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SHORT NOTE

Seabird guano boosts body size of water bears (Tardigrada) inhabiting the arctic tundra

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Abstract (1) During the Arctic summer, little auks (*Alle alle*) deposit considerable amounts of guano on land. Ecosystems subsidised in nutrients are known to hold greater biodiversity and to produce grander biomass of plants and animals compared with areas where seabirds do not nest. (2) The aim of this study was to look into the relationship between guano fertilisation and body size of invertebrates inhabiting tundra. (3) The specimens of *Macrobiotus islandicus islandicus* Richters, 1904, a tardigrade dwelling in mosses and lichens of the Arctic, from six different populations from Spitsbergen (Hornsund fjord) were measured. Tardigrades were collected from areas different in terms of seabird guano effects on the tundra ecosystem. An overall body size index for tardigrades was calculated using a principal component analysis. (4) Here, we show that the body size of *M. i. islandicus* is larger in vicinities of the little auk colonies than in areas devoid of bird nesting sites. (5) Given that fitness of many invertebrates is positively correlated with their condition, our study underlines the ecological importance of a side effect of seabirds biology—the transfer of nutrients from the sea to the land.

Keywords *Alle alle* · Ecosystem subsidy · *Macrobiotus islandicus islandicus* · Svalbard

Introduction

Foraging at sea and breeding on land, polar seabirds deposit considerable amounts of guano in the tundra during the Arctic summer. In addition, they also enrich the land with feathers, egg shells and carcasses. Given that tundra soils are generally poorly developed, all this ornithogenic input is a main source of nutrients for tundra plant assemblages

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(Stempniewicz 2005; Zwolicki et al. 2013). With an estimated 37 million breeding pairs, the most abundant planktivorous alcid in the Atlantic Ocean and probably one of the most numerous seabirds in the world is the little auk, *Alle alle* (Linnaeus, 1758). Because the vast population of little auks transports enormous quantities of organic matter from the sea to the land, which results in greater plant diversity in areas of bird cliffs than in places where birds are not nesting, this bird is considered to be a keystone species in Arctic (Dubiel and Olech 1992; Isaksen and Gavrilo 2000; Stempniewicz et al. 2007). Rich vegetation around bird colonies attracts herbivorous vertebrates such as geese and reindeer (Jakubas et al. 2008) and provides a habitat for numerous invertebrate species, including water bears (Zmudczyńska et al. 2012; Zawierucha 2013; Coulson et al. 2014).

Water bears (Tardigrada) are a phylum of small (typically ca. 300 μm long) and cosmopolitan invertebrates. Terrestrial tardigrades dwell in a variety of habitats, such as mosses, lichens, liverworts, leaf litter and soil. Despite the fact that they are a permanent and ubiquitous element of polar ecosystems (e.g. McInnes 1994; Nelson 2002), their ecology in Arctic has been very poorly investigated (e.g. Dastych 1985). In this study, we measured body size of tardigrade *Macrobiotus islandicus islandicus* Richters, 1904 (Tardigrada: Eutardigrada: Macrobiotidae), collected from proximate vicinity and side away from breeding colonies of the little auk. This is the first ever attempt to assess the effect of guano fertilisation on body size of invertebrates.

Materials and methods

The samples of mosses and lichens were collected in the Svalbard archipelago, on southern slopes and terraces of the Hornsund fjord. The samples were collected on June 2010 (samples 3 and 6), July 2010 (samples 1, 4 and 5) and August 2011 (sample 2). Given that tardigrade species differ in mean body size, in order to properly test the hypothesis whether guano influences tardigrade body size, it is essential to measure specimens of a single species collected both in the proximate vicinity as well as in the side away from little auk colonies. Of 234 analysed samples only six contained at least a dozen of suitably oriented for measurements specimens of the same species, *M. i. islandicus*. Three of these samples were collected in the proximate vicinity of the little auk colony (i.e. up to ca. 100 m from a colony edge) and other three samples were collected from sites where there were no little auk colony (i.e. areas at least ca. 800 m from the nearest colony). All six samples comprised eggs, juveniles and adults, and thus, they did not differ in terms of age structure that could affect the results.

All samples were examined for tardigrades according to standard methods described by Ramazzotti and Maucci (1983). All specimens were mounted on microscopic slides in Hoyer's medium and examined with an Olympus BX 41 Phase Contrast Microscope. All measurements were performed with the Quick Photo Camera 2.3 software. The traits were measured only if they were intact and properly positioned.

Given that eutardigrade body is soft, its length is not a reliable estimate of the body size. However, there are sclerified structures, such as the bucco-pharyngeal apparatus, that are well correlated with body size while being rigid and therefore ideal for morphometry (Higgins 1959; Bartels et al. 2011). Thus, we measured the following standard characters of the buccal apparatus: buccal tube length, stylet support insertion point, buccal tube external and internal width, first macroplacoid length, second macroplacoid length and placoid row length. Since all these traits were highly correlated (all $P < 0.001$) and thus the co-linearity of biometric variables prevented their joint inclusion in the analysis (Quinn and Keough 2002), using the measurements of all the structures, a principal component analysis has been performed. The coordinates of the first principal component were used as a body size index. Such body size index (BSI) was correlated negatively with all measurements (all $P < 0.001$) and explained as much as 89 % of variation. Because this BSI is inversely proportional to body size, we multiplied the BSI by -1 in order to obtain a more intuitive unit (i.e. -BSI).

The hypothesis that body size of *M. i. islandicus* is affected by guano fertilisation was tested using a two-way nested ANOVA, with the guano state (absent/present) as an independent fixed factor, sample identity (ID 1–6) as an independent random factor nested in the fixed factor, and the -BSI as the dependent variable. Errors for means are 84 % confidence intervals to allow non-overlapping intervals to be interpreted as significantly different (Julious 2004). Statistics were calculated with Statistica (StatSoft) and SPSS (IBM).

Table 1 Results of a two-way nested ANOVA for the differences in the body size index of *M. i. islandicus* inhabiting cryptogams growing either in the direct vicinity of the little auk colonies producing guano or in sites where soils are not fertilised by guano

Source	*df*	MS	F	*P*
Guano	1	34.0	18.2	0.012
Sample(Guano)	4	1.9	2.9	0.025
Error	129	0.7		

Both factors (absence/presence of guano and sample ID (sample identity) nested in guano are statistically significant at $p < 0.05$). See Fig. 1 for means and confidence intervals

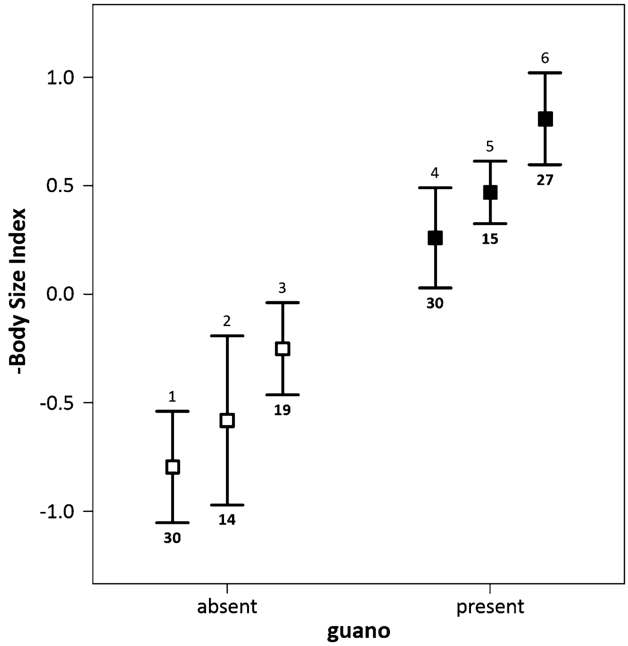

Fig. 1 Means ± 84 % confidence intervals for the differences in the body size index between populations of *Macrobiotus islandicus islandicus* inhabiting cryptogams growing either in the direct vicinity of the little auk colonies producing guano or in sites where soils are not fertilised by guano. Means are ordered from the lowest to the highest. Values above error whiskers are sample ID numbers whereas values below error whiskers represent numbers of measured specimens within each sample

Results

Both independent factors, the occurrence of guano and sample ID, significantly influenced tardigrade body size (see Table 1 for statistics and Fig. 1 for means with confidence intervals). Tardigrades collected from mosses growing in the direct vicinity of the little auk colonies were larger than those from sites where soils were not fertilised by guano. The significance of the random factor (sample ID) cannot be explained; however, it is not surprising that some other environmental factors we did not control for, such as subtle differences in slope exposition, humidity or stochastic effects, have resulted in differences between samples within both guano categories.

Discussion

Our results show that individuals of *M. i. islandicus* inhabiting areas influenced by little auk guano have relatively larger body size than those from the localities side away from the bird colony (Table 1 and Fig. 1). It has been established that the influx of nutrients is responsible for the formation of ornithogenic tundra covered by rich plant communities composed of creeping dwarf shrubs, herbs, mosses and lichens (e.g. Stempniewicz 2005; Stempniewicz et al. 2007). Even though we know very little about the biology of *M. i. islandicus*, macrobiotids in general, are considered omnivores (Ramazzotti and Maucci 1983). There is evidence that they can feed on plant cells (algae and mosses) as well as on animals that co-inhabit mosses, such as nematodes, rotifers and other tardigrades (Altiero and Rebecchi 2001). Thus, *M. i. islandicus* could benefit from guano fertilisation by consuming plants or animals or both. Nevertheless, what is important is that apart from obvious advantages such as greater reproductive success of better-fed animals, as shown, for example, in spiders (Kessler 1971) and in midges (Péry et al. 2002), tardigrades might benefit from larger body size by greater survival rates when going through cryptobiosis (a latent state enabling tardigrades to survive dry and cold periods of time). A successful transition from and to active and latent states is especially important in the Arctic regions, where polar summer is short and average temperatures are below freezing. Our findings are in accordance with Briggs et al. (2012) who found a positive impact of guano subsidies on body size and condition of geckos (*Lepidodactylus* sp.) inhabiting tropical islets in the Pacific. Also, Zmudczyńska et al. (2012) found 5–20 times higher densities and biomass of Collembola in the vicinities of Arctic seabird colonies, than in comparable control areas. Nevertheless, Zmudczyńska et al. (2012) did not show the effects of guano on collembolan body size, and thus, our study is the only available evidence for the relationship between guano fertilisation and individual invertebrate body size. However, there are also data suggesting that guano may have negative effects on invertebrate communities. Porazinska et al. (2002) and Smykla et al. (2012) showed that guano deposited by penguins in the Antarctic decreases tardigrade abundance compared with areas not inhabited by these birds. This contrasting result could be explained by the fact that penguins inhabit flat areas, where their droppings accumulate over seasons which inevitably translates into high soil salinities (Myrcha and Tatur 1991; Porazinska et al. 2002). Little auks, however, nest on cliffs and slopes from which the faeces are systematically washed down by rain and snow. This probably prevents overfertilisation and results in optimal amounts of nutrients delivered to the tundra ecosystems.

Given the fragmentary data and contrasting results, more research on other tardigrade species and also on other invertebrate groups are needed to further verify our findings and assess the impact of guano fertilisation on fitness of the tundra microfauna.

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