund University, SE-223 62 Lund, Sweden*
[2]*Department of Biological Sciences, Macquarie University, Sydney 2109, Australia*
[3]*Swedish Polar Research Programme, PO Box 50005, SE-104 05 Stockholm, Sweden*
[4]*Medins Biologi, SE-435 33 Mölnlycke, Sweden*
lars-anders.hansson@biol.lu.se

Abstract: The McMurdo Dry Valley lakes of Antarctica constitute some of the harshest and most isolated freshwater environments on Earth which might be expected to limit the biogeographical expansion of many organisms. Despite this, we found that the biodiversity of rotifer zooplankton is the highest ever recorded on the Antarctic mainland. We identified in total nine rotifer taxa, of which six are new to the Antarctic continent, in Lake Hoare, and also the first sub-adult crustacean copepod belonging to the genus *Boeckella*. A possible explanation for the high biodiversity is that many of the recorded species have arrived in the region in relatively recent times and then established invasive populations, suggesting that their distribution pattern was previously limited only by biogeographical borders. Interestingly, we show that the cosmopolitan rotifer taxa identified are relatively abundant, suggesting that they have established viable populations. Hence, our study suggests that the biogeographical maps have to be redrawn for several species.

Received 15 July 2011, accepted 5 August 2011, first published online 26 October 2011

Key words: biodiversity, Boeckella, copepod, invasion, rotifer, species-richness

Introduction

Antarctic terrestrial and freshwater ecosystems provide harsh conditions for organisms, which are exposed to low temperatures and seasonal extremes of illumination with long winters without light and summers with continuous sunlight. Moreover, many lakes on the Antarctic continent, particularly those at high latitudes, have low nutrient availabilities and are permanently ice-covered, leading to low production of algae and thereby low food supply for higher organisms. These features generally lead to low biodiversity and abundance among herbivorous zooplankton. The lakes in the Dry Valleys of the McMurdo Sound region of Antarctica constitute an extreme of these extreme systems with their permanent, several metres thick, ice cover. Both the species diversity and population sizes of zooplankton previously recorded here are low, comprising a few species of rotifers, while crustaceans have, with the exception of copepod nauplius larvae in Lake Joyce (Roberts *et al*. 2004), never been recorded. The reason for this may be either that they were not present during previous samplings, or that the samplings hitherto have mainly been focused on physical and chemical properties and on the microbial components of these lakes (Priscu 1997, Roberts *et al*. 2004, Herbei *et al*. 2010). In the present study we have therefore focused on assessing the species-richness of larger zooplankton, including rotifers and crustaceans, that is, assessing how many species that manage to maintain viable populations in this extreme environment. We have done so by sampling the water column of Lake Hoare and filtering larger volumes of lake water than in previous studies. This approach revealed a far higher number of planktonic rotifer species than previously reported and provides further evidence that a calanoid copepod of the genus *Boeckella* has a viable population in the Dry Valley lakes.

Materials and methods

Lake Hoare

Lake Hoare is situated in Taylor Valley (77°37.661'S, 162°54.574'E) one of the Dry Valleys of the McMurdo Sound region, Antarctica. Historically, the lake might have been almost completely dried out about 1000 years ago, i.e. re-colonization of organisms may have had a relatively short time to occur (Lyons 1997). In addition, re-colonization of aquatic organisms may also have been affected by the glacial history, as has been the case with, for example, copepods in the Arctic (Samchyshyna *et al*. 2008). The Dry Valleys receive < 50 mm precipitation per year and have a mean temperature of -18°C (Roberts *et al*. 2004), making them one of the driest, coldest and harshest environments on Earth. The lakes of the Dry Valleys are ice-covered throughout the year, although in late summer a moat of water opens up close to the shore. Due to the low precipitation their only inflow is generally from glacier

https://doi.org/10.1017/S095410201100071X Published online by Cambridge University Press

Table I. The Antarctic distributions of rotifers with special reference to the Brachionidae family including the genera *Brachionus*, *Keratella*, *Kellicottia* and *Notholca*. References: Lake Hoare, this study; Ross Island, Murray 1910, Cathey *et al*. 1981; Schirmacher Ponds, Kutikova 1991; Larsemann Hills, Dartnall 1995b; Vestfold Hills, Dartnall 2000; Bunger Hills, Korotkevich 1958, Kutikova 1958a, 1958b; Thala Hills, Opalinski 1972; Wilkes Land, Thomas 1965, 1972, Dartnall 2005a; Molodezhnaya, Kutikova 1991; Antarctic Peninsula, Heywood 1977, Dartnall 1980, Kuczynski 1987; South Shetland Islands, de Paggi 1982, Kuczynski 1987, Janiec 1993, Janiec & Salwicka 1996; South Orkney Islands, Dartnall & Hollowday 1985; South Georgia, Dartnall & Heywood 1980, Dartnall & Hollowday 1985, Hansson *et al*. 1996, Dartnall 2005b; Macquarie Island, Dartnall 1993, Dartnall *et al*. 2005; Heard Island, Dartnall 1995a, 2003, 2006; Kerguelen, Russell 1959, Lair & Koste 1984, de Smet 2001.

	Lake Hoare (77°S)	Ross Island (77°S)	Schirmacher Ponds (70°S)	Larsemann Hills (69°S)	Vestfold Hills (68°S)	Thala Hills (67°S)	Wilkes Land (67°S)	Molodezhnaya (67°S)	Bunger Hills (66°S)	Antarctic Peninsula	South Shetland Islands (62°S)	South Orkney Islands (60°S)	South Georgia (54°S)	Macquarie Island (54°S)	Heard Island (53°S)	Kerguelen (49°S)
Brachionus angularis Gosse	+															
Brachionus bidentatus Anderson										+						
Brachionus bidentatus inermis Rousselet										+						
Brachionus calyciflorus Pallas							+									
Brachionus havanaensis trahea (Murray)											+					
Brachionus quadridentatus (Hermanns)			+				+									
Brachionus urceolaris O.F. Müller	+										+					
Keratella americana Carlin											+					
Keratella cochlearis Gosse	+							+			+					
Keratella kostei Paggi													+			
Keratella quadrata (O.F. Müller)	+															
Keratella sancta Russell														+		+
Keratella sp.											+					
Kellicottia longispina (Kellicott)	+															
Notholca caudata Carlin													+			
Notholca foliacea (Ehrenberg)	+															
Notholca hollowdayi Dartnall															+	+
Notholca jugosa (Gosse)						+								+		+
Notholca labis Gosse													+			+
Notholca salina Foche											+	+	+			
Notholca squamula (O.F. Müller)																+
Notholca verae Kutikova									+							
Notholca walterkostei de Paggi										+	+	+	+			
Notholca walterkostei reducta												+				
Notholca sp.				+	+		+		+						+	+
Total Brachionidae species-richness	6	0	1	1	1	1	3	1	2	3	7	3	5	2	2	6
Filinia sp.	+															+
Lepadella triptera (Ehrenberg)	+											+	+	+	+	+
Philodina alata Murray	+	+			+				+							

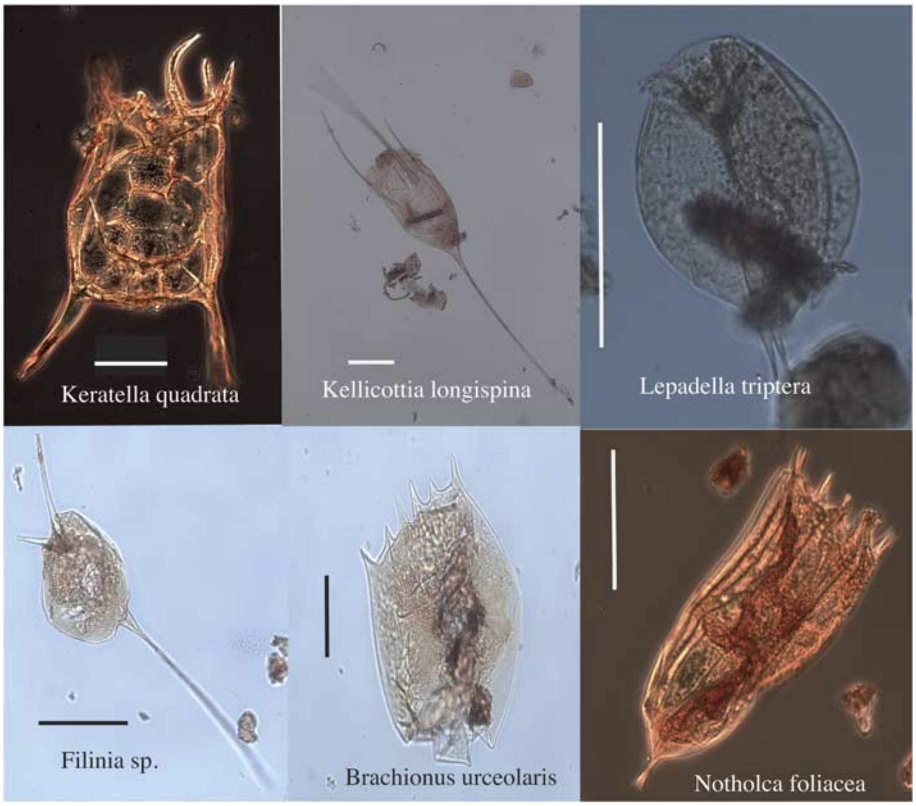

Fig. 1. Rotifers previously never recorded on the Antarctic continent, including: *Filinia* sp. (length without seta: 130 μm); *Kellicottia longispina* (Kellicott) (length without spines: 170 μm); *Notholca foliacea* (Ehrenberg) (length without spines: 135 μm); *Lepadella triptera* (Ehrenberg) (length without spines: 75 μm); *Brachionus urceolaris* Müller; (length without spines: 175 μm); *Keratella quadrata* (Müller) (length without spines: 125 μm). Scale bar in each part represents 50 μm. Picture: Jan-Erik Svensson.

meltwater and they usually lack surface outflows. Lake Hoare has a surface area of about 1.9 km^2 and maximum depth of 34 m (Roberts *et al*. 2004). The ice thickness in summer has been estimated at between 3 and 6 m (Howard-Williams *et al*. 1998, Roberts *et al*. 2004). We only recorded a thickness of about 2 m, but we did not include the 1 m thick layer of porous, partly melted snow/ice cover on top of the regular ice in our measurements.

Sampling procedure

Our sampling was on 2 February 2010 along a depth profile at 1, 4, 9 and 15 metres, but only the surface sample was taxonomically investigated here in order to focus on the pelagic fauna and excluding any possibility of contamination of animals from the benthic mat. We used a Jiffy drill to enlarge holes previously drilled by the LTER project above the deepest point (Roberts *et al*. 2004). 20 l of water were taken from each depth using a Limnos water sampler (2 l volume). In order to reduce the risk of contamination of these ecosystems with alien species all equipment was kept dry for at least a month and was rinsed in alcohol (70%) prior to sampling. Moreover, all nets were new, eliminating the risk of contamination of samples. Each 20 l sample was filtered through a 50 μm net and the zooplankton obtained were retrieved from the net, rinsed into 50 ml centrifuge tubes and preserved in Lugol's solution for later identification. In the laboratory, zooplankton from the whole volume, not just a subsample of each sampling, was counted. We used a Petri dish with eight sub-chambers, each 26–33 mm (Nalge Nunc, USA), and inspected the samples with a stereo microscope at 40x magnification. Taxonomic determinations were made using dissecting and compound microscopes, as well as Leica DMI 4000B inverted microscope at 25-945x magnification, which was also used for the photographs taken.

Results

We recorded nine species of rotifer and one calanoid copepod in the water column of Lake Hoare (Table I) and the species-richness was similar in the nearby Lake Fryxell (own observations). Most of the rotifers we found belong to the Brachionidae family including *Brachionus angularis* Gosse, which is a new record for the Antarctic. Also *Brachionus urceolaris* O.F. Müller (Fig. 1) was found in the lake and although this species has been reported from the Antarctic by Segers (2007), no location was given. *Keratella cochlearis* Gosse (Fig. 2) has been reported from the South Shetland Islands (Paggi 1983) and from Molodezhnaya (Kutikova 1991). *Keratella quadrata* (O.F. Müller) is a new record for the Antarctic and this species was very common in Lake Hoare (Fig. 1), with more than 100 individuals per litre in the surface waters. The specimens were of varying size and development of the posterior spines was extremely variable and may represent more than one species. Most specimens had a pair of similar-sized and prominent posterior spines,

Fig. 2. Rotifer species previously recorded on the Antarctic continent, including *Philodina alata* Murray, 1910 (length 225 μm) and *Keratella cochlearis* Gosse (length without spines: 75 μm). Scale bar in each part represents 50 μm. Picture: Jan-Erik Svensson.

whereas others were asymmetrical with one long and one short posterior spine. It should be noted that this was a true observation, i.e. the shorter spine had not broken off in the sampling process. Finally some specimens had a pair of very short posterior spines reminiscent of *K. testudo* (Ehrenberg, 1831) and one individual was seen that did not have posterior spines at all. *Kellicottia longispina* (Kellicott) (Fig. 1) is also a new record for the Antarctic and was very common in Lake Hoare with more than 50 individuals per litre in the surface waters. *Notholca foliacea* (Ehrenberg) (Fig. 1) is a common species in many parts of the world, but another new record for the Antarctic.

Beyond the family Brachionidae, three other species of rotifers were identified, including *Filinia* sp. The *Filinia* specimen (Fig. 1) we saw exhibited characteristics of both *F. pejleri* Hutchinson, 1964 and *F. terminalis* (Plate, 1886), but since the caudal spine seta was narrow and in most cases appeared not to originate terminally we consider *F. terminalis* as more probable. Russell (1959) reported *F. maior* Carlin, 1943, now recognized as a synonym of *F. terminalis*, from the Iles Kerguelen. However, Lair & Koste (1984) described the Kerguelen *Filinia* as a new sub species namely *Filinia terminalis kerguelensis*, which De Smet (2001) corrected to *F. pejleri.* Since the species determination of this taxa is still under discussion, we will here categorize it as *Filinia* sp. Irrespective of species, this is the first time this genus is recorded from the Antarctic continent. *Lepadella triptera* (Ehrenberg) (Fig. 1) is a small cosmopolitan species but this is the first time it has been recorded on the Antarctic continent. *Philodina alata* (Murray), with its characteristic 'protruding wings' (Fig. 2), was very common in Lake Hoare (up to 400 individuals per litre).

Fig. 3. A juvenile specimen of the calanoid copepod *Boeckella* sp. from Lake Hoare, McMurdo Dry Valleys, Antarctica. Scale bar represents 500 µm. Picture: Jan-Erik Svensson.

In addition to the above listed rotifers we recorded one complete specimen of the calanoid copepod (Fig. 3) plus the remains, assorted indistinguishable body parts, of a few others, presumably the same species. The complete specimen, a *Boeckella* (length 1.1 mm), was a juvenile thereby excluding the possibility for further taxonomic analysis beyond the genus level (Prof G. Boxshall, personal communication 2010). Several species of copepods are common on the sub-Antarctic islands, and the hitherto most southern recording of an adult copepod is at Prince Charles Mountains (71°S, Table II). Our recording of a *Boeckella* in Lake Hoare is the first time a sub-adult copepod has been recorded in freshwaters as far south as 77°S.

Discussion

Our data on zooplankton from Lake Hoare, combined with a literature review of the Antarctic and sub–Antarctic region, shows that the species-richness above *c.* 67°S declines to only one or a few species recorded (Table I). Hence, it is very surprising that the species-richness in Lake Hoare, situated at 77°S and the focus of our study, has a species-richness at the same level as the sub-Antarctic islands and that several cosmopolitan species are common components of the fauna in this lake (Table I). The presence

Table II. The distribution of calanoid copepods in Antarctic and sub-Antarctic freshwater lakes from 46–77°S. References: Lake Hoare, this study (2010); Prince Charles Mountains, Bayly & Burton 1993; Mac. Robertson Land, Bayly *et al.* 2003, Laybourn-Parry *et al.* 2006; Bunger Hills, Bayly 1994, Bayly *et al.* 2003; South Shetland Islands, Campos *et al.* 1978, Paggi 1983, Janiec 1993; South Orkney Islands, Heywood 1970; South Georgia, Mrazek 1892, Ekman 1905, Harding 1941, Hessen *et al.* 1989, Dartnall 2005b; Macquarie Island, Evans 1970, Dartnall *et al.* 2005; Heard Island, Bayly 1992, Dartnall 1995a, 2003, 2006; Kerguelen, Brady 1875, Brehm 1954, Smith & Sayers 1971, Gay 1981, 1982; Marion Island, Smith & Sayers 1971, Kok & Grobbelaar 1978; Iles Crozets, Dreux 1970, Smith & Sayers 1971.

	Lake Hoare (77°S)	Prince Charles Mountains (71°S)	Mac. Robertson Land (70°S)	Bunger Hills (66°S)	South Shetland Islands (62°S)	South Orkney Islands (60°S)	South Georgia (54°S)	Macquarie Island (54°S)	Heard Island (53°S)	Kerguelen (49°S)	Marion Island (46°S)	Crozet (46°S)
Boeckella sp.	+											
Boeckella poppei (Mrazek)		+*	+		+	+	+					
Boeckella michaelseni (Mrazek)							+					
Boeckella vallentini (Scott)										+	+	+
Boeckella brevicaudata (Brady)								+	+	+		
Parabroteas sarsi Daday de Deés						+	+					
Gladioferens antarcticus Bayly			+	+*								

*denotes that the taxa is present in epishelf lakes at this location.

https://doi.org/10.1017/S095410201100071X Published online by Cambridge University Press

of a relatively large number of planktonic species of rotifers and a calanoid copepod in Lake Hoare was a surprise and has never been reported before. Planktonic rotifers are not unknown from the Antarctic and sub-Antarctic islands (Table I), but they generally occur in small numbers. In total, 25 species of rotifers belonging to the Brachionidae family have been identified from the Antarctic and sub-Antarctic region (Table I), including a mixture of cosmopolitan and endemic species. *Lepadella triptera*, with its wide distribution (Segers 2007) which has been recorded on the sub-Antarctic islands of South Georgia (Dartnall 2005b), Marion Island (Smith & Dartnall, personal communication 2010), Iles Kerguelen (De Smet 2001), Heard Island (Dartnall 2003), and Macquarie Island (Dartnall 1993, Dartnall *et al*. 2005), as well as on Signy Island in the Maritime Antarctic (Dartnall & Hollowday 1985). *Philodina alata* is an Antarctic endemic species that was originally described from the McMurdo Sound area (Murray 1910) and has repeatedly been reported from there by Dougherty & Harris (1963) and Cathey *et al*. (1981). It has also been reported from both Bunger Hills and Obruchev Hills (Korotkevich 1958, Kutikova 1958b) and from Vestfold Hills (Dr John Gibson, personal communication 2006).

Generally the species-richness of Brachionidae declines with increasing latitude so it is puzzling that the species-richness in Lake Hoare (six rotifer species) is at the same level, or higher, than at the sub-Antarctic islands, which are situated more than 20° further north. Similarly, why does Lake Hoare plankton include four cosmopolitan species that have not been found elsewhere in Antarctica? The historical origin of the Antarctic fauna is discussed in depth by Convey *et al*. (2008). One possible explanation is that the rotifers found in our study have been there during evolutionary time, but that previous samplings were not designed to look for such low abundances. This is a possibility since only a few studies in these extreme habitats have focused on these organisms and they did not sample such large volumes of water as we did. Instead, the majority of previous studies have focused on phytoplankton, bacteria and biogeochemistry, although Roberts *et al*. (2004) noted low abundances of (unidentified) rotifers in Lake Hoare and Laybourn-Parry *et al*. (2006) found only the rotifer genus *Philodina* in the nearby Lake Fryxell. All the rotifer species we recorded in Lake Hoare were, however, also found in Lake Fryxell at relatively high abundances (0.05–400 individuals per litre, depending on taxa).

Another potential explanation is that the rotifers may have been temporally absent. Some rotifers have a periodicity of seven years (Dartnall 2005a), which may have made them "invisible" to sampling over long periods. However, having six or more species in such synchronisation makes this explanation seem unlikely. Another possibility is that resting eggs have been cryo-preserved from the period before the drying out (several thousand years) and are now hatched. Although copepod resting eggs have been shown to be viable at least 332 years (Hairston *et al*. 1995), this scenario seems very unlikely.

We also found one complete (Fig. 3), and several incomplete individuals of the copepod genus *Boeckella*, which is the first recording of a sub-adult crustacean at this high latitude, although Roberts *et al*. (2004) found copepod nauplii in Lake Joyce. These findings strengthen the conclusion that the distribution of this copepod genus has to be expanded another 6° further south than any previous freshwater copepod sightings.

Another question is how did the fauna get to the Dry Valleys and could they be recent introductions by either humans or birds (Green *et al*. 2008)? Arguments against this are that there are very strong restrictions for entering the area and very few people have been allowed to visit these lakes. However, these restrictions are relatively recent and introductions may have occurred before these rules were enacted. The harsh conditions, and the almost complete absence of birds, also reduces the possibility for invading species to enter the area and to establish this way. However, the possibility that these small animals have been unintentionally introduced by humans cannot be excluded. Another possibility is that resting eggs of rotifers have been transported by wind from other continents, a process that has been shown to transport pollen from South America to sub-Antarctic Islands (Marshall 1996). However, these islands lie far closer to another continent than the Dry Valleys and rotifer resting eggs are denser than pollen making this explanation very unlikely.

Could global climate change be a possible explanation? This hypothesis can be rejected since global warming does not appear to be affecting the Dry Valleys; instead there seems to be a net cooling in this region by 0.7°C per decade between 1986 and 2000 (Doran *et al*. 2002). Moreover, Fountain *et al*. (2006) stated that the McMurdo Dry Valleys glaciers are in equilibrium with the current climate, and thereby contrast with glacial trends elsewhere on the Antarctic Peninsula and at temperate latitudes.

Hence, the most probable explanations are that either these rotifer species have been here during evolutionary time, but not previously recorded, or they have been relatively recently introduced. However, since they all seem to exist at all depths and in viable, albeit low, abundances, any introduction must have occurred some time ago. This notion is strengthened by the fact that the temperatures, and thereby growth rates, are low, suggesting that it would take a considerable time to establish a population that can be detected by sampling. Future genetic studies may provide an answer to whether or not these rotifer taxa have been present during evolutionary time or if they are recent introductions.

There is an ongoing, and long-lasting, discussion regarding whether or not microorganisms exhibit any biogeographical patterns or should we expect that "everything is everywhere" (Fenchel *et al*. 1997, Finlay 2002). Although rotifers are generally considered to show biogeographical patterns, our results suggest that some cosmopolitan rotifer taxa are now present on this last continent suggesting that they approach the "everything is everywhere" distribution. Moreover, our study clearly shows that several rotifer species, and also the copepod *Boeckella*, are physiologically able to withstand and maintain viable populations in the harsh climate of the permanently ice-covered Dry Valleys lakes, which have been described as "end-members amongst the world's spectrum of limnological entities" (Fritsen & Priscu 1999).

Acknowledgements

Financial and logistic support for this study was provided by the Swedish Research Council (VR), the Swedish Antarctic Research Programme and the United States Antarctic Research Programme. D. Fontaneto and G. Boxshall kindly assisted with professional taxonomic guidance. We especially thank Addie Coyac at the US Antarctic Research Programme for valuable assistance throughout the field study. Two anonymous reviewers gave helpfully critical comments on an earlier version of the manuscript.

References

Bayly, I.A.E. 1992. Fusion of the genera *Boeckella* and *Pseudoboeckella* (Copepoda) and revision of their species from South America and sub-Antarctic islands. *Revista Chilena de Historia Natural*, **65**, 17–63.

Bayly, I.A.E. 1994. *Gladioferens* Henry (Copepoda: Calanoidae) discovered on Antarctica. *G. antarcticus* sp. nov. described from a lake in Bunger Hills. *Polar Biology*, **14**, 253–259.

Bayly, I.A.E. & Burton, H.R. 1993. Beaver Lake, Greater Antarctica and its population of *Boeckella poppei* (Mrázek) Copepoda: Calanoidea. *Verhandlungen der Internationalen Vereinigung für Limnologie*, **25**, 975–978.

Bayly, I.A.E., Gibson, J.A.E., Wagner, B. & Swadling, K.M. 2003. Taxonomy, ecology and zoogeography of two East Antarctic freshwater calanoid copepod species: *Boeckella poppei* and *Gladioferens*. *Antarctic Science*, **15**, 439–448.

Brady, G.S. 1875. Note on Entomostraca from Kerguelen's Land and the South Indian Ocean. *Annals and Magazine of Natural History, Series 4*, **16**, 162.

Brehm, V. 1954. Les entomostracés des Kerguelen. *Mémoires de l'Institut Scientifique de Madagascar, Série A*, **9**, 41–44.

Campos, H., Arenas, J. & Steffen, W. 1978. Antecedentes y observaciones limnoligicas en los principales lagos de la Isla Rey Jorge, Shetland del Sur, Antarctica. *Instituto Antàrcttico Chileno, Serie Cientifica*, **24**, 11–19.

Cathey, D.D., Parker, B.C., Simmons Jr, G.M., Yongue Jr, W.H. & van Brunt, M.R. 1981. The microfauna of algal mats and artificial substances in southern Victoria Land lakes of Antarctica. *Hydrobiologia*, **85**, 3–15.

Convey, P., Gibson, J.A.E., Hillenbrand, C., Hodgson, D.A., Pugh, P.J.A., Smellie, J.L. & Stevens, M.I. 2008. Antarctic terrestrial life - challenging the history of the frozen continent? *Biological Reviews*, **83**, 103–117.

Dartnall, H.J.G. 1980. Freshwater biology at Rothera Point, Adelaide Island: 1. General description of the pools and the fauna. *British Antarctic Survey Bulletin*, No. 50, 51–54.

Dartnall, H.J.G. 1993. The rotifers of Macquarie Island. *ANARE Research Notes*, **89**, 41 pp.

Dartnall, H.J.G. 1995a. The rotifers of Heard Island: preliminary survey, with notes on other freshwater groups. *Papers and Proceedings of the Royal Society of Tasmania*, **129**, 7–15.

Dartnall, H.J.G. 1995b. Rotifers, and other aquatic invertebrates from the Larsemann Hills, Antarctica. *Papers and Proceedings of the Royal Society of Tasmania*, **129**, 17–23.

Dartnall, H.J.G. 2000. A limnological reconnaissance of Vestfold Hills. *ANARE Research Notes*, **141**, 55 pp.

Dartnall, H.J.G. 2003. Additions to the freshwater fauna of Heard Island. *Papers and Proceedings of the Royal Society of Tasmania*, **137**, 75–79.

Dartnall, H.J.G. 2005a. Are Antarctic planktonic rotifers anthropogenic introductions? *The Quekett Journal of Microscopy*, **40**, 137–143.

Dartnall, H.J.G. 2005b. Freshwater invertebrates of sub-Antarctic South Georgia. *Journal of Natural History*, **39**, 3321–3342.

Dartnall, H.J.G. 2006. The freshwater fauna of Heard Island: a review of current knowledge. *In* Green, K. & Woehler, E., *eds. Heard Island: Southern Ocean sentinel*. Chipping Norton, Australia: Surrey Beatty, 105–113.

Dartnall, H.J.G. & Heywood, R.B. 1980. The freshwater fauna of South Georgia. *British Antarctic Survey Bulletin*, No. 50, 115–118.

Dartnall, H.J.G. & Hollowday, E.D. 1985. Antarctic rotifers. *British Antarctic Survey Scientific Reports*, **100**, 46 pp.

Dartnall, H.J.G., Hollwedel, W. & Paggi, J.C. 2005. The freshwater fauna of Macquarie Island, including a re-description of the endemic water-flea *Daphnia gelida* (Brady). *Polar Biology*, **28**, 922–937.

De Paggi, S.B.J. 1982. Notholca walterkostei sp. nov. y ostros Rotiferos dulceacuicolas de la Peninsula Potter. Isla 25 de Mayo (Shetland del Sur, Antartida). *Revista Asociacion de Ciencias Naturales del Litoral*, **13**, 81–95.

De Smet, W.H. 2001. Freshwater Rotifera from plankton of the Iles Kerguelen (Sub-Antarctica). *Hydrobiologia*, **446/447**, 261–272.

Doran, P.T., Priscu, J.C., Lyons, W.B., Walsh, J.E., Fountain, A.G., McKnight, D.M., Moorhead, D.L., Virginia, R.A., Wall, D.H., Clow, G.D., Fritsen, C.H., McKay, C.P. & Parsons, A.N. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature*, **415**, 517–520.

Dougherty, E.C. & Harris, L.G. 1963. Antarctic Micrometazoa: freshwater species of the McMurdo Sound area. *Science*, **140**, 497–498.

Dreux, P. 1970. Contribution a l'etudes des arthropodes terrestres et d'eau douce des terres australes Francaises. *Terres Australes et Antarctiques Francaises*, **50/51**, 41–44.

Ekman, S. 1905. Cladoceren und Copepoden aus Antarktischen und subantarktischen Binnengewassern. *Schwedischen Südpolar Expedition 1901–1903. Zoology*, **5**, 1–40.

Evans, A.J. 1970. Some aspects of the ecology of a calanoid copepod, *Pseudoboeckella brevicaudata* Brady, 1875 on a sub-Antarctic island. *ANARE Scientific Reports*, **110**, 100 pp.

Fenchel, T., Esteban, G.F. & Finlay, B.T. 1997. Local versus global diversity microorganisms: cryptic diversity of ciliated protozoa. *Oikos*, **80**, 220–225.

Finlay, B.T. 2002. Global dispersal of free-living microbial eukaryote species. *Science*, **296**, 1061–1063.

Fountain, A.G., Nylen, T.H., MacClune, K.L. & Dana, G.L. 2006. Glacier mass balances (1993–2001), Taylor Valley, McMurdo Dry Valleys, Antarctica. *Journal of Glaciology*, **52**, 451–462.

Fritsen, C.H. & Priscu, J.C. 1999. Seasonal change in the optical properties of the permanent ice cover on Lake Bonney, Antarctica: consequences for lake productivity and phytoplankton dynamics. *Limnology and Oceanography*, **44**, 447–454.

Gay, C. 1981. Ecologie du zooplankton d'eau douce des Iles Kerguelen. 1. Caractéristiques du milieu et inventaire des Entomostracés. *Comité National Français des Recherches Antarctiques*, **46**, 43–57.

Gay, C. 1982. Les eaux douces des Iles Kerguelen et leur peuplement en Entomostracés. *Comité National Français des Recherches Antarctiques*, **51**, 93–99.

Green, A.J., Jenkins, K.M., Bell, D., Morris, P.J. & Kingsford, R.T. 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. *Freshwater Biology*, **53**, 380–392.

Hairston Jr, N., van Brunt, R. & Kearns, C. 1995. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology*, **76**, 1706–1711.

Hansson, L-A., Tranvik, L., MacAlister, H., Ellis-Evans, C. & Dartnall, H. 1996. Temporal and spatial fluctuations in physical, chemical and biological variables in lakes at the Tønsberg peninsula, South Georgia. *Ecography*, **19**, 393–403.

Harding, J.P. 1941. Lower Crustacea. *Scientific Reports of the British Graham Land expedition, 1934–1937*, **1**, 319–322.

Herbei, R., Lyons, W.B., Laybourn-Parry, J., Gardner, C., Priscu, J.C. & McKnight, D.M. 2010. Physiochemical properties influencing biomass abundance and primary production in Lake Hoare, Antarctica. *Ecological Modelling*, **221**, 1184–1193.

Hessen, D., Sandoy, S. & Ottesen, P. 1989. Calanoid copepods from South Georgia with special reference to size dimorphism within the genus *Pseudoboeckella*. *Polar Biology*, **10**, 71–75.

Heywood, R.B. 1970. Ecology of the freshwater lakes of Signy Island, South Orkney Islands. 3. Biology of the copepod *Pseudoboeckella silvestri* Daday (Calanoida, Centropagidae). *Bulletin of the British Antarctic Survey*, No. 23, 1–17.

Heywood, R.B. 1977. A limnological survey of the Ablation Point area, Alexander Island, Antarctica. *Philosophical Transactions of the Royal Society*, **B279**, 39–54.

Howard-Williams, C., Schwarz, A.M., Hawes, I. & Priscu, J.C. 1998. Optical properties of the McMurdo Dry Valley Lakes, Antarctica. *Antarctic Research Series*, **72**, 189–203.

Janiec, K. 1993. The freshwater micro- and meifauna of Admiralty Bay, King George Island, South Shetland Islands. *Proceedings of the NIPR Symposium on Polar Biology*, **6**, 133–138.

Janiec, K. & Salwicka, K. 1996. Monogonont composition in different freshwater habitats on Spitzbergen (Arctic) and King George Island (Antarctic). *Memoirs of the National Institute of Polar Research, Special Issue*, **51**, 91–98.

Kok, O.B. & Grobbelaar, J.U. 1978. Observations on the crustaceous zooplankton in some freshwater bodies of the sub-Antarctic Marion Island. *Hydrobiologia*, **59**, 3–8.

Korotkevich, V.S. 1958. The distribution of plankton in the Indian sector of the Antarctic. *Doklady Akademii Nauk Sssr*, **122**, 578–581.

Kuczynski, D. 1987. Rotiferos del genero Branchionus nuevos para la Antartida. *Instituto Antartico Argentino*, **360**, 1–11.

Kutikova, L.A. 1958a. O novoy kolovratke v Antarktide. *Informatsionnyi Byulleten Sovietskoi Antarkticheskoi Ekspeditsii*, **2**, 45–46. [English translation: Kutikova, L.A. 1964. A new rotifer from the Antarctic. *Soviet Antarctic Expedition Information Bulletin*, **1**, 88–89.]

Kutikova, L.A. 1958b. K fauna kolovratok s poberezh'ya Vostochnoy Antarktide. *Informatsionníoўí Byulleten Sovetskoi Antarkticheskoí Ekspeditsii*, **3**, 99. [English translation: Kutikova, L.A. 1964. Rotifers from the coast of East Antarctica. *Soviet Antarctic Expedition Information Bulletin*, **1**, 162.]

Kutikova, L.A. 1991. Rotifers of the inland waters of East Antarctica. *Informatsionnyi Byulleten' sovetskoi Antarkticheskoi Ekspeditsii*, **16**, 87–99. [In Russian.]

Lair, N. & Koste, W. 1984. The rotifer fauna and population dynamics of Lake Studer 2 (Kerguelen Archipelago) with description of *Filimia terminalis kerguelensis* n. spp. And a new record of *Keratella sancta* Russel [sic] 1984. *Hydrobiologia*, **108**, 57–64.

Laybourn-Parry, J., Madan, N.J., Marshall, W.A., Marchant, H.J. & Wright, S.W. 2006. Carbon dynamics in a large ultra-oligotrophic epishelf lake (Beaver Lake, Antarctica) during summer. *Freshwater Biology*, **51**, 1119–1130.

Lyons, W.B., Howard-Williams, C. & Hawes, I., eds. 1997. *Ecosystem processes in Antarctic ice-free landscapes*. Proceedings of a Workshop on Polar Desert Ecosystems, Christchurch, New Zealand. Rotterdam: Balkema, 281 pp.

Marshall, W.A. 1996. Biological particles over Antarctica. *Nature*, **383**, 680.

Mrazek, A. 1892. Süsswasser Copepoden. *Hamburger Magalhaennsiische Sammelreise*, **2**, 2–29.

Murray, J. 1910. Antarctic Rotifera. *Reports on the Scientific Investigations of the British Antarctic Expedition, 1907–09, Biology*, **1**, 41–65.

Opalinski, K.W. 1972. Flora and fauna in freshwater bodies of the Thalla Hills Oasis (Enderby Land, eastern Antarctica). *Polskie Archiwum Hydrobiologii*, **19**, 383–398.

Paggi, J.C. 1983. Estudios limnológicos en península Potter, Isla 25 de Mayo (Shetland del Sur), Antàrctido: Morffologia y Taxonomía de *Pseudoboeckella poppei* Mrazek 1901 (Crustacea: Copepoda). *Contribuciónes del Instituto Antárctico Argentino, Buenos Aires*, **303**, 1–34.

Priscu, J.C. 1997. The biogeochemistry of nitrous oxide in permanently ice-covered lakes of the McMurdo Dry Valleys, Antarctica. *Global Change Biology*, **3**, 301–315.

Roberts, E.C., Priscu, J.C., Wolf, C., Lyons, W.B. & Laybourn-Parry, J. 2004. The distribution of microplankton in the McMurdo Dry Valley Lakes, Antarctica: response to ecosystem legacy or present-day climatic controls? *Polar Biology*, **27**, 238–249.

Russell, C.R. 1959. Rotifera. *B.A.N.Z. Antarctic Research Expedition, 1929–31, Reports, Series B*, **8**, 81–88.

Samchyshyna, L., Hansson, L-A. & Christoffersen, K. 2008. Patterns in the distribution of Arctic freshwater zooplankton related to glaciation history. *Polar Biology*, **31**, 1427–1435.

Segers, H. 2007. Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. *Zootaxa*, **1564**, 1–104.

Smith, W.A. & Sayers, R.L. 1971. *Entomostraca*. *In* van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A., *eds. Marion and Prince Edward islands. Report on the South African biological and geological expedition, 1965–1966*. Cape Town: Balkema, 427 pp.

Thomas, C.W. 1965. On populations in Antarctic meltwater pools. *Pacific Science*, **19**, 515–521.

Thomas, C.W. 1972. Two species of Antarctic rotifers. *Antarctic Journal of the United States*, **7**(5), 186–187.