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BIODIVERSITY RESEARCH

Aerial colonization of high Arctic islands by invertebrates: the diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) as a potential indicator species

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Abstract. The restricted animal communities of the high Arctic islands are due, in part, to extreme geographical isolation. Migration via wind currents is one mechanism by which invasion of new species may occur. Here, we describe immigration of the non-resident migratory moth, *Plutella xylostella*, into Svalbard during 2000. This was associated with a warm south-easterly air mass that crossed from W. Russia: moths appear to have covered the 800 km to Svalbard in under 48 h, flying at an altitude between 500 and 1500 m. These events thus provide a case study for wind-dispersed movements of invertebrates to high Arctic regions. Climate change scenarios predict increased frequency of such air masses and also of the warm dry weather associated with increased aerial insect transport. The general factors determining successful colonization of the high Arctic by wind-dispersed animals are discussed, using *P. xylostella* as a model species whose important life history and physiological attributes are well known.

Key words. adaptation, colonization, ecophysiology, host plant, migration, survival.

INTRODUCTION

Successful mapping of the distribution response of organisms to changing climate requires an understanding of their migration characteristics and their physiological responses to an altered 'climatic envelope' (Davis *et al.*, 1998; Baker *et al.*, 2000). The island archipelagos of the high Arctic, however, are geographically remote, limiting the potential for gradual and ordered diffusion of invading species in response to climatic amelioration (see Clark, 1998), with the intervening expanses of ocean/pack ice and continental ice sheets representing formidable barriers to colonization. Climate change scenarios predict, nevertheless, that the high Arctic will experience the greatest and most rapid climatic shifts that will occur within the next 100 years (Serreze *et al.*, 2000; IPCC, 2001) and that these will be associated with changes in atmospheric circulation patterns (Walsh *et al.*, 1996; Hanssen-Bauer & Førland, 1998, 2001). This implies that the simple high Arctic faunas (e.g. Coulson & Refseth, in press) will become potentially more susceptible to invasion by more southerly species — provided the animals can reach there and survive.

Here we examine current evidence for aerial insect invasions into the Svalbard archipelago lying at 74°81′N, 10°35′E, almost 800 km from mainland Europe. We place particular emphasis

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on the diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae), presenting a detailed climatic analysis for the period coinciding with a major immigration into Svalbard during 2000. *P. xylostella*, an invasive non-indigenous species, is particularly conspicuous on Svalbard because of its pale colouration, relatively large size and abundance. The absence of other flying Lepidoptera species make it immediately obvious. We argue that invasion by *P. xylostella* coincides with, and thereby signals, the opening of a synoptic meteorological window that provides a potential gateway to the high Arctic for many aerially dispersing arthropods. These other arthropods, including Diptera, Hymenoptera, Hemiptera, Arenaea and Tardigrada, are usually smaller and less conspicuous than *P. xylostella* and their immediate arrival on Svalbard is likely to pass relatively unnoticed, despite their potential ecological significance. For example, we have recently recorded the presence of common species of parasitoid Hymenoptera that are unlikely to have escaped prior notice in earlier extensive faunal sampling programmes (Coulson *et al*., 2002).

P. xylostella, because its ecophysiology and general ecology are well known (Harcourt, 1957; Talekar & Shelton, 1993), serves as a useful model species against which to test general principles regarding the invasion by new species at high latitudes. It is a well-known migrant (Williams, 1958; Kaisila, 1962; Shaw, 1962; Lindroth *et al*., 1973) with a worldwide distribution and it has already successfully colonized the remote subAntarctic Marion Island (Chown & Avenant, 1992). Elsewhere it has no resting winter stage, is multivoltine and develops slowly throughout the winter at warmer latitudes. In Europe and Russia it overwinters in the south and migrates northwards into temporary breeding areas, such as the United Kingdom and Scandinavia during spring, where larvae often become pests of cruciferous crops and weeds.

Ten species of non-resident migratory insect, mainly of European origin, have been recorded sporadically from Svalbard over the last 170 years (Parry, 1828; Elton, 1925; Elton & Longstaff, 1934; Kaisila, 1973; Lokki *et al*., 1978), suggesting that species immigration is a sporadic but perhaps not infrequent event. Several species have sometimes been observed together. It raises the question of under what conditions successful immigration takes place and what are the barriers that these insects must overcome to become established? Invasion is essentially a catenary process that can be split into sequential phases involving initial population build-up in a remote source area, long-range migration into the new area, followed by survival and establishment of a breeding population in the new habitat. At each stage interaction between the physical environment and the ecophysiological tolerances of the invading species determines whether a stage is successfully negotiated. Successful establishment requires each successive stage to be completed successfully.

Initially we discuss data for the mass immigration of *P. xylostella* into Svalbard during summer 2000, when adult moths survived and remained active over an extended period. We then consider, using *P. xylostella* as a model species, the ecological and physiological barriers that must be overcome for the successful establishment of wind-dispersed arthropods on Svalbard in particular and the high Arctic in general. It is worth noting that Bjørnøya, the only potential island staging post between Svalbard and Europe presents essentially similar ecological barriers to Svalbard.

RECONSTRUCTION OF THE *PLUTELLA XYLOSTELLA* IMMIGRATION OF SUMMER 2000

During summer 2000, *P. xylostella* was first seen on 20 July (until 10 August) near Ny-Ålesund, Kongsfjord, Spitsbergen (78°55′N, 11°54′E) and was recorded subsequently on successively later dates at Semeldalen, Van Mijenfjord (22 July–10 August), Recherchefjord, Bellsund (2 August), Coraholmen, Ekmanfjord (3 August) and Heclahuken, Sorgfjord (7 August). The initial sighting at Ny-Ålesund records accurately the first arrival of the insect. By comparison, despite extensive summer fieldwork at Ny-Ålesund during 1991–94 and 1997–2000, the only Svalbard record of *P. xylostella* within these periods was for Fugelsangen, NW Spitsbergen in 1998.

On 17–19 July a warm airstream at 850 hPa (standard pressure level to describe the state of the atmosphere at an altitude of around 1500 m) flowed north-westwards (Fig. 1). The migrating

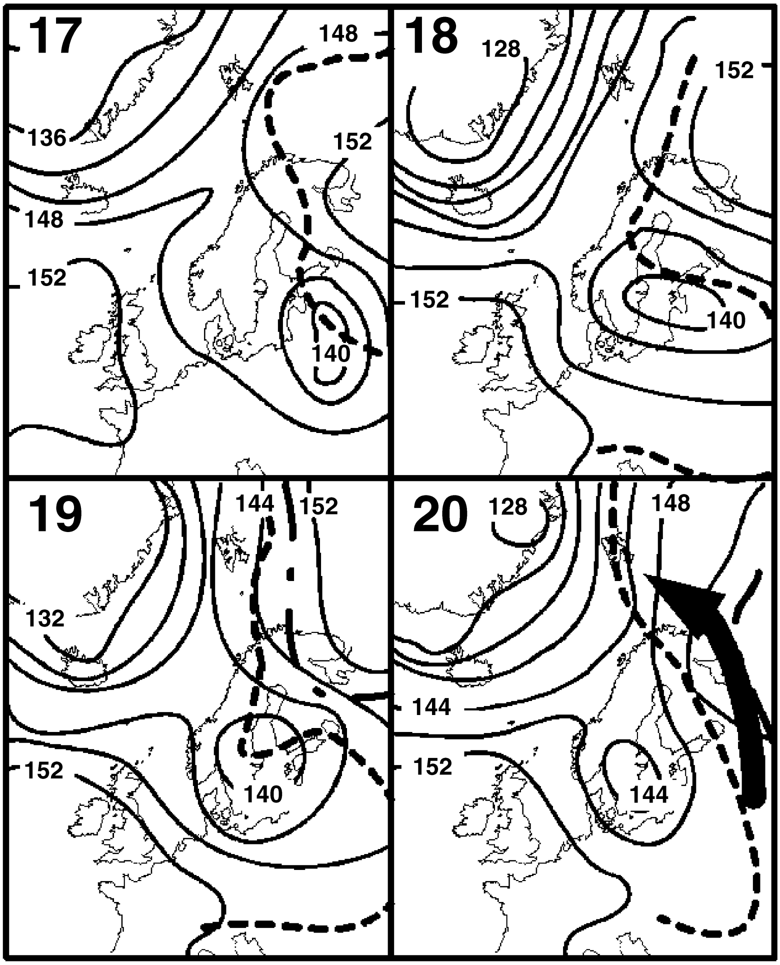

Fig. 1 Synoptic charts (12 UTC) for Eastern Europe and Scandinavia at 850 hPa (*c.* 1500 m) for *P. xylostella* migration during the period 17–20 July 2000. Contours ($\times$ 10) at 40-m intervals —, 10 °C isotherm ---, 15 °C isotherm – – – – –. Migration path indicated by thick arrow.

P. xylostella were then most likely in eastern Carelia and the Kola Peninsula (see later for supporting data). The air current had a favourable velocity of 13 m/s and a temperature of 10–15 °C at around 1500 m. By 20 July, a corner of this warm air mass extended to Svalbard (Fig. 1). The way to Svalbard thus opened on 19 July, before which immigration from the same south-east direction was blocked by unfavourable winds.

Surface maps provide a similar picture (Fig. 2). On 19 July 00 : 00 (UT) the warm sector of an anticyclone centred over the Baltic countries had reached Finland; south-east of the high pressure over northern Russia warm air was drawn toward the north-west (Fig. 2). Night temperatures were as high as 18–23 °C. On 20 July at 00 : 00, similar night temperatures were recorded north-west of the Kola Peninsula, and on Svalbard strong easterlies were experienced, but the temperature was only 9 °C (Fig. 3).

Air temperature measurements vs. altitude profiles for Bjørnøya (between Kola and Svalbard) and Ny-Ålesund on 18 and 20 July (Fig. 3) illustrate the movement of this warm air mass, reaching Svalbard on 20 July. They show a cold surface layer of air with a temperature maximum

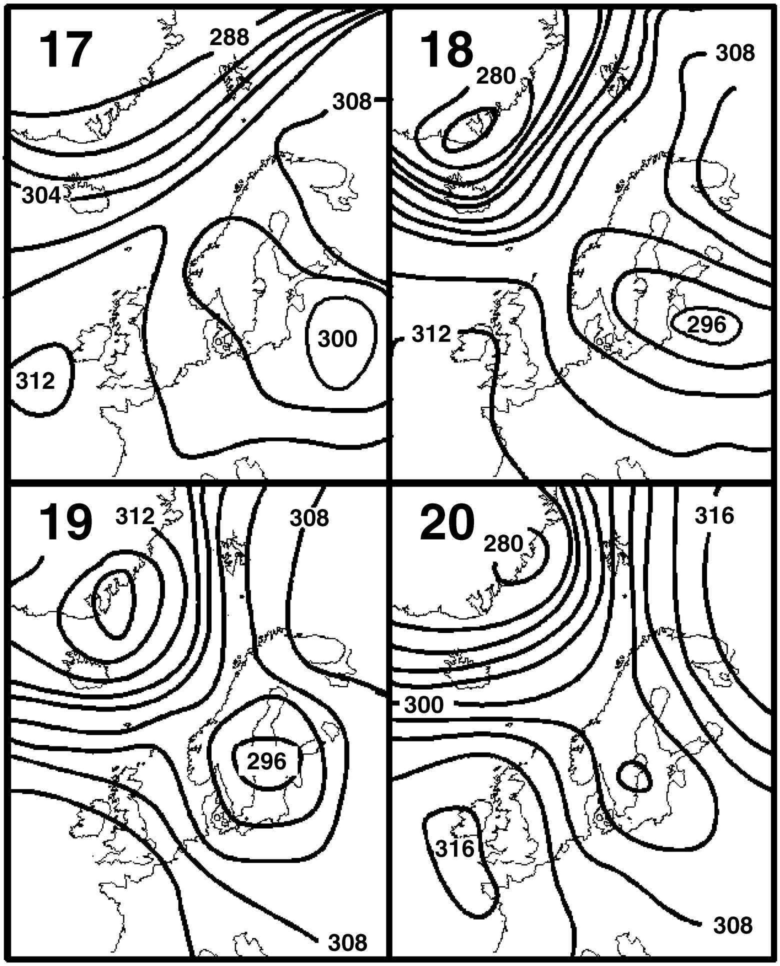

Fig. 2 Surface synoptic charts for Eastern Europe and Scandinavia for *P. xylostella* migration during the period 17–20 July, 2000. Isobars are at 4 hPa intervals.

at around 600 m, which is likely to correspond to the optimum height for flight of *P. xylostella.*

Spot directions and speeds of the air currents at 850 hPa (1500 m) were as follows: Moscow 17 July SE 7.8 m/s, Kola Peninsula 18 July SSE 6.6 m/s, Bjørnøya 19 July SSE 5.1 m/s and 20 July S 5.1 m/s. The distance of the Kola coast to Svalbard is approximately 800 km. With a mean air current of 5 m/s it would take around 40 h to cover the distance to Svalbard, equating to departure from the mainland on 18 July (Figs 1 and 2). Thus, the most probable time of passage for *P. xylostella* was early on 20 July at 400–600 m at Bjørnøya, reaching Svalbard later the same day at around 600 m, corresponding with the first sighting at Ny-Ålesund.

The warm south-easterly winds formed a layer of cool cloudy air in contact with the sea (Fig. 3). However, the height of the temperature maximum over Ny-Ålesund on 20 July was significantly lower than over Bjørnøya on 18 July. If *P. xylostella* tracked the temperature profile then this will have tended to bring them closer to the land surface over W. Svalbard, where the visual cues required for landing could begin to operate effectively.

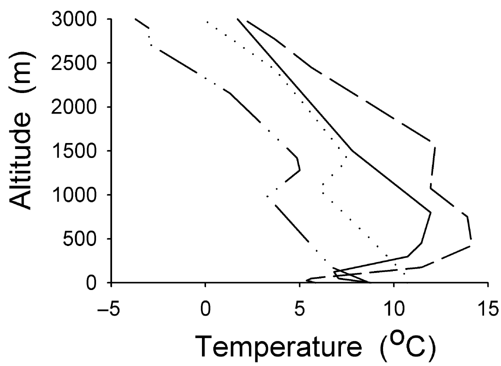

Fig. 3 Air temperature vs. altitude profiles for Bjørnøya and Ny-Ålesund, Svalbard on 18 and 20 July 2000 showing movement of mass of warm air. Bjørnøya 18 July —, Bjørnøya 20 July – – –, Ny-Ålesund 18 July – - – - –, Ny-Ålesund 20 July ···.

GENERAL ECOLOGICAL AND PHYSIOLOGICAL CONSIDERATIONS

Source population build-up

The number of *P. xylostella* arriving on Svalbard implies the presence of a large source population somewhere further south, at a time coincident with the opening of the synoptic window for migration to Svalbard. Summer 2000 was particularly good for Lepidoptera migrating north (Mikkola 2001). *P. xylostella* first appeared in Tammisaari, SW Finland in early spring (20–21 April trap sample), an event that usually presages large summer populations. However, it then remained scarce throughout the summer in Finland, suggesting insufficient numbers there to support the Svalbard migration and that these immigrant moths probably originated from further east in Russia. Furthermore, the fact that *P. xylostella* was not accompanied by other species when arriving on Svalbard tends to support this contention. At the time of the migration into Svalbard, significant numbers of two other large Lepidoptera species, *Pontia daplidice* and *Noctua interposita*, were migrating northwards in Finland on the same weather system. If the Svalbard *P. xylostella* had formed part of this migration, then one might reasonably expect the other two species to have arrived on Svalbard simultaneously with the *P. xylostella.*

Migration

Take-off

Most dispersing winged insects, including *P. xylostella*, require warm dry conditions for take-off. Climate models predict warmer and dryer summers in Fennoscandia, weather patterns usually associated with increased aerial insect movement (Drake & Farrow, 1988; Greenstone, 1990). The *P. xylostella* 2000 migration illustrates the importance of unusually warm air temperatures (18–23 °C at night) in initiating such a migration event.

Similarly, for nonwinged invertebrates, small surface-active species are most likely to be dispersed in a similar manner utilizing thermals to enter the warm airstream. Holm (1958), for example, suggested that the diminutive size of Svalbard spider species reflects the success of smaller species dispersing by wind. Thus, current climate warming scenarios imply an increased likelihood of species entering the northerly airstream and arriving on Svalbard.

Aerial passage

Once airborne, sufficient invertebrates must survive aerial passage to reach the target destination (Pedgley *et al.*, 1995). Invertebrates have often been sampled from altitudes over 1500 m (Glick, 1939; Drake & Farrow, 1988) but *P. xylostella* demonstrates that it is unnecessary to reach high altitude to cover long distances. Crucially, air temperature typically decreases with height above ground (commonly 0.65–0.98 °C 100 m^{-1}) and animals ascending to a great height risk chill injury and death. This is particularly relevant for summer-acclimated individuals that are cold-intolerant. Lower altitudes also favour actively flying species as temperatures will remain at, or above, the minimum required for flight (Rainey, 1974). In Japanese *P. xylostella*, the optimum temperature for flight under laboratory conditions is 23 °C, ranging from 18 to 28 °C, which compares unfavourably with the air mass temperatures of 10–15 °C recorded in our study (Shirai, 1991). However, this does not allow for additional warming of flight muscles through insolation and basking and on Svalbard *P. xylostella* flies actively at air temperatures below 10 °C. Nevertheless, particularly under cloudless conditions, it is likely that *P. xylostella* disperses at suboptimal air temperatures. Clearly, there is a lower temperature threshold beyond which migration becomes ineffectual but this will also interact with travel exposure time.

Travel time

Short travel time is important for actively flying species to avoid depletion of food reserves that power flight muscles and to avoid high cumulative mortality within the dispersing population. Although *P. xylostella* have been observed landing on and rising from the surface of the North Sea (Williams, 1958), it seems unlikely that this is possible from the surface of the Arctic Ocean with lower water temperatures, pack ice and often a more disturbed surface. Shorter transit duration also favour desiccation-susceptible species such as aphids that require a food source to maintain positive water balance. Dry air, however, is advantageous since it reduces the occurrence of fog and precipitation when warm air is chilled by contact with cold arctic seas and landmasses. The evidence, from small aphids to the relatively larger Lepidopterans, such as *P. xylostella*, which have successfully reached Svalbard in significant numbers, suggests that the estimated journey time of around 48 h to cover the 800 + km recorded does not provide an insurmountable physiological barrier to initial colonization, even in non cold-tolerant species.

Establishment

Food plant availability

For herbivorous immigrants, such as *P. xylostella* the presence of suitable larval food plants (a wide range of Cruciferae for *Plutella*) is a prerequisite for establishment. The common crucifers on Svalbard include *Draba* spp. and *Cochlearia groenlandica*. *P. xylostella* is known to feed successfully on *C. groenlandica* in northern Scandinavia but plant populations are smaller, less productive and more widely scattered on Svalbard. Similarly, *Draba* spp. usually grow as small isolated plants, making them less apparent to potential herbivores.

Thermal adaptation

Animal species arriving on Svalbard must be 'preadapted' to short cool summers with 24 h daylight (mid-April to mid-August) and long cold winters. Climatic conditions at Ny-Ålesund illustrate the general problems that invading insects will encounter. Mean monthly temperature is above 0 °C for only three summer months of the year and never rises above 5 °C (Bale *et al*., 1997). Maximum air temperature reaches 17 °C but frosts may occur in any month. Winter air temperatures may fall to –42 °C. For *P. xylostella* with a developmental threshold of 7.3 °C (Butts & McEwen, 1981), and no cold resistant hibernating stage (Talekar & Shelton, 1993) summers are probably too cool and short and winters too cold and long for extended survival and reproduction. Nevertheless, *P. xylostella* is well established on Marion Island where the mean monthly air temperature ranges from 3.6 to 7.5 °C, largely below the stated threshold for development elsewhere. This suggests a measure of rapid cold adaptation may develop once the moth is exposed to suboptimal temperatures, although Marion Island does not experience the extended subzero temperatures of the Svalbard winter. These ecophysiological barriers to successful invasion by *P. xylostella* currently appear insurmountable and further climatic amelioration appears necessary before populations become established. Nevertheless, the example of *P. xylostella* illustrates clearly the challenges that may be overcome by better 'preadapted' and more resilient species.

Date of arrival on Svalbard is clearly important for successful colonization. Early arrival shortly after snow melt (late June) would be beneficial for most species, providing a sufficiently long summer season for the first generation to complete development. Date of arrival, however, is currently unpredictable and depends on when invertebrates are in an appropriate life stage to disperse and when a suitable airstream becomes available. Most immigrations, particularly for *P. xylostella*, tend to be recorded in late summer. However, climate change will act to ensure that invertebrates are in migratory phases earlier in the season and may increase the frequency of suitable air movements, leading to increased and earlier immigration into Svalbard. Nevertheless, species most likely to extend their range further north are those in which photoperiod (day length) does not strictly control their life cycle and those that possess a potential mechanism for surviving winter in a cold-hardy inactive state.

Reproduction
Species establishment requires successful population growth, with animals reproducing subsequent to their migration flight. For actively flying species, such as *P. xylostella*, visual landing cues through broken cloud cover may enhance the chances of successful colonization by concentrating reproductive individuals into a restricted area, an important adaptive consideration for species in which sexual reproduction is normally postmigration (Southwood, 1962).

CONCLUSIONS

Migration of invertebrates into the high Arctic is a stochastic event coincident with suitable synoptic meteorological conditions. For these animals to reach Svalbard they should be sufficiently abundant in the source region, northern Scandinavia or western Russia, at the appropriate time. The warming of continental areas (IPCC 2001) will enable species such as *P. xylostella* to extend their distributions northwards into Fennoscandia and western Russia, making them more 'available' to suitable airstreams. Warming will also encourage earlier annual northward migration of species, providing an extended time window for migration into the Arctic. Successful migration will most probably occur when the opening of the 'synoptic window' coincides with peaks of migration linked to maximum population densities. For *P. xylostella* this window occurs during summer, even though moths emerging then have shorter flight duration and range than those emerging earlier in spring (Shirai, 1991).

While the barriers to aerial immigration into Svalbard are breached sporadically, the successful establishment of breeding populations is more problematic. Given current climatic conditions it is unlikely that *P. xylostella* will establish populations on Svalbard in the near future, despite the presence of known host plants. Short growing season, lack of photoperiod cues, low mean summer temperatures and harsh winters mitigate against establishment for a species without obvious specialized overwintering stages. Nevertheless, other species that are less constrained climatically, but which are less visually obvious migrants, may be able to utilize the same opportunities to reach Svalbard as *P. xylostella. Plutella xylostella* thus remains a potential indicator species signalling the opening of the synoptic window through which many other less conspicuous species will be transported into the high Arctic.

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