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Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal

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Summary

1. The ability of six species of high Arctic soil arthropod to survive oceanic transport in or on sea water was tested experimentally.
2. Five species of Collembola, *Hypogastrura tullbergi* (Schäffer), *Onychiurus groenlandicus* (Tullberg), *Onychiurus arcticus* (Tullberg), *Folsomia quadrioculata* (Tullberg) and *Tetracanthella arctica* Schött were exposed on the surface film of seawater in chambers agitated within a shaking water bath.
3. All five species survived for over 14 days, at the end of which survival among species varied between 27 and 100%.
4. In a separate experiment the cryptostigmatic mite *Camisia anomia* Colloff and the 'wettable' collembolan *T. arctica* survived submersion in sea water for longer than 2 weeks. Survival of *C. anomia* exceeded 75% but that of *T. arctica*, when submerged, fell to 12%.
5. Survival times are sufficient to permit ocean current transport from northern Norway to Svalbard in the high Arctic, a distance of around 700 km. The implications of the experiments for long-distance *trans*-oceanic dispersal of non-specialized soil arthropods are discussed.

Key-words: Barents Sea, Collembola, colonization, mite, Svalbard

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Introduction

There is much speculation as to how flightless terrestrial organisms have colonized remote islands. Explanations predominantly involve dispersal by strong winds, rafting on logs or vegetation and transportation by animals including people (e.g. Falla 1960; Lindroth *et al*. 1973; Fridriksson 1975; Coulson 2000). Evidence is largely circumstantial and there are few if any experimental data to demonstrate that ocean currents provide viable mechanisms that allow terrestrial animals to disperse over long distances.

We have recently considered the origins, following deglaciation, of the faunas of high Arctic islands such as the Svalbard archipelago including Björnoya and Jan Mayen (Coulson 2000). Here, in the high Arctic, a potential dispersal agent for animals exists in the form of driftwood washed into the Arctic oceans from the major river systems of Russia, Siberia and North America. Such driftwood is transported by ocean currents or caught up and carried by the Transpolar Current in the pack ice, to be deposited later at remote locations (Haggblom 1982; Eggertsson 1994; Dyke *et al*. 1997; Johansen 1998; Johansen & Hytteborn 2001). For example driftwood on Svalbard and Jan Mayen originates predominantly from the White Sea area of Russia and the from the Yenisey river system in Siberia (Eggertsson 1994; Johansen 1998).

Cryptostigmatic mites and Collembola are ubiquitous components of terrestrial soil communities and are the numerically dominant arthropods in the high Arctic (Bengtson, Fjellberg & Solhoy 1974). Several temperate species are adapted for life in marine littoral environments or, in the case of Collembola, on water surface films (e.g. Luxton 1967a,b; Christiansen 1978; Ehrnsberger, Sterzynska & Szeptycki 1997; Sterzynska & Ehrnsberger 2000). Some specialized species survive repeated salt- or freshwater inundation (Ernst 1995; McMeechan, Manica & Foster 2000) and are thus potentially susceptible to dispersal by saltwater. We therefore investigated whether common Arctic species of *terrestrial* cryptostigmatic mites and Collembola could similarly survive for extended periods on or in sea water, and whether this could serve as a mechanism aiding long-distance dispersal. Our results, described below, demonstrate that a wide range of species are capable of surviving for extended periods on the surface of agitated sea water and, perhaps more surprisingly, some species survive continual submersion.

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Materials and methods

Three separate experiments were conducted on five species of Collembola *Hypogastrura tullbergi* (Schäffer), *Onychiurus groenlandicus* (Tullberg), *Onychiurus arcticus* (Tullberg), *Folsomia quadrioculata* (Tullberg) and *Tetracanthella arctica* Schött and one species of cryptostigmatic mite, *Camisia anomia* Colloff. These were all common species associated with moss tundra growing within 1 km of the shoreline. Experimental animals were collected from sites adjacent to Ny-Ålesund, West Spitsbergen, Svalbard (78°55′ N, 11°54′ E), and experiments were conducted at the Natural Environment Research Council's Ny-Ålesund field laboratory. Availability of animals, coupled with a restricted field season, placed some limitations on experimental design.

The first experiment tested the ability of soil arthropods with hydrophobic cuticles to survive on the seawater surface film. Seawater (salinity = 26·3 g l^{-1}) was collected from the tidal central area of the outer Kongsfjord to minimize the dilution effects of runoff from glacial melt water. Four species of Collembola, *F. quadrioculata*, *H. tullbergi*, *O. groenlandicus* and *T. arctica*, were allowed to float on the sea water in 4-cm diameter sealed pots. Pots were maintained at *c.* 6–10 °C in a shaking water bath and continuously rocked to provide maximum agitation of the water while avoiding strong surface turbulence. For each species there were five animals per pot, replicated 44 times. Eleven replicates were examined on four subsequent sampling dates, after approximately 1, 3, 7 and 16 days. Results from earlier trials conducted in Liverpool using animals from laboratory culture provided guidelines for the sampling intervals used.

A second parallel experiment was conducted with the hydrophobic collembolan *O. arcticus* but the number of animals available led to a more limited experimental design using four replicate pots, each containing five animals. Pots were removed from the water bath at intervals over 14 days, the number of live animals counted without disturbance, and the pots then returned to the water bath. Each examination took less than 5 min.

The third experiment measured the ability of the wettable/sinkable species *C. anomia* and *T. arctica* to survive extended periods of submersion in sea water. It had previously been noted that the mite *C. anomia* was often active in fresh water following standard heat extraction and that the less hydrophobic collembolan *T. arctica* continued activity when sunk through the water surface film by gentle pressure with a fine paint brush. Experimental animals were exposed under 2 cm of sea water in 2-cm diameter sealed glass vials stored at *c.* 6–10 °C. These vials contained either five (*C. anomia*) or six (*T. arctica*) individuals and were replicated 12 times per species. Animals were examined regularly over 16 days by opening the vials but remained submerged throughout the experimental period. Inactive animals recorded as dead occasionally became active later and mortality data were adjusted to remove this anomaly.

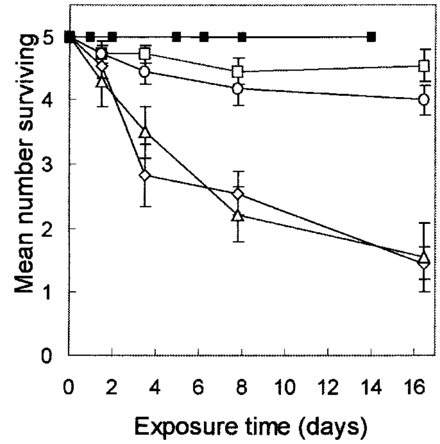

Fig. 1. Survival of Collembola species over time on the surface of agitated seawater. ◇ *F. quadrioculata*, □ *H. tullbergi*, △ *O. groenlandicus*, ○ *T. arctica* and ■ *O. arcticus*. Error terms are SE. Note that data for *O. arctica* are based on repeated observation of the same individuals whereas those for the other species are based on replicate samples.

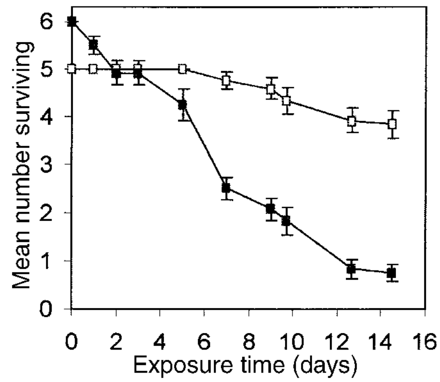

Fig. 2. Survival of *C. anomia* (□) and *T. arctica* (■) over time following submersion in sea water. Error terms are SE.

Results

All species in experiment 1 displayed the ability to survive the 16-day exposure to agitated sea water (Fig. 1). By the end of the experiment, however, there were significant differences in survival between species (one-way ANOVA $F_{3,40} = 22{\cdot}91$, $P < 0{\cdot}001$). Survival in *H. tullbergi* and *T. arctica* exceeded 80% whereas that for *O. groenlandicus* and *F. quadrioculata* was lower, but still about 30%. Experiment 2 suggested that *O. arcticus* was equally capable of surviving the similar experimental exposure, with its survival rate of 100% after 14 days matching that of *H. tullbergi* (Fig. 1).

Experiment 3 (Fig. 2) produced intriguing results. Both *C. anomia* and *T. arctica* survived submarine immersion for 15 days, with the survival rate for *C. anomia* exceeding 76%. By comparison with *C. anomia*, survival in *T. arctica* was significantly lower with 12% of animals surviving treatment (one-way ANOVA on percentage data (arcsin-transformed) $F_{1,22} = 92{\cdot}9$, $P < 0{\cdot}001$).

Discussion

Our results demonstrate that hydrophobic species of Collembola, such as *H. tullbergi* (91%), *O. arcticus* (100%), *O. groenlandicus* (34%) and *F. quadrioculata* (29%), can successfully survive periods of up to 16 days on the surface of agitated sea water. The less hydrophobic *T. arctica*, when held on the water film, showed similar long-term survival capacity (82%), without a general tendency to be lost through sinking. For each species much of the mortality occurred in the early part of the experiment and was probably associated with specimen handling rather than the direct effects of exposure to salt water. Further losses that cannot be attributed to sea water accrued from individuals becoming trapped on the vessel sides, effectively becoming isolated above the water level. The ability to survive salt water thus ranged across species with very different biologies, from surface-active, relatively drought-resistant species (*H. tullbergi*), through soil-dwelling desiccation-susceptible species (*O. arcticus*, *O. groenlandicus* and *F. quadrioculata*) to a species that inhabits wet moss (*T. arctica*).

Perhaps the more surprising result was the ability of both the cryptostigmatic mite (*C. anomia* 76%) and the collembolan (*T. arctica* 12%) to survive continued submersion in sea water, without access to atmospheric oxygen, for over 14 days. At the end of the experiment the survivors were still active under water. As a matter of interest the samples of *C. anomia* were brought back to the UK and maintained at 5 °C for a further 37 days, at the end of which 16% of the mites were still alive and active when warmed gently. Survival in cold sea water has similarly been noted in the Antarctic mites *Alaskozetes antarctica* (Michael) and *Cyrtolaelaps racovitzai* (Trouessart) (Strong 1967). It appears that when suspended in cold, well-oxygenated sea water (6–10 °C) the problems of oxygen availability and of the osmotic stresses of sea water, usually invoked for littoral species (Witteveen & Joosse 1987; Witteveen, Verhoef & Letschert 1987; Witteveen & Joosse 1988), are easily surmounted. It seems that animals obtain sufficient oxygen by diffusion across the cuticle. The respiration rate of adults of *Nothrus silvestris* (Nicolet), a close relative of *C. anomia* is around $7{\cdot}6 \times 10^{-3}$ μl O_2 h^{-1} (Webb 1969). Assuming that *C. anomia*, which is of similar size, has an equivalent rate of oxygen consumption, then in 16 days five adult *C. anomia* will consume 14·5 μl O_2. This is around a quarter to a third of the oxygen that would be present in the experimental tube, assuming initial oxygen saturation at 8 °C.

It is interesting to note that both *C. anomia* and *T. arctica* are less hydrophobic species that are often found in moss habitats and may already be partially preadapted for extended immersion in water. *Tetracanthella arctica* is particularly interesting in that it can survive on both the surface film and when submersed. Osmotic and desiccation stresses appear similarly to be overcome by hydrophobic species that are held on the water surface film. Sea water with a salt content of 26·3 g l^{-1}, as used in our experiments, creates an atmospheric relative humidity of about 98·2% within the experimental chamber. This is equivalent to soil humidity levels at the permanent wilting point of plants and imposes a potential desiccation stress on exposed animals (Bayley & Holmstrup 1999). For Collembola, which are particularly susceptible to desiccation, this suggests that our experimental animals obtained water from sea water or synthesized osmoprotectants.

How do terrestrial arthropods get into the sea? The obvious mechanism is in surface runoff water entering streams. Hertzberg (1997) and Hertzberg, Leinaas & Ims (1994), working on a relatively flat Arctic site on Svalbard with open vegetation, found some limited evidence for the surface water transport of Collembola. Observations of accumulations of Collembola on the surface of small pools and along the edges of eroding braided streams and runnels suggest that animals are transported by water, often in considerable numbers (S. J. Coulson *et al*., unpublished data; S. Hayward, personal communication). Gressitt & Yoshimoto (1974), however, recorded limited dispersal of mites and Collembola by wind at Point Barrow, Alaska.

These results have important implications for the transoceanic dispersal of Arctic mites and Collembola. They suggest that direct dispersal over considerable distances, on or in sea water, is feasible, without the need to invoke the attachment to driftwood. Attachment to such a potential carrier may, however, further enhance survival. Couple the ability of these arthropods to endure sea water with the ability to survive low temperatures for extended periods (Bale *et al*. 1997), then it is possible to conceive of animals surviving incorporation into and transportation in the pack ice, followed by successful release several years later. For example *H. tullbergi*, *O. groenlandicus* and *F. quadrioculata* have all been shown to survive a temperature of below −22 °C for over 4 years when frozen in damp soil (Coulson & Birkemoe 2000). Perhaps it not surprising that these two species are very broadly distributed within the Arctic and elsewhere (Fjellberg 1994). Recent studies of colonization by Collembola and mites of the Lovén Islands (3 km from the shore), which have recently emerged from below a tidewater glacier within Kongsfjord, West Spitsbergen (S. J. Coulson *et al*., unpublished data) provide similar evidence of effective dispersal across a saltwater barrier. *Hypogastrura tullbergi*, *F. quadrioculata* and *C. anomia* were already present on Leirholmen, the most recently emerged island, approximately 100 years old.

Experiments were conducted on organisms with predominantly Arctic distributions but there is every reason to suppose that transoceanic dispersal by mites and Collembola, employing the mechanisms described, is a wider phenomenon. Minimum survival

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times in our experiments are sufficient for animals potentially to travel considerable distances. For example, a conservative estimate of the average surface velocity of the Norwegian current, which sweeps past the north-west coast of Norway up past Björnoya and along the west coast of Spitsbergen, is 0·5 m s^{-1} (Poulain, Warn-Varnas & Niiler 1996; Loeng & Saetre 2001). This gives a potential journey time to Svalbard from the Norwegian coast of around 16 days, over a distance of about 700 km. Furthermore, several mites and Collembola are parthenogenetic and it would only require a single surviving individual for successful colonization to take place.

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