RESEARCH/REVIEW ARTICLE

Tardigrades of Alaska: distribution patterns, diversity and species richness

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Abstract

During the summer of 2010, a biotic survey of tardigrades was conducted along a latitudinal transect in central Alaska from the Kenai Peninsula, via Fairbanks and the Arctic Circle to the coastal plain. Work was centred at the Toolik and Bonanza Creek Long Term Ecological Research Network sites and supplemented by opportunistic collections from the Kenai Peninsula and Anchorage areas. The 235 samples collected at 20 sites over 10 degrees of latitude yielded 1463 tardigrades representing two classes, three orders, 10 families, 23 genera and 73 species from 142 positive samples. A total of 50 species are new to Alaska, increasing the state's known species richness to 84. Several environmental metrics, such as pH, substrate, elevation, location and habitat were measured, recorded and analysed along the latitudinal gradient. Contrary to expectations, pH did not appear to be a predictor of tardigrade abundance or distribution. Density and species richness were relatively consistent across sites. However, the assemblages were highly variable within and between sites at only 14–20% similarity. We detected no correlation between species diversity and latitudinal or environmental gradients, though this may be affected by a high (59.9%) occurrence of single-species samples (containing individuals of only one species). Estimates of species richness were calculated for Alaska (118) and the Arctic (172). Our efforts increased the number of known species in Alaska to 84, and those results led us to question the validity of the estimate numbers.

Biodiversity is most often thought of as species richness or the number of species in a given area (Costello 2001), while declining biodiversity is a measure of species extinction (Chapin et al. 2000). The total number of species, the relationships between them and rates of extinction are particularly unclear (Jackson 2008). This is especially true for microscopic invertebrates in several under-studied taxonomic groups, such as the tardigrades (Costello et al. 2006).

Vicente (2010) used tardigrades and their significant survival capability as a case study to infer the danger of extinction for all other edaphic and hemi-edaphic micro-invertebrate taxa. He acknowledges that without baseline data sets, the impact(s) of global warming, habitat destruction and environmental pollution on micro-invertebrate diversity are difficult to measure. Clearly, there is a great need for biodiversity studies to support conservation of tardigrades and other minor taxonomic groups (Vicente 2010).

McInnes (1994) documented ca. 700 species of limno-terrestrial tardigrades, recorded more than half of those to the European Palearctic, but only 22 as cosmopolitan. Pilato & Binda (2001) considered 53 to be cosmopolitan and 493 Palearctic, but only 195 (39.5%) as Nearctic.

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Meyer & Hinton (2007) increased Nearctic numbers to 206 species. The current checklist (Guidetti & Bertolani 2005; Degma & Guidetti 2007; Degma et al. 2012) reports more than 1150 tardigrade species, of which ca. 170 are marine and over 1000 are limno-terrestrial species. Even so, the European (Palearctic) species bias does not make biological sense and is most likely explicable in terms of unequal sampling effort.

The first report of a tardigrade from Alaska was by Mathews (1938), who listed *Pseudechiniscus suillus* from south of Juneau. The second mention was 27 years later, when Schuster & Grigarick (1965) reported six species from Sand Point on the Alaskan Peninsula. Almost another 20 years passed before Dastych (1982) and Meininger & Spatt (1988) reported 27 and 12 species, respectively, from several sites along the Alaskan Highway, bringing the total to 32 (Table 1).

McInnes (1994) reports only four articles referencing Alaska, omitting Mathews (1938), but including Dastych (1991) for re-describing *Isohypsibius sattleri* (Richters, 1902), a species he had found in 1982. In her revision of the genus *Minibiotus*, Claxton (1998) reported the species *Minibiotus intermedius* from Denali National Park. Meyer & Hinton (2007) reviewed more than 100 publications relating to Nearctic species diversity realm, reporting 62 species from the "AS region", which includes Alaska and northern Canada. They cite the above Alaskan species and articles, along with the 30 species reported from Axel Heiberg Island, Canada (79°N, 90°W) (Weglarska & Kuc 1980).

More recently, Schill, Forster, Dandekar & Wolf, 2010 described *Paramacrobiotus fairbanksi* from the Fairbanks area. We have added a new *Oreella* species (Calloway et al. 2011), bringing the total of known species in Alaska to 34, representing 53% of the Nearctic fauna (Meyer & Hinton 2007), but only 3% of global species richness.

We collected tardigrades along a north–south transect through central Alaska, comparing tardigrade communities in terms of sample similarity, density differences and composition in relation to pH and other environmental factors. We used our data to estimate tardigrade diversity for Alaska and the Arctic.

Materials, methods and study area

Study area

During the summer of 2010, a biotic survey of tardigrades was conducted along a latitudinal transect in central Alaska from the Kenai Peninsula, via Fairbanks and the Arctic Circle to the coastal plain. These were supplemented by additional collections gathered between 2007 and 2010 between −147° and −151° longitude (Fig. 1, Table 1).

Sampling sites were grouped into four latitudinal "regions". (1) "Kenai" (60–61°N) comprised nine distinct sites between 60 and 62°N. (2) "Bonanza" (64°N) was made up of three sites in and around the Bonanza Creek Long Term Ecological Research site (LTER). (3) "Arctic Circle" (66°N) sampling took place on and near the Arctic Circle. (4) "Toolik" (68–69°N) samples were collected in the area of the Toolik LTER (Fig. 1, Table 1).

Sampling and processing

Hand-collected moss, lichen and leaf litter samples were placed in article bags labelled with global positioning system coordinates, substrate and habitat, and allowed to dry at ambient temperatures, prior to laboratory processing.

Dry samples were weighed on an auto-taring scale (Thermo Fisher Scientific, Waltham, MA) to ±0.1 g and 10 ml of spring water (pH ca. 7.00) added per gram of sample. After 30 min, the sample was stirred, distressed and the pH taken via a LabPro pH sensor and Logger Pro data retrieving software (Vernier Software & Technology, Beaverton, OR). On the following day, all tardigrades were removed from the sample using an EMZ dissecting microscope (Meiji Techno America, Santa Clara, CA, USA), at 20–30 ×, reflected light and an Irwin loop. Tardigrade numbers were divided by sample dry weight to derive comparative density data.

Specimens were permanently mounted on slides in polyvinyl alcohol (PVA) media for identification (Miller 1997). Additional specimens were preserved for subsequent DNA analysis or scanning electron microscope imaging. All slides associated with this study are archived at the Academy of Natural Sciences in Philadelphia. Tissues samples are stored at −80°C at Brigham Young University, remnants of the habitat samples are currently stored at Fresno City College, and collection metadata are contained in an online database (http://tegrity.fresnocitycollege.edu/johansson/).

Tardigrades were identified using a BX 51differential interference contrast (DIC) microscope (Olympus, Center Valley, PA, USA) along with the keys of Pilato & Binda (2011), Nelson & McInnes (2002), Rammazzotti & Maucci (1983) and current literature. Mounted specimens were photographed via an Olympus DP72 high-resolution digital camera mounted on the DIC microscope. Classification is derived from Degma et al. (2012).

Table 1 Tardigrade collections in Alaska, 2009, arranged from north to south latitudes.

Cluster	Site code[a]	Site	Latitude	Longitude	Elevation (m)	No. of samples	No. of positive samples	No. of specimens	No. of species
Toolik Lake	T	Roadside Creek	69.05930	148.49978	312.1	3	1	6	1
Toolik Lake	S	Sagway River	68.46167	148.50859	472.4	9	4	75	17
Toolik Lake	R	Slope Mountain	68.42592	149.02228	674.2	3	2	24	4
Toolik Lake	Q	Kupa River	68.38813	149.24832	755.9	5	1	1	1
Toolik Lake	P	Toolik field station	68.37695	149.35592	722.1	23	9	181	26
Toolik Lake	O	Brooks Range	68.14498	149.25371	906.8	14	3	25	9
Arctic Circle	N	Arctic Circle	66.33334	150.48644	361.8	1	1	3	1
Arctic Circle	M	Finger Mountain	66.21462	150.27686	650.7	12	7	92	18
Bonanza Creek	L	Alyeska Pipeline	64.92909	147.62944	238.7	3	1	6	1
Bonanza Creek	K	Winner Creek	64.51492	147.49820	205.7	13	6	11	3
Bonanza Creek	J	Bonanza Creek	64.42325	148.19439	160.6	31	22	176	20
Kenai Peninsula	I	Crows Creek	61.02707	149.07223	802.5	85	66	584	38
Kenai Peninsula	H	Girdwood Outlook	60.92840	149.34700	11.3	2	1	13	1
Kenai Peninsula	G	Granite Mine	60.57183	148.13301	183.2	5	3	89	5
Kenai Peninsula	F	Kenai Lake	60.49012	149.74716	247.2	1	1	5	1
Kenai Peninsula	E	Moose Pass	60.47070	149.40123	981.5	5	4	29	7
Kenai Peninsula	D	Seward Highway	60.39510	149.29020	375.2	9	3	29	5
Kenai Peninsula	C	Swetman Mine	60.36646	149.34685	165.5	3	1	25	2
Kenai Peninsula	B	Lost Lake	60.26337	149.42240	594.4	3	2	2	2
Kenai Peninsula	A	Brown Bear Prospect	60.20323	149.21058	177.7	5	4	87	13
Total						235	142	1463	

[a]See Fig. 1.

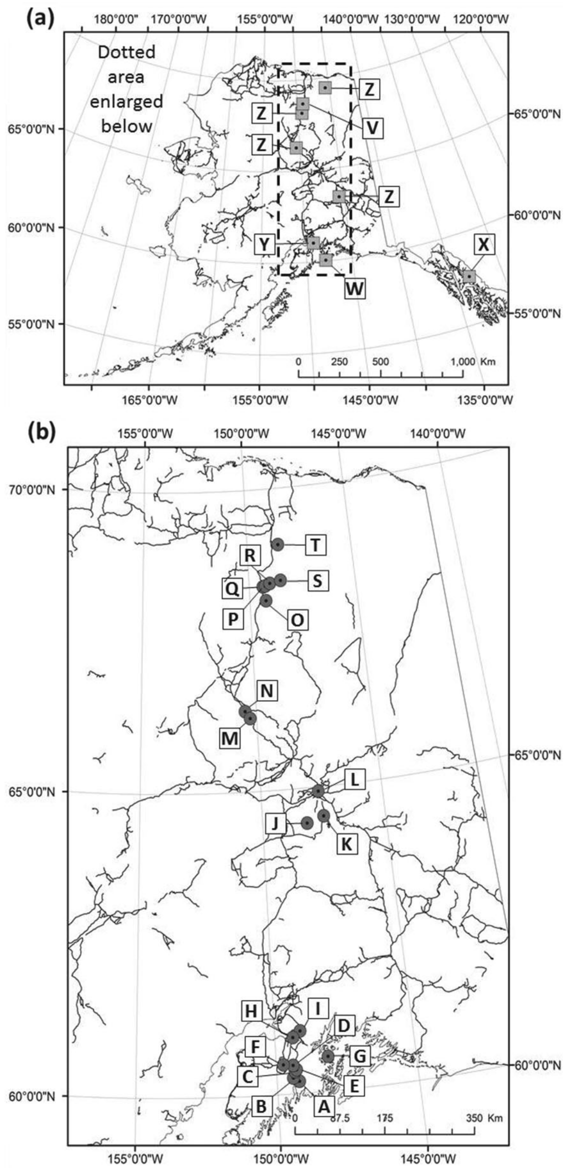

Fig. 1 Tardigrade collections: (a) prior collections by Meininger & Spratt (1988; V), Calloway et al. (2011; W), Mathews (1938; X), Schuster & Grigarick (1965; Y) and Dastych (1982; Z), and (b) collections in this study (letters correspond to site codes in Table 1).

Statistical methods

To determine the potential influence of pH, we compared the pH of tardigrade-positive with tardigrade-negative samples using ANOVA to test for differences.

To determine the probability of finding positive tardigrade samples with the same frequency along our latitudinal gradient, we normalized the data via an arcsine transformation for a Pearson's correlation analysis of individual samples. This test was also applied in determining if species richness changed along the latitudinal gradient. ANOVA, using PROC GLM in the SAS software package (SAS Institute 2006), was used to test for differences in density and species richness with the defined clusters as our dependent variable. We used the Bray-Curtis similarity index metric and analysis of similarity (ANOSIM) order to identify how community composition changed between samples both within and between sites, applying a fourth-root transformation to reduce variance within the density data. We deemed this appropriate because so many of the samples consisted of only a few individuals, often representing a single species (Legendre & Legendre 1998).

Estimates of species numbers. EstimateS version 8.2 software (Colwell et al. 2012) was used to estimate probable total tardigrade species numbers for central Alaska and the whole Arctic, reducing conflicts by eliminating genus-only identifications (Bartels & Nelson 2007). Data were divided into moss versus lichen habitats and high (>66°N) versus low (55–65°N) latitudes. Accumulation curves and estimated the species richness values were calculated for central Alaska based on the median of seven EstimateS estimators. Finally, the two habitat estimators were summed and percentage overlap (species occurring in both) was subtracted to estimate total species richness.

Results. A total of 142 of the 235 (58.9%) samples taken from the 20 sites were positive for at least one tardigrade species. The 1463 individual tardigrades collected represent 2 classes, 3 orders, 5 super-families, 10 families, 23 genera and 73 species. Some 50 species are new to Alaska, bringing species richness to 84 (Table 2). Some 41 species were unique to particular regions, including low-latitude Kenai (23), high-latitude Toolik (10), mid–low latitude Bonanza and Arctic Circle (2). Furthermore, 40 (54.7%) species occurred at only one site and 12 (16.4%) in all four regions.

There were no significant pH differences between samples that contained tardigrades and those that did not (d.f.$_{1,146}$ $F = 0.177$, $P = 0.675$). Correlation analysis indicated no significant (coefficient 0.189, $P = 0.365$) relationship between the probability of a positive sample and latitude. Indeed positive sample probability was relatively consistent throughout our study sites. There was no relationship between species richness and latitude (Pearson's correlation coefficient = −0.053, $P = 0.600$).

ANOVA indicated that tardigrade density did not vary significantly across each cluster d.f.$_{3,96}$ $F = 0.338$,

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Table 2 Tardigrades of Alaska

Family	Genus	Species	1938[a]	1965[a]	1982[a]	1988[a]	1998[a]	2010[a]	2012[a]	Site codes (north to south)[b]
Oreellidae										
	Oreella									
		O. chugachii Calloway, Miller, Johansson & Whiting, 2012							X	K
Echiniscidae										
	Echiniscus									
		E. arctomys Ehrenberg, 1853							X	C, G, I, M, P
		E. blumi blumi Richters, 1903							X	M
		E. columinis Murray, 1911[d]							X	G, I, K
		E. merokensis merokensis Richters. 1904			X				X	A
		E. oihonnae Richters, 1903							X	J
		E. postojnensis Mihelcic, 1967[c]							X	I
		E. quadrispinosus quadrispinosus Richters, 1902							X	J, M
		E. robertsi Schuster & Grigarick, 1965		X						
		E. testudo Doyère, 1840							X	I
		E. trisetosus Cuénot, 1932							X	R
		Echiniscus sp. A							X	J
		Echiniscus sp. B							X	A, E, G, I, J, P, R, S
	Hypechiniscus									
		H gladiator gladiator (Murray, 1905)		X	X				X	I, O
	Pseudechiniscus									
		P. facettalis Petersen, 1951							X	P
		P. suillus Ehrenberg, 1853	X	X					X	I
		P. victor Ehrenberg, 1853							X	S
		Pseudechiniscus sp.							X	I, P
Milnesiidae										
	Milnesium									
		M. eurystomum Maucci, 1991[e]							X	I, M, P
		Milnesium sp.			X				X	I, J, M, O, P, S
		Milnesium n. sp.							X	J, O, S
Eohypsibiidae										
	Bertolanius (*Amphibolus*)									
		Bertolanius sp.				X				
Calohypsibiidae										
	Calohypsibius									
		C. ornatus Richters, 1900		X					X	I, M
Hypsibiidae										
	Diphascon (*Diphascon*)									
		D. alpinum Murray, 1906		X	X				X	J
		D. bullatum Murray, 1905			X					
		D. iltisi Schuster & Grigarick, 1965			X				X	P
		D. nodulosum Ramazzotti, 1957							X	I
		D. oculatumoculatum Murray, 1906							X	I, J, K, M, P

Table 2 *Continued*

Family	Genus	Species	1938[a]	1965[a]	1982[a]	1988[a]	1998[a]	2010[a]	2012[a]	Site codes (north to south)[b]
		D. oculatumalpinum Mihelcic, 1964							X	I
		D. pingue pingue Marcus, 1936				X			X	I, J, P
		D. ramazzottii Robotii, 1970[e]							X	O
		D. rugosum Bartoš, 1935			X					
		D. stappersi Richters, 1911							X	P
		Diphascon sp.							X	A, E, G, H, I, J, M, P
	Diphascon (*Adropion*)									
		D. arduifrons Thulin, 1928							X	I, P
		D. belgicae Richters, 1911							X	I, P
		D. prosirostre Thulin, 1928			X	X			X	A
		D. scoticum Murray, 1905			X	X			X	I
	Hypsibius									
		H. convergens Urbanowicz, 1925			X				X	M, Q
		H. dujardini Doyère, 1840				X			X	J
		H. pallidus Thulin, 1911			X	X			X	C, D, I, J, L, O, P, S
		Hypsibius sp.								B, F, G, P
	Mesocrista									
		M. marcusi Rudescu, 1964[c]							X	I, P
		M. spitzbergensis (Richters, 1903)			X	X				
	Platicrista									
		P. angustata Murray, 1905			X	X			X	D, J, K, M
		P. cheleusis Kathman, 1990							X	I
		P. itaquasconoide Durante Pasa & Maucci, 1975[c]							X	I
Ramazzottidae										
	Ramazzottius									
		R. oberhaeuseri Doyère, 1840			X				X	B, I, J, M, R
		Ramazzottius sp.							X	I, J
Isohypsibioiidae										
	Isohypsibius									
		I. brevispinosus Iharos, 1966[e]							X	I
		I. duranteae Maucci, 1964[c]							X	S
		I. pauper Mihelcic, 1971[c]							X	S
		I. prosostomus Thulin, 1928							X	A, I, S
		I. sattleri Richters, 1902			X				X	J
		I. tuberculatus (Plate, 1888)			X					
		Isohypsibius sp. A			X				X	J
		Isohypsibius sp. B							X	E, I, M, P, S
	Pseudobiotus									
		Pseudobiotus sp.							X	S, T
Macrobiotidae										
	Adorybiotus									
		A. granulatus (Richters, 1903)			X	X			X	L, M, Q

Table 2 *Continued*

Family	Genus	Species	1938[a]	1965[a]	1982[a]	1988[a]	1998[a]	2010[a]	2012[a]	Site codes (north to south)[b]
		*Adorybiotus*sp.							X	M
	Macrobiotus									
		M. australis Pilato & D'Urso, 1976[c]							X	Q
		M. crenulatus Richters, 1904[e]							X	I, K, P
		M. echinogenitus Richters, 1904			X					
		M. furciger Murray, 1907[d]							X	X
		M. grandis Richters, 1911							X	A
		M. harmsworthi Murray, 1907			X	X			X	H, K, L, M, O, Q, R
		M. hufelandi C.A.S. Schultze, 1833		X	X	X			X	A, C, F, H, I, K, L, M, O, Q, R
		M. islandicus Richters, 1904		X	X				X	K
		M. montanus Murray, 1910			X					
		M. occidentalis Murray, 1910							X	K, N, Q
		M. pallarii Maucci, 1954							X	H
		M. recens Cuénot, 1932							X	H
		M. spectabilis Thulin, 1928			X				X	A, I, N
		Macrobiotus sp.							X	X
	Minibiotus									
		M. intermedius Plate, 1888			X		X		X	H, L, M, Q
		Minibiotus sp.							X	A, I, Q
	Paramacrobiotus									
		P. areolatus Murray, 1907							X	A, M
	Richtersius									
		R. coronifer Richters, 1903[e]							X	I, J, L, Q
	Tenuibiotus									
		T. fairbanksi Schill, Forster, Dandekar & Wolf, 2010						X		
		T. hystricogenitus Maucci, 1988[c]							X	Q
		T. willardi Pilato, 1977			X					
Murrayidae										
	Dactylobiotus									
		D. ambiguus (Murray, 1907)[e]							X	Q
	Murrayon									
		M. hastatus Murray, 1907							X	T
		M. hibernicus Murray, 1911			X					
		Totals	1	7	27	11	1	1	73	Total species 84

[a]1938 is Mathews 1938; 1965 is Schuster & Grigarick 1965; 1982 is Dastych 1982; 1988 is Meininger & Spatt 1988; 1998 is Claxton; 2010 is Schill et al.; and 2012 is this study.
[b]See Table 1 for site codes.
[c]New records for North America.
[d]New record for the Americas.
[e]New records for the United States.

$P = 0.798$), while Tukey's Honestly Significant Difference (HSD) test showed none of the clusters to be significantly different from each another (Fig. 2) suggesting a relatively constant tardigrade density across the latitudinal gradient.

However, ANOVA did show that species richness varies between clusters (d.f.$_{3,96}$ $F = 2.63$, $P = 0.055$), while Tukey's HSD test indicated the only significant pairwise difference was (high) Anchorage compared to (low) Bonanza (Fig. 3). ANOSIM suggests sample similarity within samples is very low, averaging 14–19% (Table 3), but is significantly dissimilar between clusters, irrespective of distance between samples (Global $R =$ 0.037, $P = 0.093$). Further examination of our data, using both principle component analysis and cluster analysis strongly supported our previous results.

EstimateS estimators proposed an Alaskan species richness of between 90 and 160 species; the median (Jack1 for both habitats) of all estimators estimates total species richness at 118 species or ca. 10% of global diversity.

Discussion

Taxonomic notes

Echiniscus arctomys sensu stricto, *Diphascon* (*Diphascon*) *rugosum* sensu stricto and *Tenuibiotus willardi* sensu stricto were previously reported from Alaska as "cf." or uncertain identifications. Mechalczyk et al. (2012) recently re-described *Milnesium tardigradum* from European material and stated that the presence of the species outside Europe was unconfirmed. Thus, all previous records from North America must be considered *Milnesium* sp. and we have found no *Milnesium tardigradum* (sensu Mechalczyk et al. 2012) in our Alaskan collections, but we are confident these contain at least one new species to be described later.

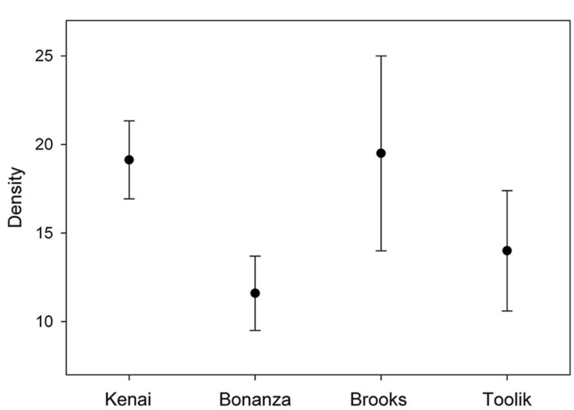

Fig. 2 Density of tardigrades from our four clusters of sites. No significant differences were found.

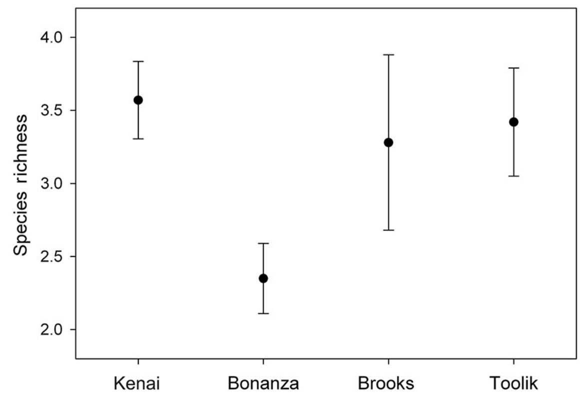

Fig. 3 Tardigrade richness from our four clusters of sites. Only the Bonanza and Kenai sites were significantly different from one another.

Ecological notes. While the survey was expected to add to the known tardigrade diversity of Alaska, a 150% increase is remarkable, as was the large number of species that occurred at only one sampling site. While we had collected large numbers of *Oreella chugachii* at one site, repeated sampling, over three years, in close proximity (within 500 m) yielded no other *O. chugachii* populations despite consistent finds at the original site. This unusual distributional pattern leads us to question species number estimates. It is unlikely that over 70% (84 of 118) of the predicted number of species in Alaska have been captured with this limited sampling scheme. Given Alaska's great size and apparent abundance of suitable habitat, we are convinced we could not be close to capturing all the extant species.

Although pH is often cited as an important factor influencing the distribution (e.g., site suitability), density and species richness of tardigrades (Meininger et al. 1985; Hoffman 1987; Dastych 1988; Meininger & Spatt 1988; Mitchell et al. 2009), not all studies have shown a strong influence of pH on species distributions (Johansson et al. 2011). This study does not support the influence of pH on either the probability of samples containing tardigrades nor on species richness. Certainly, upper and lower pH limits reduce distribution of tardigrades and those ranges may vary by species, but in our study, the presence or absence of tardigrades in microhabitats within a suitable range of pH appears to be either random or controlled by other unmeasured variables.

These observations are consistent with the idea that the tardigrade communities along the study transect may be structured as much by stochastic factors associated with dispersal as they are by variables associated with habitat suitability (Convey & McInnes 2005). For example, while pH may be important in influencing site suitability, it fails to emerge as "significant" because so many sites (including pH-suitable ones) remain unoccupied.

These results suggest minimal differences between the structure of tardigrade communities across Alaska with respect to species richness and density. The variation was insufficient to produce any significant patterns. Many taxonomic groups exhibit latitudinal diversity gradients (Rosenzweig 1995; Wu et al. 2009; Wu et al. 2011), but it does not appear to hold for tardigrades in this particular study area, suggesting the distribution data are not complete, or at least representative. It is likely the geographic distributions of many species are underestimated because Artic species diversity is grossly underestimated.

Interestingly, within and among site, similarity indices were both within a relatively narrow range (14–20%) indicating that samples in close proximity to one another were no more likely to share a similar tardigrade assemblage as any other two random locations across Alaska (Table 3). The low similarity in Alaskan tardigrade communities is largely the result of a few cosmopolitan species and a large number of species that appear in single/very few samples. Clearly, more work needs to be done to determine if, and at what spatial and temporal scales, common distributional patterns hold for these microscopic animals.

Meyer & Hinton (2007) reported that the Arctic and sub-Arctic tardigrade fauna was taxonomically quite different than that of the remaining North America. Our results tend to corroborate that observation. Comparison of the species make-up of other large-scale surveys in North America show that our Alaskan species list has only 14% overlap (19 out of 139 species occurred in both studies) with the Great Smoky Mountain National Park (GSMNP; Bartels & Nelson 2007), and a 21% overlap (21 out of 102 species) with the western North American study done by Schuster & Grigarick (1965).

Table 3 Similarity (%) within and among clusters for tardigrade communities across Alaska.

	Kenai Peninsula	Bonanza	Brooks Range	Toolik
Kenai Peninsula	17.76	16.42	20.20	13.96
Bonanza		18.92	18.55	14.34
Brooks Range			18.99	15.49
Toolik				14.08

Bartels & Nelson (2007) examined 6220 specimens from 231 samples in GSMNP and developed a list of 73 species. Using EstimateS version 7.5, they estimated the probable species richness in the park to be 96 with a range of 86–105 species. Following their methods, we estimated the probable species richness for central Alaska to be 118, within a range of 90–160 species. Considering that the GSMNP is located at temperate latitudes and is 0.13% of the land mass of Alaska, these are not directly comparable studies. However, the model they established is informative as to the prediction of the diversity of a defined area.

The new list (Table 2) of 84 species from central Alaska (55–69N, 149°W) surpasses the results of the other major Arctic collections. Peterson (1951) reported 34 species from sites around Greenland (62–82°N, 40°W). Weglarska & Kuc (1980) reported 63 species from Axel Heiberg Island, Canada (79°N, 90°W). Dastych (1985) reported 48 species from Spitsbergen (79°N, 19°E). Biserov (1999) reported 59 species from the Novaya Zemlya (74°N, 56°E). Biserov (1996) also reported 71 species from the Taimyr Peninsula (74°N, 96°E) and finally, Biserov (1998) reported 42 species from the Pacific islands of Komandorskyie (55°N, 167°E). Combined, these reports identify more than 127 species from north of 55°N, of which 58 (46%) were reported from only a single area and only nine species (7%) occurred in all Arctic areas. After combining these reports with the Alaskan collections, our EstimateS 8.2 estimators predicted that a total of 170 species (range 132–195) are likely to occur in the whole Arctic. Further whole-Arctic analysis is beyond the scope of this study.

To summarize, previous studies have only documented a small portion of the Nearctic tardigrade community. While general ecological patterns may apply to this group of meiofauna, the spatial scale at which this study was conducted failed to identify any traditional distributional patterns. The relatively large number of species that occurred at a single site may also have obscured patterns. Identification of which environmental parameters, if any, strongly influence the distribution of tardigrades remains elusive. We feel that additional data of the spatial–temporal variation in abundance of tardigrades and the processes that generate them are needed to understand the basic ecology of this under-studied group.

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