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Succession and phenology of the generalist predator *Mitopus morio* (Fabricius, 1799) (Opiliones) in a glacier foreland

SIGMUND HÅGVAR & DANIEL FLØ

Hågvar, S. & Flø, D. 2015. Succession and phenology of the generalist predator *Mitopus morio* (Fabricius, 1799) (Opiliones) in a glacier foreland. *Norwegian Journal of Entomology* 62, 210–215.

The 73 km^2 large Hardangerjøkulen glacier in southern Norway is shrinking due to climate change. Near the Midtdalsbreen glacier snout, surface-active invertebrates were sampled by pitfall trapping at sites with different age since deglaciation (3, 40, 63, 79, 160, and 205 years). Throughout this 1.1 km long gradient, *Mitopus morio* (Fabricius, 1799) (Opiliones) was a common surface active predator, with highest catches on 40 and 63 year old ground. The species greatly outnumbered the total catches of spiders except for the oldest site, and also outnumbered the total catches of carabid beetles at three of the sites (on 40, 160 and 205 year old ground). *M. morio* followed the receding glacier edge closely and was an important predator in the pioneer invertebrate community. On three year old, vegetation-free ground, pitfall catches of *M. morio* were only slightly lower than that of the dominant carabid beetle *Bembidion hastii* C.R. Sahlberg, 1827. *M. morio* was active throughout the snow-free season. It had a one-year life cycle, hatching at snowmelt and with egg-laying adults in the autumn. Phenology expressed by pitfall catches may vary between years and is probably influenced by weather.

Key words: *Mitopus morio*, Opiliones, chronosequence, alpine, primary succession, community assembly.

Sigmund Hågvar, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway. E-mail: sigmund.hagvar@nmbu.no

Daniel Flø, The Norwegian Institute of Bioeconomy Research, P.O. Box 115, NO-1431 Ås, Norway. E-mail: daniel.flo@nibio.no

Introduction

Mitopus morio (Fabricius, 1799) (Figure 1) is a common harvestman (Opiliones) in Norway, occurring in many habitats from lowland to high altitudes (Slagsvold 1976). The species is a generalist predator which consumes both living and dead invertebrates (Phillipson 1960a,b, Hågvar & Ohlson 2013). Although being a rather large invertebrate, it is able to complete its life cycle during the short, snow-free season in alpine habitats. Using pitfall traps during three years in five high mountain habitats at Finse, southern Norway, Hågvar *et al*. (1978) showed that *M. morio* was the most surface-active macroinvertebrate species in all habitats, usually giving higher catches than spiders as well as the two beetle families Carabidae and Staphylinidae.

The 73 km^2 large Hardangerjøkulen glacier in southern Norway has been receding since A.D. 1750, with increasing rate during the last decades (Hågvar & Ohlson 2013). In front of Midtdalsbreen glacier snout near Finse (60°34’30’’N, 7°27’40’’E), there is a 1.1 km long foreland in which the soil age since deglaciation is rather well known for the last 250 years, mainly due to characteristic moraines. The foreland is in the treeless low- and mid-alpine zone, between 1300 and 1400 meters above sea level. This gradient, where distance from the glacier edge is a substitute for time, is

FIGURE 1. *Mitopus morio* (Fabricius, 1799) (Opiliones) is a common generalist predator, occurring from lowland to alpine habitats. Photo: Ed Nieuwenhuys.

called a chronosequence (Kaufmann 2001). It is like an ecological laboratory, where invertebrate succession can be studied. So far, succession has been described among soil mites (Acari) (Hågvar *et al*. 2009), soil springtails (Collembola) (Hågvar 2010), and surface-active spiders (Aranea) and beetles (Coleoptera) (Bråten *et al*. 2012, Hågvar 2012). From the two year long pitfall program in the foreland described by Bråten *et al*. (2012), a large material of *M. morio* remains unpublished. Here we present data on succession and phenology of this important generalist predator, spanning an age gradient from 3 to 205 years in the glacier foreland.

Material and methods

During 2007 and 2008, intensive pitfall trapping were performed at sites with known age, in order to describe the primary succession of surface-active invertebrates. In 2007, twenty pitfall traps of 6.5 cm diameter were operated during the snow-free season at sites with the following ages: 39, 62, 78, 159, and 204 years. Next year, a barren, three year old moraine was added as a sampling site (Figure 2). Table 1 shows distance from glacier edge and mean vegetation cover for the six sampling sites. More detailed information on the foreland, sampling sites and sampling procedure was given by Bråten *et al*. (2012). Traps were emptied every second week. In 2011, an additional sampling was performed on the 2005-moraine, with 50 traps. All data are presented as catches per 20 traps during two-week periods.

Results

Seasonal variations in catches for sites which were sampled both years are shown in Figure 3. In 2007, the sampling started later than in 2008, but lasted longer. Both years, the highest maxima were on 39–40 year old ground, which had a vegetation cover of only 6%. The next highest maxima were on 62–63 year old ground. The lower part of the

TABLE 1. Age since deglaciation, distance from glacier edge, and mean vegetation cover in the six sampling sites.

Sampling site No.	1	2	3	4	5	6
Age (2008)	3	40	63	79	160	205
Distance from glacier (m)	15	70	470	810	1010	1100
Mean vegetation cover (%)	0	6	91	80	80	96

FIGURE 2. The barren 2005-moraine photographed in 2009. Roofs covering pitfall traps are seen. Photo: Sigmund Hågvar.

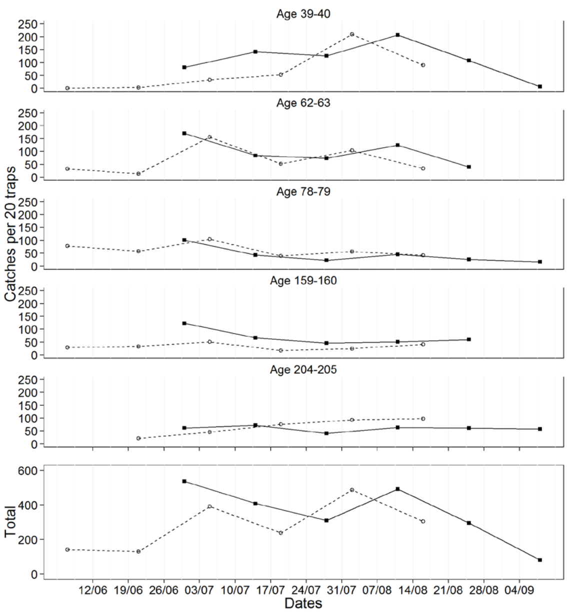

FIGURE 3. Pitfall catches (per 20 traps) of *Mitopus morio* (Fabricius, 1799) on sites with different age since deglaciation. Whole line: 2007, stippled line: 2008. Each value has been placed in the middle of a two-week trapping period.

figure shows the total catches for all sites.

The catches on the 2005-moraine in 2008 and 2011 is illustrated in Figure 4. Maximum catch per 20 traps in 2008 was 57 animals, which was about one fourth of the maximum catch in the 40 year old site, but similar to the highest catch on 160 year old ground (Figure 3). In 2011, July catches were similar to 2008, but August catches were lower.

In Figure 5, the total catches at different sites within each year have been related to time since deglaciation. In 2007, the highest catches were on 39-year-old soil, which had the most scarce vegetation cover. Also in 2008, this site had high catches, but also 63 and 79 year old sites with a dense vegetation cover had similar total catches. The three-year-old moraine without vegetation had a considerable catch of 158 specimens, nearly as much as on 160-year-old ground. In none of the two years had the two oldest sites the highest catches. Figure 5 illustrates that *M. morio* uses the whole glacier foreland including freshly exposed ground, but the relative catches within the age gradient may vary between years.

Discussion

Phenology of *M. morio*

Hågvar *et al*. (1978) showed that the phenology pattern of *M. morio* varied between three succeeding years in the Finse area. Moreover, the relative catches between habitats could vary both between years and throughout the season. They suggested that high general catches in August 1969 and 1971 were due to warm and dry weather. In a large study from several Norwegian localities Slagsvold (1976) demonstrated a correlation between mean air temperature and pitfall catches of this species.

In the studied material, two peaks

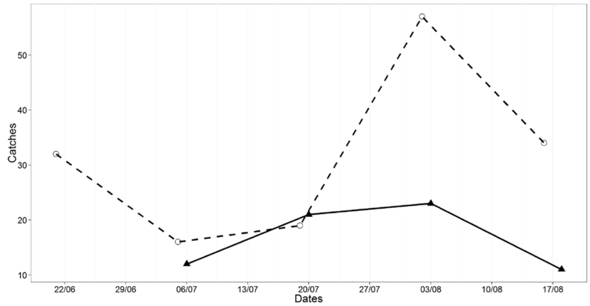

FIGURE 4. Pitfall catches (per 20 traps) of *Mitopus morio* (Fabricius, 1799) on a moraine formed in 2005. Whole line: 2011, stippled line: 2008. Each value has been placed in the middle of a two-week trapping period.

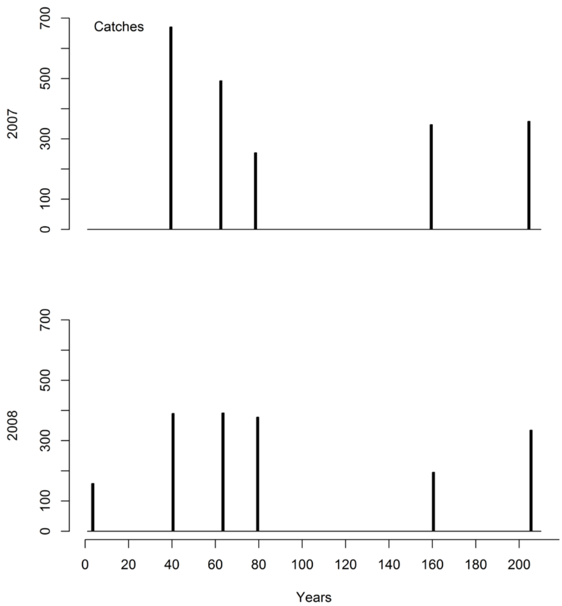

FIGURE 5. Total pitfall catches of *Mitopus morio* (Fabricius, 1799) in 2007 and 2008 on sites with different age since deglaciation.

appeared in the total catches both years (Figure 3, bottom): one in early July and one in early August. This could be due to high density of young animals in July and high activity of large adults and preadults in August. However, this pattern is not consistent between all sampling sites. The local climate at each sampling site is probably important, and this may depend highly on vegetation cover and distance from the glacier.

Succession and role in the foreland

The catches on three year old ground in 2008 (Figure 4) show that *M. morio* followed the receding glacier edge closely. The species belongs to the pioneer community, which is established on pristine, barren ground before any vegetation is visible. According to Phillipson (1960a,b), *M. morio* is a generalist predator, consuming both living and dead prey. Gut analyses of 29 specimens from the three-year-old moraine showed that they fed on both inblown (Flø & Hågvar 2003) and resident invertebrates (Hågvar & Ohlson 2013, Hågvar & Pedersen 2015). Among resident prey were chironomid midges, which developed in young ponds on the moraine. The sediment-living chironomid larvae assimilated ancient carbon released by the melting glacier, and adult midges had a radiocarbon age of 1040 years. By eating these midges, which were "marked" with ancient carbon, *M. morio* specimens achieved a radiocarbon age of 570 years (Hågvar & Ohlson 2013). We assume that adult chironomid midges often end on the ground, for instance during bad swarming conditions, and they frequently dropped into our traps. In addition, four resident springtail species were eaten. Among airborne (allochthonous) prey were aphids and butterflies (Hågvar & Ohlson 2013, Hågvar and Pedersen 2015).

Hodkinson *et al*. (2001, 2002) and Coulson *et al*. (2003) have pointed to the ecological paradox that various predators as spiders (Aranea), ground beetles (Carabidae), and harvestmen (Opiliones) are generally observed before herbivores and plants on pioneer ground, for instance in glacier forelands. According to classic ecology, a primary succession should start with plants, followed by herbivores, and then allow predators to establish. They assumed that airborne prey was the answer, either due to wind transport or to active flight. However, as shown above, even the barren ground may produce prey, partly as chironomid midges hatching from young ponds, and partly as pioneer springtails (Collembola). Hågvar & Ohlson (2013) and Hågvar & Pedersen (2015) showed that the relevant springtails were in fact herbivores, grazing on invisible biofilm with diatom algae, or on barely visible pioneer mosses. Hågvar & Ohlson (2013) called the barren ground "the invisible carbon source community", being supported partly by ancient carbon delivered by the glacier, and partly by early, but cryptic photosynthesis in algae and mosses.

Pitfall traps measure surface activity, and the catches depend on three factors; 1. The density of animals. 2. The degree of activity of individuals, and 3. Restrictions to active movement due to obstructions, mainly vegetation (e.g. Southwood 1966, Westerberg 1977, Westerberg & Granström 1977). The second factor is influenced by developmental stage and microclimate. Only in habitats with similar surface structure and vegetation, as well as microclimate, may catches be taken as relative measures of density. The high catches on 40-year-old ground (Figure 3) may be explained by a combination of nearly vegetation-free ground, and sufficient age of the site for efficient colonisation. A barren ground has few obstacles for movements and may be considerably heated by the sun.

Although not being a measure of relative density, pitfall data on surface activity could reflect relative differences in predation pressure. According to Phillipson (1960a), *M. morio* identifies prey by touch, which means that the number of prey items encountered increases with walking speed. Being a large invertebrate with widespread legs, an individual is able to sample prey from a considerable surface area during a day's walk. *M. morio* can walk rather fast and is active at daytime. An efficient predation technique combined with a great habitat tolerance may explain its ability to fulfil its life cycle during the short snow-free season.

Two other important predator groups in the glacier foreland are carabid beetles and spiders. In three sites (on 40, 160 and 205 year old ground), catches of *M. morio* outnumbered the total catches of carabid beetles. On three year old, vegetation-free ground, total catches of *M. morio* were only slightly lower than that of the dominant carabid beetle *Bembidion hastii* C. R. Sahlberg, 1827. Although spiders have different hunting methods, it can be noted that *M. morio* greatly outnumbered the total catches of spiders, except for in the oldest site (Bråten *et al*. 2012).

Hågvar *et al*. (1978) documented that *M. morio* was a very common predator in five common, but rather different alpine habitats in the Finse area. The present data show that the species is a significant predator even in younger habitats, and belongs to the pioneer community close to the receding glacier. Its high habitat tolerance and the ability to colonise pioneer ground has been confirmed by other studies. An extensive pitfall study by Vater (2006) in several glacier forelands in southern Norway concluded that *M. morio* belonged to the pioneer invertebrates. For instance, the species dominated the pitfall catches on 0-20 year old ground near Storbreen in Jotunheimen, and was taken abundantly also in older sites (Vater 2012). Matthews and Vater (2015) and Vater & Matthews (2015) further elaborated the pioneer function of *M. morio*, as well as its persistence in later successional stages in various Norwegian glacier forelands. Also in the Alps, *Mitopus* species (*M. morio* or *Mitopus glacialis* (Heer, 1845)), belong to the pioneer invertebrates in glacier forelands (Kaufmann 2001, Raso *et al*. 2014).

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Received: 5 November 2015
Accepted: 23 November 2015