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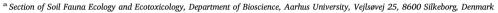
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Screening of cold tolerance in fifteen springtail species

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ABSTRACT

Springtails (Collembola) are ubiquitous and help ecosystem processes such as the decomposition of dead plant material. Their ability to survive low winter temperatures is an important trait that partly defines their geographic distribution. The cold tolerances of 15 laboratory-reared species of springtails were investigated. Springtails were cold acclimated in the laboratory over two months in order to simulate a seasonal change in temperature during autumn. Springtails were then exposed to decreasing sub-zero temperatures and at the same time simulating the moisture conditions in frozen soil. The cold tolerance of the species reflected well the climate of region of origin. Differential scanning calorimetry of individual springtails showed that melting points of body fluids did not become lower due to long-term cold acclimation (from 20° to 1.5° C). However, both water content and melting point of two arctic species (*Hypogastrura viatica* and *Protaphorura macfadyeni*) decreased drastically during exposure to sub-zero temperatures indicating cryoprotective dehydration (CPD). These arctic species survived exposure to -9° C for two weeks and -20° C for at least one week using CPD. Four other subarctic or cool temperate species also used CPD and survived -9° C for weeks, whereas springtails in culture from less cool temperate regions had poor cold tolerance.

1. Introduction

Springtails (Collembola) are widely distributed on every continent and are an important group of soil invertebrates that enhance the decomposition of dead plant material in various ecosystems (Hopkin, 1997). As for other ectothermic organisms, springtails' activities, growth, reproduction and population dynamics are strongly influenced by habitat temperature (Hopkin, 1997; Janion-Scheepers et al., 2018). Survival of extreme low temperatures in the habitat is an important component of fitness, which has prompted much research dealing with cold tolerance in this group of animals (Cannon and Block, 1988; Holmstrup, 2014; Zettel, 2000).

Springtails belong to the freeze-avoiding species (freezing of body fluids is lethal), and depend on the ability to remain unfrozen when temperature of their habitat is below the melting point of body fluids (Cannon and Block, 1988; Sømme, 1982). In general, freeze-avoiding species have physiological adaptations promoting the ability to supercool (Lee, 2010). In arthropods, these adaptations may include accumulation of low-molecular mass cryoprotectants (e.g. polyols or sugar alcohols), the masking or elimination of ice-nucleators and production of antifreeze proteins stabilizing the supercooled state (Zachariassen, 1985). Springtails are generally good supercoolers because they contain

small volumes of aqueous solutions with their minute body size (Zachariassen et al., 2004). Supercooling capacity is often enhanced if springtails have ceased feeding and emptied their gut for ice-nucleating food particles (Sømme and Block, 1982; Worland and Lukesova, 2000; Worland, 2005).

Many cold hardy springtail species, especially those that live in soil and litter, rely on cryoprotective dehydration (Sørensen and Holmstrup, 2011). This cold tolerance strategy is relevant for small soil invertebrates that have only little cuticular resistance to desiccating conditions, which includes many springtail species (Holmstrup, 2014; Holmstrup et al., 2002). Springtails relying on cryoprotective dehydration become gradually dehydrated at sub-zero temperatures due to the difference in vapor pressure between ice surrounding the animal and supercooled body fluids, and continue to desiccate until vapor pressure equilibrium is attained. These species therefore must tolerate both low temperature and extensive water loss during winter (Holmstrup et al., 2002).

Most studies on springtail cold tolerance have been concerned with measurement of the supercooling point (the temperature where the animal spontaneously freezes during cooling; SCP) in order to explain their survival in polar or alpine cold environments (Cannon and Block, 1988). This metric is easy to measure and can sometimes be a good

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proxy of cold tolerance in cold-hardy species living in polar or alpine environments, whereas it is not necessarily indicative of cold tolerance in chill-susceptible species from temperate environments (Bale, 1993; Baust and Rojas, 1985; Cannon and Block, 1988; Sinclair et al., 2015). Further, SCP has little relevance for cold tolerance in species that use cryoprotective dehydration (Holmstrup et al., 2002).

Compared to the number of papers on supercooling abilities of springtails, rather few studies have established lower lethal temperatures in long-lasting controlled laboratory experiments (Cannon and Block, 1988; Coulson and Birkemoe, 2000; Sørensen and Holmstrup, 2011). Cold tolerance of springtails and other soil invertebrates living in cold regions where soils are frozen every winter (e.g. arctic or subarctic regions) can be deduced from the mere presence of these species when combined with temperature measurements of soil layers where springtails overwinter (Addison, 1981; Birkemoe and Sømme, 1998; Convey et al., 2015; Coulson et al., 2000). Consequently, the potential cold tolerance of many polar species is well-known, whereas cold tolerance of temperate species/populations is much less studied.

The present study was an attempt to establish tolerance of long-term exposure to sub-zero temperature in 15 species of springtails from temperate and cold regions. In addition to assessment of survival after exposure to sub-zero temperatures, the investigation included thermal analysis (differential scanning calorimetry) of individual springtails giving information about SCP, body fluid melting points, and a quantification of the proportion of body water that was osmotically active.

2. Materials and methods

2.1. Springtail cultures

Fifteen species belonging to four families were used for the experiments (Table 1). Most species were collected in the field during previous field studies of the author, whereas a few were supplied from cultures of other laboratories. Sinella curviseta was provided in 2000 by M. L. Draney, University of Wisconsin, USA, from an old laboratory culture called the Crossley Culture. Onychiurus yodai was supplied by J. Qin, Chinese Academy of Sciences, Shanghai, China. Orchesella cincta was provided by S. Bahrndorff, Aalborg University, Denmark. Most species were maintained for several years in Petri dishes with moist plaster of Paris mixed with charcoal, and fed dried baker's yeast or green algae (only O. cincta) ad libitum. All species were kept at 20 °C with 12 h light and 12 h darkness. An exception from this procedure was Megaphorura arctica, that was collected in August 2017, on a beach near Sauðárkrókur, Iceland, and kept at 5 °C on a substrate consisting of decomposing brown algae until used in experiments ca. three months later.

2.2. Cold acclimation and cold tolerance

In order to gradually acclimate springtails to winter conditions, temperature was lowered from 20° to $1.5\,^\circ$ C in darkness over ca. two months simulating seasonal changes before exposure to sub-zero temperatures (Fig. 1). During this period, the springtails were not given additional food, but the plaster of Paris was watered when necessary to keep it moist.

When the springtails had been acclimated at 1.5 °C for about one month they were transferred to other containers that simulate exposure in frozen soil. Springtails were placed in vials (1.6 cm diameter and 3 cm high) closed with a fine mesh. The vials were placed in a 200 ml plastic beaker (7 cm diameter and 4 cm high) containing ca. 25 g of crushed ice. The plastic beakers were closed with a tightly fitting lid lined with rubber. The beakers containing ice and sample vials were placed in custom made freezing cabinets where temperature could be controlled with a precision of \pm 0.2 °C. Initially the beakers were held at -3 °C and then stepwise cooled to -20 °C (Fig. 1). Actual temperature (Fig. 1) was logged throughout the cold acclimation and cold

List of the species investigated and their region of origin (with approximate latitudinal and longitudinal coordinates). In addition, annual mean temperature and mean temperature of coldest month is indicated (data from Danish Meteorological Institute).

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Superfamily	Family	Species	Region of collection	Time in culture (approximately)	Latitude	Longitude	Annual mean temperature (°C)	Time in culture (approximately) Latitude Longitude Annual mean temperature (°C) Mean temperature of coldest month (°C)
Poduromorpha	Hypogastruridae	Hypogastruridae Hypogastrura assimilis	Rønde, Denmark	18 y	56°29 N	10°48 E	7.8	0
		Hypogastrura viatica	Ny Aalesund, Svalbard	4 y	N 86.82	11°87 E	- 5.2	- 15.3
		Ceratophysella denticulata	Jægerspris, Denmark	4 y	25°86 N	11°97 E	8	- 0.1
	Onychiuridae	Protaphorura fimata	Göttingen, Germany	20 y	51°49 N	9°84 E	8.5	- 0.4
		Protaphorura macfadyeni	Nuuk, Greenland	4 y	64°20 N	51°42 W	-1.4	- 8
		Protaphorura pseudovanderdrifti	Hveragerði, Iceland	3 y	64°00 N	21°10 W	4.6	- 0.3
		Protaphorura tricampata	Jægerspris, Denmark	6 y	25°86 N	11°97 E	8	- 0.1
		Megaphorura arctica	Sauðárkrókur, Iceland	3 months	65°52 N	19°44 W	3.3	- 2.1
		Onychiurus yodai	Shanghai, China	5 y	31°36 N	120°28 E	15.4	3.3
Entomobryomorpha Isotomidae	Isotomidae	Folsomia candida	Berlin, Germany	25 y	52°38 N	13°34 E	8.9	- 0.9
		Folsomia fimetaria	Askov, Denmark	20 y	55°27 N	9°05 E	7.5	- 0.1
		Proisotoma minuta	Jægerspris, Denmark	4 y	25°86 N	11°97 E	8	- 0.1
	Entomobryidae	Sinella curviseta	Vancouver, Canada	15 y	20°08 N	123°01 W	9.8	2.8
		Orchesella cincta	Alès, France	3 y	44°08 N	3°59 E	13.6	5.4
		Heteromurus nitidus	Rome, Italy	15 y	41°59 N	12°35 E	15.4	7.1

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