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Area, depth and elevation of cryoconite holes in the Arctic do not influence Tardigrada densities

Krzysztof ZAWIERUCHA[1*], Tobias R. VONNAHME[2,3], Miloslav DEVETTER[2,4], Małgorzata KOLICKA[1], Marta OSTROWSKA[5], Sebastian CHMIELEWSKI[6] and Jakub Z. KOSICKI[5]

[1] *Zakład Taksonomii i Ekologii Zwierząt, Uniwersytet im. Adama Mickiewicza w Poznaniu, Umultowska 89, 61-614 Poznań, Poland*

[2] *Centre for Polar Ecology, University of South Bohemia, Branišovská 31, 37005 České Budějovice, Czech Republic*

[3] *Max-Planck Institute for Marine Microbiology, Bremen, Germany*

[4] *Institute of Soil Biology, Biology Centre CAS, Na Sádkách 7, 37005 České Budějovice, Czech Republic*

[5] *Zakład Biologii i Ekologii Ptaków, Uniwersytet im. Adama Mickiewicza w Poznaniu, Umultowska 89, 61-614 Poznań, Poland*

[6] *Zakład Zoologii Systematycznej, Umultowska 89, 61-614 Poznań, Poland*

* *corresponding author: k.p.zawierucha@gmail.com*

Abstract: Water bears (Tardigrada) are known as one of the most extremophile animals in the world. They inhabit environments from the deepest parts of the oceans up to the highest mountains. One of the most extreme and still poorly studied habitats which tardigrades inhabit are cryoconite holes. We analysed the relation between area, depth, elevation and tardigrades densities in cryoconite holes on four glaciers on Spitsbergen. The mean (±SD) of cryoconite area was 1287.21±2400.8 cm^2, while the depth was on average 10.8±11.2 cm, the elevation 172.6±109.66 m a.s.l., and tardigrade density 24.9±33.0 individuals per gram of wet material (n = 38). The densities of tardigrades on Hans Glacier reached values of up to 168 ind. cm^3, 104 ind. g^{-1} wet weight, and 275 ind. g^{-1} dry weight. The densities of tardigrades of the three glaciers in Billefjorden were up to 82 ind. cm^2, 326 ind. g^{-1} wet weight and 624 ind. g^{-1} dry weight. Surprisingly, although the model included area, depth and elevation as independent variables, it cannot explain Tardigrada density in cryoconite holes. We propose that due to the rapid melting of the glacier surface in the Arctic, the constant flushing of cryoconite sediments, and inter-hole water-sediment mixing, the functioning of these ecosystems is disrupted. We conclude that cryoconite holes are dynamic ecosystems for microinvertebrates in the Arctic.

Key words: Arctic, Svalbard, Tardigrada, cryoconite holes, ecology, glaciers.

Introduction

Cryoconite holes are small, water-filled, cylindrical reservoirs occurring on the surface of glaciers throughout the world (*e.g.* Wharton *et al.* 1983, 1985; Mueller *et al.* 2001). Currently these holes are considered to be extreme micro-ecosystems (*e.g.* Mueller *et al.* 2001; Fountain *et al.* 2004; Hodson *et al.* 2008). The functioning of such habitats is possibly caused by a decrease in the albedo on the surface of a cryoconite-covered glacier and by the presence of various groups of microorganisms (McIntyre 1984; Takeuchi *et al.* 2001; Hodson *et al.* 2010; Kaczmarek *et al.* 2016). Pioneer observations and studies of cryoconite holes took place in Greenland between the 19th and 20th century (Drygalski 1897) and have continued through present day. So far, representatives of Rotifera, Nematoda, Annelida, Tardigrada and Arthropoda have been found in cryoconite holes in various zoogeographical regions (*e.g.* Zawierucha *et al.* 2015a). One of the most common taxa known to inhabit glaciers in polar regions are tardigrades (Dastych 1985; Zawierucha *et al.* 2015b).

Tardigrada, also known as water bears, are small microinvertebrates (*ca.* 50–2000 μm) inhabiting terrestrial and aquatic environments (Ramazzotti and Maucci 1983; Nelson *et al.* 2015). Because of their adaptations to unfavorable conditions they are known as one of the toughest animals on earth. They can survive at the bottom of the deep sea, on high mountains and even in space (Guidetti *et al.* 2012; Nelson *et al.* 2015). In cryoconite holes they may act as grazers and top predators in a multi-trophic food web (Vonnahme *et al.* 2016; Zawierucha *et al.* 2015a). Tardigrades and rotifers are proposed to have an impact on the size of microalgae colonies and to be important for nutrient recycling by feeding and digestion of their prey in cryoconite holes (Vonnahme *et al.* 2016). Studies designed to explore tardigrade fauna in cryoconite holes were conducted by *e.g.* De Smet and Van Rompu (1994), Grøngaard *et al.* (1999), Séméria (2003), Dastych *et al.* (2003) and Dastych (2004). Only Porazinska *et al.* (2004) conducted well-designed ecological studies on cryoconite-dwellng tardigrades in the Antarctic. Despite the papers which have been published so far, our knowledge of tardigrade ecology in cryoconite holes is still severely limited (Zawierucha *et al.* 2015a).

The relationship between area and species richness have been frequently discussed in the literature (*e.g.* Gaston and Blackburn 2000). The first studies to explore the relationship between area and population density were done by MacArthur and Wilson (1967), MacArthur *et al.* (1972) and Root (1973). However, little attention has been given to the relationship between area and individuals of higher taxon (*e.g.* phylum) densities. Connor *et al.* (2000) showed that the population density (insects, birds) is positively correlated with the area, but the authors did not discuss the correlation between generally individual densities of higher taxa and the area in general. According to Gaston and Matter (2002), individuals–area relationships need more detailed discussion and the relationship should always include densities per accompanying area. In glacier ecology only Porazinska *et al*. (2004) have proved that the diameter, the amount of sediment, and the concentrations of Na^+ were able to predict tardigrade abundances in Antarctica. In cryoconite holes at lower elevations the concentration of sediment is higher than in those located at higher elevations (Porazinska *et al*. 2004). Significant variations in tardigrade abundance between lower and higher elevations have also been observed in Antarctic cryoconite holes with different sediment content (Porazinska *et al*. 2004).

Since glaciers and ice sheets are forgotten biomes and one of the fastest disappearing habitats (Anesio and Laybourn-Parry 2012), studies on the ecology of animals in these habitats are urgently needed (Zawierucha *et al*. 2015a). So far, the most comprehensive ecological studies of cryoconite holes were conducted on bacterial communities (*e.g*. Stibal *et al*. 2006, 2008; Edwards *et al*. 2014) and knowledge of the larger organisms and top predators in cryoconite holes – microanimals – is seriously limited (Zawierucha *et al*. 2015a). In this study the relationship between area, depth and elevation of cryoconite holes and tardigrade densities is presented and some differences between Arctic and Antarctic systems are discussed.

Material and methods

Cryoconite material was collected from four glaciers on Spitsbergen (48 samples): I – ten samples from Hans Glacier (July, 2014) located in Hornsund; II – twenty-two from Nordenskiöld Glacier (July, August, 2014); III – four samples from Ebba Glacier (August, 2012) and IV – twelve from Hørbye Glacier (August, 2013, July, August, 2014) located in Billefjorden (Fig. 1).

Cryoconite samples from Hans Glacier were collected with disposable plastic Pasteur pipettes from the bottom of selected cryoconite holes and transferred to 15 cm^3 plastic test tubes. After collection, the samples were preserved in 96% ethyl alcohol. From each sample 1 cm^3 of sediments was scanned for tardigrades with a stereomicroscope. Then the wet sediments were weighed and again after drying them at room temperature for two days, the number of tardigrades were calculated per one gram of material.

Cryoconite holes on three glaciers around Billefjorden (Ebba Glacier, Hørbye Glacier, Nordenskiöld Glacier) were collected randomly using a large (500 cm^3) pooter (Southwood and Henderson 2000) within a 4.5 cm plastic ring (15 cm^2 area). All sampling equipment was washed with meltwater from the sampling site prior to sampling. In the lab, the samples were allowed to settle, the supernatant was removed and subsamples of sediment were counted in a counting chamber under a stereomicroscope. The sediments were weighed in a wet state and again after drying them at 50°C for 12 h. Taxa were identified using the key to the World Tardigrada (Ramazzotti and Maucci 1983).

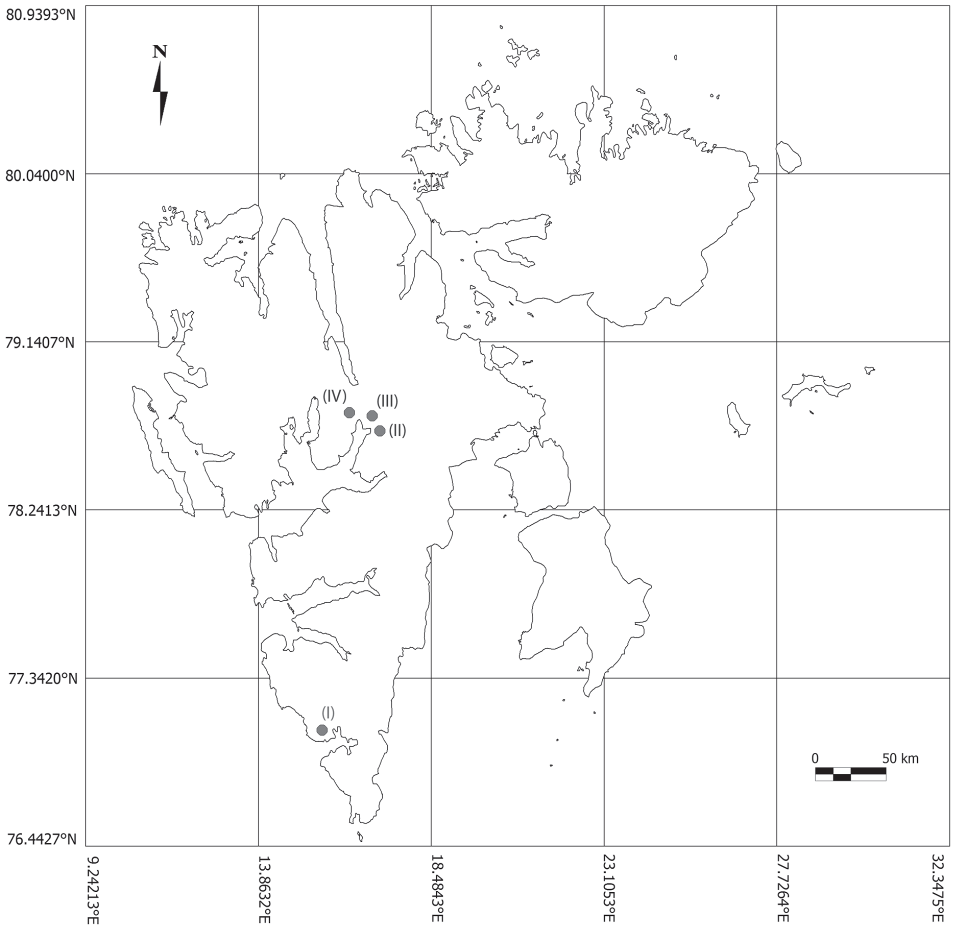

Fig. 1. Svalbard archipelago with sampled glaciers. I – Hansbreen, II – Nordenskiöldbreen, III – Ebbabreen, IV – Hørbyebreen.

The depth of cryoconite holes on all glaciers was measured on site with a ruler. The area of each cryoconite hole was calculated from calibrated photographic documentation with the Olympus cellSens Entry 1.11 software.

Data analysis

Full data, *i.e.* depth, area, elevation and the calculated number of tardigrades per gram of wet material, were obtained for 41 samples. However, three samples were excluded from all the analyses because of the extremely high: tardigrade densities (326 ind. g^{-1} sediment), depth (49 cm) and area (162831.9 cm^2). Thus, in analysis 38 samples have been used. For each cryoconite hole the relative area, depth, elevation and tardigrade density were calculated as the residual expressed as the differences between observed values and mean value. Thus, all the variables define how much the observed values (area, depth and elevation) in each cryoconite hole deviate from the average estimated for all samples. For the calculations we used General Linear Models (GLM) and backward selection of non-significant factors. All the calculations were performed with R 2.12.0 (R Development Core Team 2010). GLMs were developed for standarized area, depth and elevation as independent variables and for standarized tardigrade abundances as a dependent variable (n = 38). Among 48 cryoconite samples data for: tardigrade densities per gram of wet sediments, depth and area for six, three and seven samples respectively, were not available. Thus, in Table 1, data for 41 samples are presented.

Results and discussion

Tardigrada were present in 42 from 48 samples, which is 87.5% of all the collected samples. Five taxa were found in cryoconite holes, they are: *Hypsibius dujardini* (Doyère, 1840), *Hypsibius* sp. A, *Pilatobius recamieri* (Richters, 1911), one species of Ramazzottiidae Sands, McInnes, Marley, Goodall-Copestake, Convey and Linse, 2008, *Isohypsibius* sp. A. The mean (±SD) of cryoconite area was 1287.21±2400.8 cm^2, while the depth was on average 10.8±11.2 cm, the elevation 172.6±109.66 m a.s.l., and tardigrade density 24.9±33.0 ind. per g^{-1} wet weight (n = 38). The average numbers of tardigrades were 32 ind. cm^3, 23 ind. g^{-1} wet weight, 58 ind. g^{-1} dry weight in Hornsund and 6.13 ind. cm^2, 24.43 ind. g^{-1} wet weight, 46 ind. g^{-1} dry weight in Billefjorden (for all collected samples in Billefjorden). The densities of tardigrades on Hans Glacier reached values of up to 168 ind. cm^3, 104 ind. g^{-1} wet weight and 275 ind. g^{-1} dry weight. At Billefjorden up to 82 ind. cm^2, 326 ind. g^{-1} wet weight and 624 ind. g^{-1} dry weight were found. The model, which included area, depth and elevation as independent variables, cannot explain the Tardigrada density in cryoconite holes (GLM, F = 0.71, p = 0.54, R^2 = 0.059). Mean values of a.s.l., area, depth and number of tardigrades for each glacier (41 cryoconite samples) are presented in Table 1.

Quantitative data on the ecology and diversity of aquatic tardigrades are limited and different methods of collection and calculation were used in previous studies (*e.g.* Kathman and Nelson 1987), which makes the comparison of water bear assemblages in freshwater habitats impossible. The ecology of glacier tardigrades is almost unknown with only three papers published on this topic so far (De Smet and Van Rompu 1994; Dastych *et al.* 2003; Porazinska *et al.* 2004). But quantitative data for tardigrades were presented in only two of these papers (Dastych *et al.* 2003; Porazinska *et al.* 2004). According to Dastych *et al.* (2003) the abundance of tardigrades in glacier pools of water in the Alps

Table 1

Mean values of a.s.l., area, depth and number of tardigrades for Hansbreen, Nordenskiöldbreen, Ebbabreen, Hørbyebreen.

	N	Mean a.s.l. [m] (95% CL)	Mean area [cm^2] (95% CL)	Mean depth [cm] (95% CL)	Mean no. of tardigrades [ind g^{-1} of sediment] (95% CL)
Hansbreen	10	79.7 (64.3 – 95.0)	358.5 (55.6 – 661.4)	8.5 (4.2 – 12.7)	23.4 (0 – 49.4)
Nordenskiöld-breen	17	148.2 (115.0 – 181.4)	11875 (8199.3 – 31949.7)	19.0 (10.9 – 27.1)	22.8 (8.2 – 37.3)
Ebbabreen	4	319.2 (77.9 – 560.5)	1317.0 (137.0 – 2771.0)	12.9 (1.5 – 24.3)	136.1 (71.9 – 344.2)
Hørbyebreen	10	265.1 (211.0 – 319.1)	626.9 (412.4 – 841.4)	4.0 (0.5 – 7.5)	9.2 (1.8 – 16.6)

consisted of up to 75 individuals and up to 3.60 ind. cm^3 (360 ind. 100 cm^3) of meltwater current (Dastych *et al*. 2003). However, the data presented in Dastych *et al*. (2003) is not comparable to ours due to a different quantitative methodology (estimation of tardigrades per cryoconite hole or pooled samples in Dastych *et al*. (2003)). The densities of tardigrades in the present study are higher than in the studies conducted in the Antarctic (McMurdo Dry Valley) by Porazinska *et al*. (2004). In the Antarctic the highest concentration of tardigrades were *ca*. 12.5 ind. g^{-1} (1250 individuals per 100 g of dry sediment). However, Everitt (1981) reported that maximum tardigrades abundance in wet algal mats in tundra pond can reach 470 specimens g^{-1}, which is higher than the numbers currently observed in cryoconite holes.

Significant differences in tardigrade abundance between lower and higher elevations have also been observed in the Antarctic cryoconite holes with variations in the amount of sediments (Porazinska *et al*. 2004). Tardigrades were not significantly more abundant in cryoconite holes located in lower elevations in the present study.

Surprisingly, *ca*. 90% of samples examined in the present study contained tardigrades. This number of positive samples is similar to the results of previous studies conducted in tundra in the Svalbard – 71.7%–80% (Dastych 1985; Zawierucha *et al*. 2015b, 2016).

The lack of a significant relationship between tardigrade abundances and the abiotic factors examined can be explained by a more dynamic supraglacial hydrological system, frequent melting events, and less stable cryoconite holes in the Arctic, which can influence organism assemblages (Mueller *et al*. 2001; Fountain *et al*. 2004; Mueller and Pollard 2004). The hydrological system between cryoconite holes is important for the transport of nutrients and for the development of a drainage system near their surface (Gajda 1958). In the initial state, cryoconite holes are capable of storing water. Combined with supraglacial channels, they form a dynamic drainage system, which has conseqences for the internal morphology of the cryoconite holes, for example by enhancing heat transport or altering chemical properties (MacDonell and Fitzsimons 2008). On the glacier surface, stripping events take place, during which the cryoconite holes are melted away in a few days (Fountain *et al*. 2004; MacDonell and Fitzsimons 2008; Vonnahme *et al*. 2016). Additionally, partial stripping, which can impact the transport of fresh or relocated sediments, has been observed (MacDonell and Fitzsimons 2008).

Cryoconite holes in the Antarctic are wider, deeper and mostly covered with ice, which makes them more stable than the Arctic ones (Mueller *et al*. 2001; Fountain *et al*. 2004). High meltwater production and open cryoconite holes in the Arctic may negatively affect cryoconite communities because of inter-hole water-sediment mixing (Mueller and Pollard 2004). In comparison to the Antarctic ones, the Arctic cryocnite holes have a lower concentration of nutrients, which may be caused by the flushing or dilution effect (Mueller *et al*. 2001).

In the Arctic, factors depending on direct surroundings are most likely the important factors determining tardigarde abundances in cryoconite holes. Vonnahme *et al*. (2016) found a positive relationship between tardigrade abundances and the impact of guano input by sea birds on the same glaciers in Billefjorden. This very local phenomenon supplies a small, hydrologically connected area on the glacier with a large amount of nutrients (Zárský *et al*. 2013). These nutrients can fuel the base of the food web, which can act as a food source for higher trophic levels, such as tardigrades.

A new term – biocryomorphology – was embedded by Cook *et al*. (2015), which describes ice-organisms interaction. Glacier organisms can influence the size of cryoconite holes (McIntyre 1984), therefore, despite perturbations on the ice surface, high densities of tardigrades may influence speed of ice melting and cryoconite hole size. The shape of cryoconite hole together with glacier hydrology may be also a factor, which influences tardigrade communities. Thus, our data are the first attempt to complement the gaps in term of ice (area, depth, elevation of cryoconite holes) – invertebrate densities.

It could be stated that area, depth, and elevation do not influence tardigrade densities in cryoconite holes in the Arctic as much as the amount of nutrients, value of meltwater and the flushes of sediment.

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