

# The effect of summer temperature on the distribution of *Ceramica pisi* (Lepidoptera: Noctuidae) in Iceland

BRYNJA HRAFNKELSDÓTTIR<sup>1</sup>, EDDA S. ODDSDÓTTIR<sup>1</sup> AND GUDMUNDUR HALLDÓRSSON<sup>2</sup>

<sup>1</sup>Icelandic Forest Research, Mogilsa, IS-162 Reykjavik, Iceland ([brynja@skogur.is](mailto:brynja@skogur.is); [edda@skogur.is](mailto:edda@skogur.is))

<sup>2</sup>Soil Conservation Service of Iceland, Gunnarsholt, IS-851 Hella, Iceland ([gudmundurh@land.is](mailto:gudmundurh@land.is))

## ABSTRACT

The distribution of *Ceramica pisi* has been expanding in Iceland after 1990, concurrent with a recent rise in mean annual temperature. A previous study showed that the winter survival of *C. pisi* is primarily related to pupal mass. We monitored the development of *C. pisi* larvae over cool, mild, and warm summers in southern Iceland and calculated the total mass-related survival of *C. pisi* larvae/pupae through pupation and winter. A significant positive relationship was found between a) summer growing degree days and the proportion of larvae that reached critical mass for winter survival, and b) larval mass and likelihood of pupation. We conclude that increased summer temperature is the primary cause of the distribution range shift of *C. pisi* in Iceland, and this has facilitated increased population density of the species, in combination with increased availability of food resources due to host shift over to Nootka lupin.

**Keywords:** broom moth, geographical range shifts, global warming, mass-related survival, phenology, summer day degrees, Nootka lupin

## YFIRLIT

*Áhrif sumarhita á útbreiðslu og stofnsveiflur ertuyglu á Íslandi*

Útbreiðsla ertuyglu á Íslandi hefur verið að aukast eftir 1990, samhliða hækkun á meðalhita. Fyrri rannsóknir sýndu að vetrarlífur ertuyglu er fyrst og fremst háð þyngd púpna. Við fylgdu með þroskun ertuyglulirfa á svölu, mildu og hlýju sumri á Suðurlandi og reiknuðum heildarlífur lírfa/púpna frá púpun til vetrarloka. Marktækt jákvætt samband fannst á milli a) daggráðusummu sumars og hlutfalls lírfa sem höfðu náð lágmarksþyngd til að lifa af veturinn og b) þyngdar lírfa og líkinda á púpun. Okkar niðurstaða er að hærri sumarhiti sé höfuðorsök breytinga á útbreiðslu ertuyglu á Íslandi og hafi stuðlað að aukinni stofnstærð tegundarinnar ásamt auknu fæðuframboði sem tengist breyttu hýsilvali frá því að ertuygla fór að nýta sér lúpínu til fæðu.

## INTRODUCTION

Climate change is expected to be a significant driver in northward range shifts in species distribution in the northern hemisphere (Parmesan et al. 1999). Insects can respond rapidly to changes in temperature (Ayres & Lombardero 2000, Logan et al. 2003), which can affect their distribution range, development rate, survival rate, and the length of growing

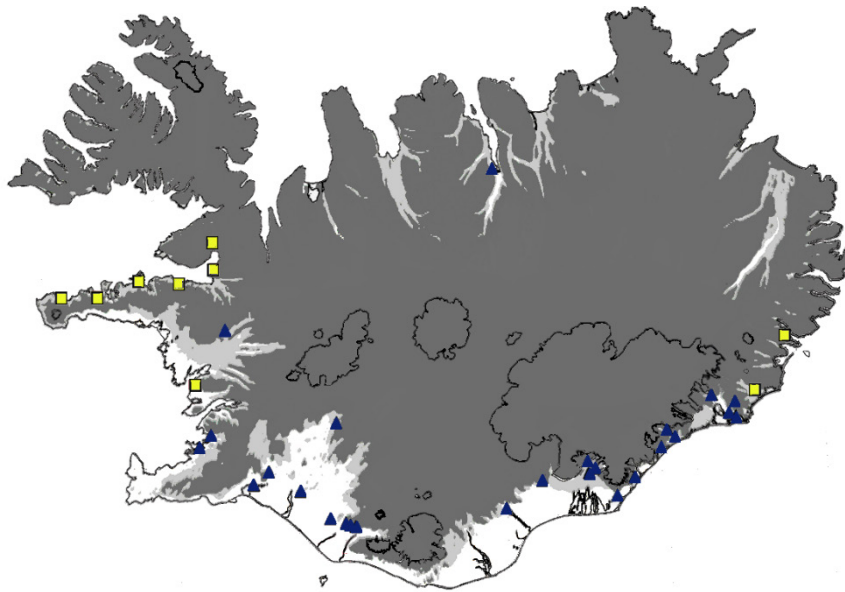
season (Parmesan et al. 1999, Bale et al. 2002, Crozier 2004, Pureswaran et al. 2018). Low winter temperatures often limit the northward distribution of insects, especially for species that are active during cold periods (Ungerer et al. 1999, Sinclair et al. 2003, Battisti et al. 2005). However, cold-hardy insect species are more likely to benefit from longer and warmer

summers during their larval development, rather than milder winters, as they often overwinter in the diapause stage (Bale & Hayward 2010).

Increasing temperature in low-temperature climates generally increases the speed of larval development (Bale 2002). The rate of development has often been shown to be connected to the accumulation of heat, frequently called growing degree days (GDD), rather than chronological time (Zalom & Wilson 1982, Cayton et al. 2015). The GDD metric is widely used to predict phenological events in the life history of plants and insects (Herms 2004) and has been shown to perform significantly better than date in predicting the emergence of Lepidoptera species (Cayton et al. 2015). Using GDD has also been an effective way to predict insect response to climate change, for example that of butterfly species (Hodgson et al. 2011, Cayton et al. 2015).

*Ceramica pisi* Linnaeus. (Lepidoptera, Noctuidae) is a native species in Iceland. It occurs throughout northern Scandinavia, south to the Mediterranean Sea, and east to Japan (Wolff 1971). In Iceland *C. pisi* overwinters

as pupae. The adults start to emerge in early May. Egg laying is primarily in June. Larvae emerge from late June until late July and pupate in late August to early September (Ólafsson 2009, Hrafnkelsdóttir & Oddsdóttir 2010, Hrafnkelsdóttir et al. 2012). Before 1990, its main distribution area in Iceland was the lowlands of the southern part of the country (Figure 1; Wolff 1971, Ólafsson & Björnsson 1997), which coincides with the area with the highest degree-day summation for Iceland during 1961-1990 (Figure 1; Björnsson et al. 2007). The mean temperature in Iceland has increased by 0.47°C per decade during the period 1980-2015 (Björnsson et al. 2018). Since 1990, the distribution range of *C. pisi* has been expanding north, primarily in the lowlands of western Iceland, but a minor expansion has also been observed in southeast Iceland (Figure 1; Hrafnkelsdóttir 2020). This coincides with the recent increase in mean annual temperature since 1990, which has been most pronounced in western Iceland (Björnsson et al. 2018). The first recorded outbreak of *C. pisi* in Iceland was in 1991 on *Lupinus nootkatensis* in Skaftafell,



**Figure 1.** GDD map (threshold value 5°C) for the period of 1961-1990 (redrawn from Björnsson *et al.*, 2007) and distribution of *Ceramica pisi* in Iceland before 1990 (triangles) and new records during 2009-2018 (squares) (Hrafnkelsdóttir, 2020). Dark grey area <500 GDD, light grey 500-600 GDD white 600-800 GDD.

southeast Iceland (Sigurðsson et al. 2003). Subsequently, many extensive outbreaks have occurred on lupin as well as young tree plantations in South Iceland (Sigurðsson et al., 2003, Halldórsson et al. 2013).

The larvae of *C. pisi* are polyphagous, but species of the Fabacea genus are known to be favored (Cindea 1979). Wolff (1971) reviewed the distribution and biology of Lepidoptera in Iceland, based on earlier reports and his own findings. He listed *Comarum palustre*, *Rhinanthus minor*, *Parnassia palustris* and *Rumex* sp. as host plants of *C. pisi*. More recently Ólafsson & Björnsson (1997) and Sigurðsson et al. (2003) added to the host plant list *Juncus arcticus*, *Lathyrus maritimus*, *Lupinus nootkatensis*, *Salix* spp., *Betula pubescens*, *Populus trichocarpa*, *Pinus contorta*, *Picea sitchensis*, and *P. engelmannii*. Presently, *C. pisi* in Iceland is primarily found on *L. nootkatensis*, which was first introduced in 1885 as an ornamental plant and again in 1945 for land reclamation (Schierbeck 1886, Bjarnason 1957). It invades native ecosystems readily and is considered an invasive species in Iceland (Magnússon 2010). Presently it covers around 300 km<sup>2</sup> (Guðjohnsen & Magnússon 2019).

The causes of the ongoing changes in the distribution of *C. pisi* in Iceland are not known. Keena and Moore (2010) found that temperature had a clear effect on larval development, the likelihood of pupation, and the potential spatial distribution of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in the United States. Studies have shown that insect size can be important for winter survival (Hokkanen 1993, Liu et al. 2007) and Hrafnkelsdóttir et al. (2019) found that winter survival of *C. pisi* pupae in Iceland was positively correlated with pupal mass, but not related to subzero temperatures.

In the present study, we examined the hypotheses that the recent increase in summer temperature caused the observed changes in the distribution of *C. pisi* in Iceland and facilitated changes in the population dynamics of the species. We monitored the development of *C. pisi* larvae at three locations at different times (dates and years) and compared the proportion of larvae that had reached the critical mass

for winter survival to summer GDD. We also collected larvae and observed them undergoing pupation under outdoor conditions to establish the relationship between larval mass and the likelihood of pupation, as well as the ratio between larval and pupal mass. Our hypotheses were: (a) that increased summer temperatures after 1990 increased the likelihood of larvae reaching the critical mass for successful pupation and winter survival, (b) the likelihood of successful pupation is positively correlated to larval mass, and (c) total mass-related survival through pupation and winter is positively related to the GDD during the egg and larval development in the preceding summer.

## MATERIALS AND METHODS

### *Study sites and monitoring of larval development*

Larval development was monitored by sampling larvae from three separate *L. nootkatensis* fields (sampling locations) in southern Iceland with different elevations and distances from the sea. The sampling was conducted over four summers of different temperature profiles. The average June-August temperature for each sampling year and sampling location is shown in Table 1. Temperature data for sampling locations were gathered from the nearest weather station (The Icelandic Meteorological Office, personal communication). The geographical coordinates, the elevation of each sampling location and the nearest weather station are shown in Table 2. The placement of sampling locations is shown in Figure 2.

**Table 1.** Mean June-August temperature during larval sampling years (NS=no sampling).

Location	Mean June-August temperature during sampling years (°C)*			
	2014	2016	2017	2018
Geítasandur	11.5	11.6	10.7	10.1
Þjórsárdalur	NS	NS	10.8	NS
Ölfus	11.4	11.5	NS	NS

\* (The Icelandic Meteorological Office, personal communication).

**Table 2.** Geographical characteristics, elevation, and distance between different sampling locations and nearest weather stations.

Sampling location/ weather station	Geographical coordinates		Nearest weather station			
	Latitude	Longitude	Latitude	Longitude	Altitude (m.a.s.l)	Dist. (km)
Geitasandur/Hella	N 63.809258	W -20.209994	N 63.8257	W -20.3654	36/20	7.8
Þjórsárd./Mörk á Landi	N 64.098077	W -19.955172	N 64.0293	W -20.0189	159/125	8.3
Ölfus/Eyrarbakki	N 63.892431	W -21.305491	N 63.8692	W -21.1602	4/3	7.6

**Figure 2** Map of Iceland showing the sampling locations (•) of *Ceramica pisi* larvae in the present study.

Sampling dates and years varied between locations, as shown in Table 3. Four sampling sites were randomly selected at each sampling location. The distance between sampling sites ranged between 100 and 200m. Five sampling plots (0.5 x 0.5m) were selected within each sampling site, by randomly searching for plants infested by *C. pisi* larvae and by sampling the first encountered *C. pisi* infested plants. The distance between sampling plots therefore varied between sites and sampling times, but never less

than 5-10m. This approach was used as earlier observations had shown that the distribution of larvae is quite patchy. All lupin stems within each plot were cut at the base and carefully placed into a large plastic box in batches of ca. five stems. Only plots with less than 75% leaf defoliation were sampled to avoid the effects of food shortage on larval growth. Each batch of stems was then shaken/beaten thoroughly into the box until all larvae had detached from the vegetation and fallen into the box. The larvae were then put into small plastic containers with small holes for ventilation and labeled with the number of sampling site and plot.

#### Larval measurements

Larvae collected during regular sampling were kept under outdoor conditions in the shade and deprived of food for ca. 20h to ensure that all gut content had emptied. After 20h, larvae were weighed individually on a scale (AA-160; Denver Instrument Company, Arvada, Colorado) to the nearest 0.0001g. The proportion of larvae that had reached the critical mass for winter survival was calculated for each sampling time and location. The critical mass for winter survival was set at 300 mg, as Hrafnkelsdóttir et

**Table 3.** Overview of sampling dates of larvae at all three sampling sites. NS = no sampling.

Year	Sampling location		
	Geitasandur	Þjórsárdalur	Ölfus
2014	14/8, 21/8, 29/8	NS	5/8, 14/8, 20/8
2016	3/8, 9/8, 16/8, 25/8, 30/8	NS	3/8, 9/8, 25/8, 31/8
2017	3/8, 10/8, 17/8, 21/8, 28/8, 4/9	3/8, 10/8, 28/8, 4/9	NS
2018	9/8, 17/8, 25/8, 3/9	NS	NS

al. (2019) showed that 5% winter survival of *C. pisi* pupae was at 157 mg, which is equivalent to 294 mg larval mass, according to the current pupation study.

#### *Pupation study*

For the pupation study, *C. pisi* larvae were collected in Ölfus on 31 August 2016 and kept in the shade under outdoor conditions. The larvae were deprived of food for 20h before weighing, then put into 13 mL (40 × 23 mm) plastic cups (1 larva per cup) and left for pupation under outdoor conditions. Pupation was monitored until 11 October 2016, when all pupae were weighed. Larvae that did not pupate were counted. This information was used to establish: (a) the ratio between larval and pupal mass, and (b) the pupation mass-related survival. Based on this, the likelihood of mass-related pupation survival for all larvae across each sampling location, year and sampling time was calculated. After transforming larval mass to pupal mass, the likelihood of mass-related winter survival for all potential pupae across all sampling locations, years, and sampling dates was calculated, based on Hrafnkelsdottir et al. (2019). Total mass-related survival was then calculated as pupation survival × winter survival.

*C. pisi* larvae were also sorted into different mass groups of 100mg intervals to analyze the minimum mass they must gain to be able to finish pupation.

#### *Calculation of Growing Degree Days*

Daily maximum and minimum temperature data from weather stations nearest to the larval sampling locations were obtained from the Icelandic Meteorological Office (personal communication). GDD for each day was calculated with the formula given below (Eq. A) (Herms 2004, Murray 2008) and summarized from 1 June to the relevant larval sampling date.

$$\text{(Eq. A) GDD} = \left[ \frac{(T_{\text{MAX}} + T_{\text{MIN}})}{2} \right] - T_{\text{BASE}}$$

where  $T_{\text{MAX}}$  is the daily maximum temperature,  $T_{\text{MIN}}$  is the daily minimum temperature, and

$T_{\text{BASE}}$  is the base temperature for the lower development threshold of the larvae. As the lower development threshold is not known for *C. pisi*, 5°C was chosen as the base temperature, since it reflects the principal threshold for butterfly larvae growth (Hill et al., 2003) and is often used as the minimum threshold for insect development in northern Europe (Luoto et al. 2006, Ekholm et al. 2019). GDD from the beginning of April, May, June, and July until the relevant sampling date was calculated, as those months coincide with different stages of the life cycle of *C. pisi*. The GDD formula was applied for every day of the season that was tested and accumulated daily. The best fit between larval development and GDD was found to be cumulative GDD from 1 June, which coincides with the beginning of egg laying (Ólafsson 2009).

#### *Statistical analysis*

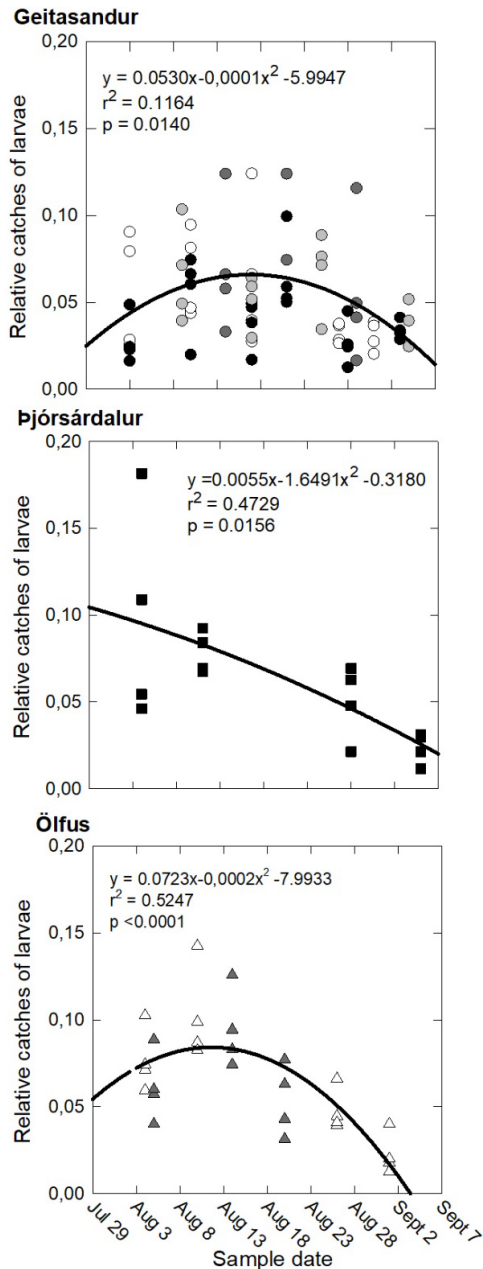
Data were analyzed with SAS enterprise guide (Davis 2007) and SigmaPlot (Systat Software Inc 2008). The correlation between sampling dates and relative larval catches was examined with polynomial quadratic regression analysis. Linear regression analysis was used to examine the relationship between GDD and larval mass, the relationship between larval and pupal mass, and the relationship between GDD and total (pupation × winter) survival. The effect of larval size on pupation survival and total survival was examined with a nonlinear regression analysis. The Kruskal-Wallis test was used to examine differences in larvae mass between sites and years.

## RESULTS

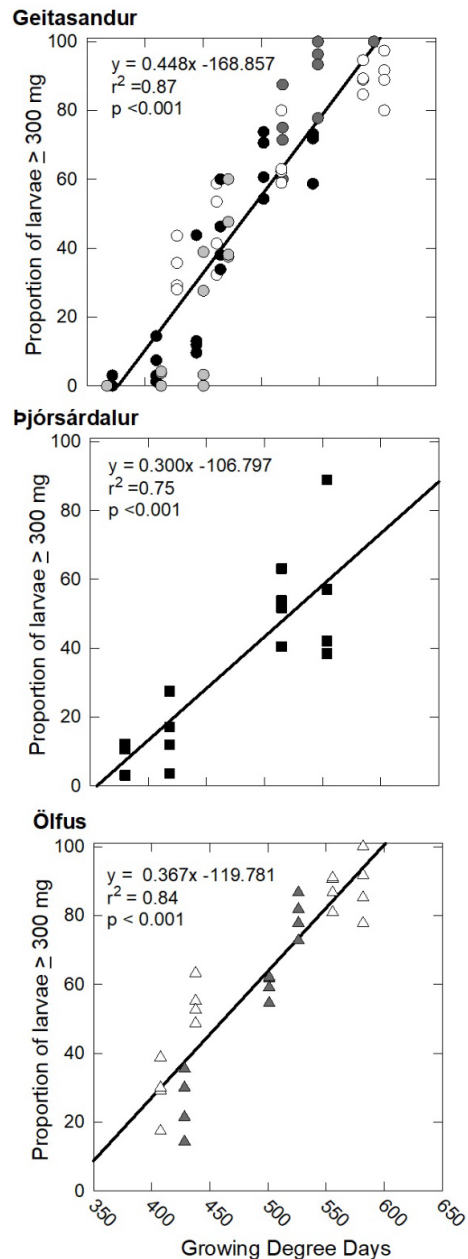
### *Larval sampling*

A total of 5084 larvae were collected and weighed over the sampling period, 182 on average at each sampling time. The number of larvae varied greatly across sampling sites, dates, and years (Figure 3, Table 3). The number of larvae ranged between 27 and 354 in Geitasandur, 57 and 237 in Þjórsárdalur, and 29 and 553 in Ölfus.

The analysis showed a significant polynomial (quadratic model) regression



**Figure 3** Relationship between relative catches of *Ceramica pisi* larvae (catches/average catches per sampling location per year) on different sampling dates at the three sampling locations: ● Geitasandur (2014, 2016-2018), ■ Þjorsárdalur (2017), and ▲ Ölfus (2014, 2016). Colors represent different sampling years; 2014 (dark grey), 2016 (white), 2017 (black) and 2018 (light grey).



**Figure 4.** The relationship between GDD and the proportion of *Ceramica pisi* larvae that had reached  $\geq 300$  mg larval mass for each sampling location, across all years and sampling dates. Sampling locations were: ● Geitasandur (2014, 2016-2018), ■ Þjorsárdalur (2017), and ▲ Ölfus (2014, 2016). Colors represent different sampling years; 2014 (dark grey), 2016 (white), 2017 (black) and 2018 (light grey).

**Table 4.** The proportion of larvae  $\geq 300$  mg (%) after a cool summer (470 GDD) as in 2018, mild summer (560 GDD) as in 2017, and warm summer (600 GDD) as in 2014 and 2016. Also shown is the ratio of larvae  $\geq 300$  mg, comparing mild summer vs cool summer, warm summer vs mild summer, and warm summer vs cool summer.

Sampling location	Proportion of larvae $\geq 300$ mg (%)			Ratio of larvae $\geq 300$ mg between:		
	470 GDD	560 GDD	600 GDD	M/C*	W/M**	W/C***
Geitasandur	41,7	82,0	99,9	2,0	1,2	2,4
Ölfus	52,7	85,7	100	1,6	1,2	1,9
Þjórsárdalur	34,2	61,2		1,8		

\*Mild summer (560 GDD) vs cool summer (470 GDD)

\*\*Warm summer (600 GDD) vs mild summer

\*\*\* Warm summer vs cool summer

between relative catches and sampling dates across all sampling years and locations (d.f.=27;  $P = 0.002$ ) (Figure 3). The  $r^2$  of the relationship was 0.4044, indicating that up to 41% of the variability in relative catches could be explained by sample date. In Geitasandur and Ölfus, a marked decrease in the number of caught larvae was observed after the middle of August, which most likely indicated the beginning of pupation. In Þjórsárdalur in 2017 a general decrease in the number of larvae from the beginning of sampling was observed (Figure 3).

#### Larval measurements

The average mass of larvae ranged from 49 to 533mg across all sampling locations, dates, and years. The larval mass ranged between 6 to 743 mg in Geitasandur, 4 to 772mg in Þjórsárdalur and 7 to 833mg in Ölfus. The lowest single larval mass observed was 4mg at Þjórsárdalur on 9 August 2017, and the highest mass observed was 833mg in Ölfus on 14 August 2014.

#### Summer GDD and larval growth

In order to establish the effect of summer temperature on the proportion of larvae potentially ready to survive the following winter, we compared the proportion of larvae that had reached larval mass  $\geq 300$  mg to June GDD across all sampling years and dates. A highly significant positive relation was found between GDD and the proportion of larvae that had reached larval mass  $\geq 300$  mg in all sampling locations ( $P < 0.001$ ; Figure 4). The  $r^2$  of the relationship was 0.81 (d.f.=71) in Geitasandur,

0.79 (d.f.=15) Þjórsárdalur and 0.63 (d.f.=31) in Ölfus, indicating that GDD explained up to 81%, 79% and 61% of the proportion of larvae with mass  $\geq 300$  mg. At 470 GDD, which was the GDD summation in the beginning of September 2018, the proportion of larvae  $\geq 300$  mg ranged between 34.2 – 41,7%, but was nearly 100% at 600 GDD, which was the GDD summation by the end of August in 2014 and 2016 (Table 4).

#### Pupation study

To establish the ratio between final larval mass and pupal mass for *C. pisi*, we compared the mass of larvae collected in Ölfus on 31 August 2016 to their pupal mass. The analysis showed a highly significant regression between larval and pupal mass across all sampled larvae (d.f.=5;  $P < 0.001$ ). The  $r^2$  of the relationship was 0.682, indicating that up to 68% of the variability of pupal mass observed could be explained by larval mass.

Some larvae did not pupate but died or transformed into intermediates retaining larval characteristics. This was true of 100% of 100-300 mg larvae, 48% of 300-500 mg larvae, and 12% of the 500-700 mg larvae. A test using the same methodology, except that the larvae were set for pupation in batches of different mass intervals, gave similar results: 88% of  $< 300$ mg larvae, 33% of 300-500mg larvae and 13 % of 500-700mg larvae did not pupate.

*C. pisi* larvae were sorted into different mass groups of 100mg intervals to analyze the minimum mass they must gain to be able to finish pupation. There was a significant

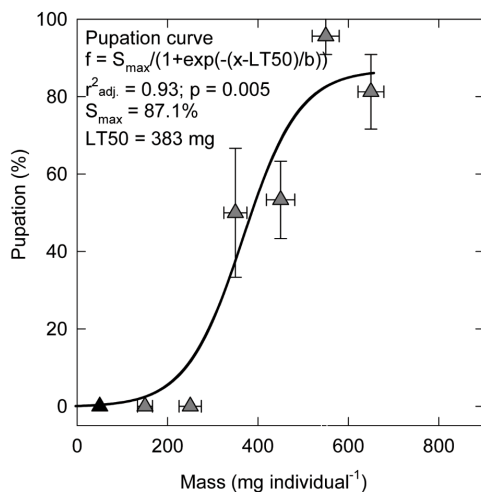
correlation between the pupation rate of different mass groups and a sigmoid curve fitted to the pupation of different mass groups ( $P = 0.005$ ,  $r^2 = 0.93$ )(Figure 5).

The sigmoid model was:

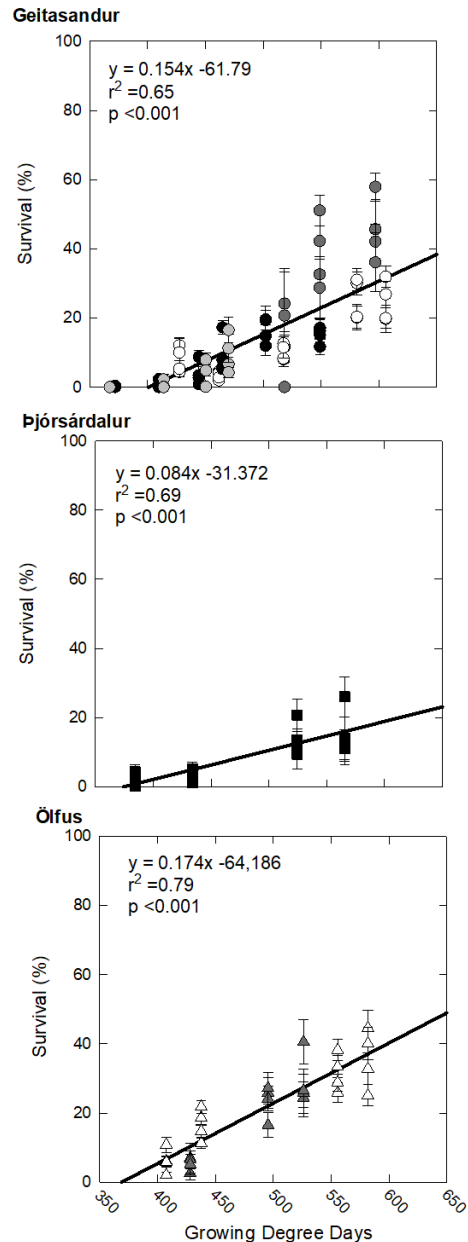
$$(Eq. B) \quad S_{pupation} = \frac{S_{max}}{\left(1 + \exp\left(\frac{x-LT50}{b}\right)\right)}$$

Where  $S_{pupation}$  is larval pupation,  $x$  is the larval mass (mg),  $S_{max}$  (maximum size-related pupation) is 87.1 %,  $b$  (a constant) is 62 and  $LT50$  (50% likelihood of pupation) is 383 mg.

The Sigmoid curve of pupation rate of different larval mass groups showed that the  $LT50$  occurred at 383 mg larval mass, and that the larval mass-related pupation was as high as 95% at 650 mg but only 5% at 191 mg (Figure 5).



**Figure 5.** The relationship between pupation success and mass of *Ceramica pisi* larvae (collected on 31 August, 2016). Each point represents a 100-mg interval in larval mass. The line represents the fitted sigmoid pupation curve (Eqn B). Also shown are  $r^2$  adjusted and  $P$  values from the fitted sigmoid survival curve along with  $S_{max}$  (maximum size-related survival) and  $LT50$  (50% likelihood of pupation related to mass). Vertical bars show the SE of larval mass. As collecting time was late in the growing season, no larvae collected were under 100 mg, so the black triangle does represent assumed pupation (%).



**Figure 6.** The relationship between GDD and total expected mass-related total survival of *Ceramica pisi* larvae/pupae (pupation survival \* winter survival) for each sampling location, across all years and sampling dates. Sampling locations were: ● Geitasandur (2014, 2016-2018), ■ Þjórsárdalur (2017), and ▲ Ölfus (2014, 2016). Colors represent different sampling years; 2014 (dark grey), 2016 (white), 2017 (black) and 2018 (light grey).



**Table 5.** Mass-related survival after a cool summer (470 GDD) as in 2018, mild summer (560 GDD) as in 2017, and warm summer (600 GDD) as in 2014 and 2016. Also shown is the ratio of mass-related survival, comparing mild summer vs cool summer, warm summer vs mild summer, and warm summer vs cool summer.

	Mass-related survival (%)			Ratio of mass-related survival		
	470 GDD	560 GDD	600 GDD	M/C*	W/M**	W/C***
Geitasandur	10,6	24,5	30,6	2,3	1,3	2,9
Ölfus	18,9	31,7	37,5	1,7	1,2	2,0
Þjórsárdalur	8,1	15,7		1,9		

\*Mild summer (560 GDD) vs cool summer (470 GDD)

\*\*Warm summer (600 GDD) vs mild summer

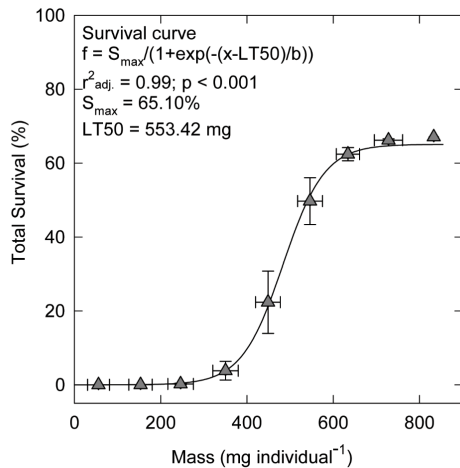
\*\*\* Warm summer vs cool summer

The Sigmoid model further predicted that other unexplained reasons accounted for 12.9% ( $100 - S_{\max}$ ) of non-pupation.

The analysis showed a highly significant regression between GDD and total mass-related survival across all sampling years and dates ( $P < 0.001$ ; Figure 6). The  $r^2$  of the relationship was 0.65 (d.f.=71) in 2014, 0.69

(d.f. =15) in 2016, 0.67 (d.f. =31) in 2017, indicating that up to 65%, 69% and 67% of the variability of survival could be explained by GDD from June 1 (Figure 6). At 470 GDD the total mass-related survival ranged between 8.1-18.9%, but between 30.6-37.6 at 600 GDD (Table 5).

A sigmoid curve was fitted to the total mortality of different mass groups ( $P < 0.001$ ,  $r^2 = 0.99$ ) (Fig. 7) according to eq.B, where  $S_{\text{total survival}}$  is the total expected mass related survival,  $x$  is the larval mass (mg),  $S_{\max}$  (maximum total expected mass related survival) is 65.10 %,  $b$  (a constant) is 48 and  $LT50$  (50% likelihood of pupation) is 553.42 mg.



**Figure 7.** The relationship between larval mass of *Ceramica pisi* and total mass-related survival of larvae/pupae (pupation survival\*winter survival) across all locations, years, and sampling dates. The line represents the fitted sigmoid survival curve (Eqn B). Also shown are  $r^2$  adjusted and  $P$  values from the fitted sigmoid survival curve along with  $S_{\max}$  (maximum size-related survival) and  $LT50$  (50% likelihood of mass-related survival). Vertical and horizontal bars show the SE of pupal survival and larval mass.

## DISCUSSION

Earlier findings of Hrafnkelsdottir et al. (2019) showed that winter survival is strongly linked to pupal mass. Our results were linked to those findings to establish the total mass-related survival across pupation and overwintering. In the present study, we found a significant correlation between June GDD and the proportion of larvae that had reached the critical mass for winter survival, between larval mass and the likelihood of pupation, and between June GDD and total mass-related survival through pupation and winter. The proportion of larvae that had reached the critical mass for winter survival and total mass-related survival was found to be greatly increased after warm summers compared to cool summers (Table 4; Table 5). Increased summer temperature would

therefore be expected to facilitate the northward distribution of *C. pisi*, especially in the northern part of West Iceland, where the warming after 1990 has been most intense (Figure 1).

Several studies show that the northern distribution of insects is limited by temperature (f.ex. Cannon 1998, Parmesan et al. 1999) and frequently by the thermal summation during the insects' developing stage (Ayres & Scriber 1994, Bale et al. 2002). A northward spread of Lepidoptera species on birch has recently been observed in northern Scandinavia (Jepsen et al. 2013). The historical distribution of *C. pisi* in Iceland was confined to areas with the highest GDD (Wolff 1971, Ólafsson & Björnsson 1997, Björnsson et al. 2018), which indicates that the species is near its thermal range limits in Iceland. Its recent spread has been into areas where warming after 1990 has been greatest. This indicates strongly that the northward distribution of *C. pisi* in Iceland is linked to the warming after 1990. It could be argued that the historical distribution of *C. pisi* was limited by lack of suitable host plants outside its former range. However, as all host plants of *C. pisi* reported by Wolff (1971) are native species common all over Iceland, especially in the lowlands (Kristinsson 2010), this is clearly not the case.

The average temperature in Iceland is expected to rise by 1.3–2.3°C by the middle of this century, compared to the period 1986–2005 (Björnsson et al. 2018). According to our results, this is likely to enhance the distribution and population density of *C. pisi* in Iceland. Increased damage by *C. pisi* in young tree plantations can therefore be expected, as well as increased pressure on *Lupinus nootkatensis*, which might reduce its invasiveness. Hrafkelsdóttir et al. (2020) showed that three years of defoliation on the lupin can reduce seed production and thereby the potential spread of the plant. Svavarsdóttir et al. (2016) showed that cutting in July during 2011–2015 had a significant negative effect on the density and cover of lupin. Repeated insect outbreaks may have similar effects.

Our study indicates strongly that the

recent northward expansion and changes in the population dynamics of *C. pisi* in Iceland have been driven by climate change, the latter concurrent and in combination with host shift over to the Nootka lupin. This may have a substantial effect on lupin ecosystems and pose a new threat to afforestation efforts in Iceland.

#### ACKNOWLEDGMENTS

We thank Minningarsjóður Hjálmars R. Bárðarsonar and Elsa S. Bárðarson (Hjálmars R. Bárðarsonar and Elsa S. Bárðarson Memorial Fund) and Vísinda og rannsóknasjóði Suðurlands (The Science and Research fund of South Iceland) for financial support. We also thank The Icelandic Meteorological Office for providing temperature data, Björn Traustason for assistance with making the map and Bjarni D. Sigurdsson, Halldór Sverrisson and Dennis Riege for good advice.

#### REFERENCES

- Ayres MP & Lombardero MJ 2000.** Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment* 262(3): 263–286. DOI: [10.1016/S0048-9697\(00\)00528-3](https://doi.org/10.1016/S0048-9697(00)00528-3)
- Ayres MP & Scriber JM 1994.** Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecological Monographs* 64(4): 465–482. DOI: [10.2307/2937146](https://doi.org/10.2307/2937146)
- Bale J 2002.** Insects and low temperatures: from molecular biology to distributions and abundance. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 357(1423): 849–862. DOI: [10.1098/rstb.2002.1074](https://doi.org/10.1098/rstb.2002.1074)
- Bale JS & Hayward SAL 2010.** Insect overwintering in a changing climate. *Journal of Experimental Biology* 213(6): 980–994. DOI: [10.1242/jeb.037911](https://doi.org/10.1242/jeb.037911)
- Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC,**

- Symrnioudis I, Watt AD & Whittaker JB 2002.** Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8(1): 1-16.  
DOI: [10.1046/j.1365-2486.2002.00451.x](https://doi.org/10.1046/j.1365-2486.2002.00451.x)
- Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A & Larsson S 2005.** Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological applications* 15(6): 2084-2096.  
DOI: [10.1890/04-1903](https://doi.org/10.1890/04-1903)
- Bjarnason H 1957.** Um innflutning plantna [plant importing]. Ársrit Skógræktarfélags Íslands 24: 64-79 [In Icelandic].
- Björnsson H, Olason EO, Jónsson T & Henriksen S 2007.** Analysis of a smooth seasonal cycle with daily resolution and degree day maps for Iceland. *Meteorologische Zeitschrift* 16(1): 57-69.  
DOI: [10.1127/0941-2948/2007/0188](https://doi.org/10.1127/0941-2948/2007/0188)
- Björnsson H, Sveinbjörnsdóttir ÁE, Daniélsdóttir AK, Snorrason Á, Sigurðsson BD, Sveinbjörns-son E, Viggósson G, Sigurjónsson J, Baldursson S & Þorvaldsdóttir S 2018.** Hnattrænar loftslagsbreytingar og áhrif þeirra á Íslandi: Skýrsla vísindanefndar um loftslagsbreytingar [Global climate change and its effects in Iceland. Report from the national scientific panel on climate change], p. 120, Umhverfisráðuneytið, Reykjavík [In Icelandic].
- Cannon RJ 1998.** The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology* 4(7): 785-796.  
DOI: [10.1046/j.1365-2486.1998.00190.x](https://doi.org/10.1046/j.1365-2486.1998.00190.x)
- Cayton HL, Haddad NM, Gross K, Diamond SE & Ries L 2015.** Do growing degree days predict phenology across butterfly species? *Ecology* 96(6): 1473-1479.  
DOI: [10.1890/15-0131.1](https://doi.org/10.1890/15-0131.1)
- Cindea E 1979.** Investigations on the biology and control of some pests of edible pea crops. *Probleme de Protectia Plantelor* 7(2): 87-96.
- Crozier L 2004.** Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85(1): 231-241.  
DOI: [10.1890/02-0607](https://doi.org/10.1890/02-0607)
- Davis JB 2007.** Statistics using SAS enterprise guide, SAS Institute, Cary.
- Ekholm A, Tack AJ, Bolmgren K & Roslin T 2019.** The forgotten season: the impact of autumn phenology on a specialist insect herbivore community on oak. *Ecological Entomology* 44(3): 425-435.  
DOI: [10.1111/een.12719](https://doi.org/10.1111/een.12719)
- Guðjónsen SK & Magnússon B 2019.** Útbreiðsla og flatarmál lúpínubreiða á Íslandi 2017 [Spread and area of Nootka Lupin fields in Iceland in 2017], p. 31, Náttúrufræðistofnun NÍ-19001 (Icelandic Institute of Natural History), Gardabær Iceland [In Icelandic].
- Halldórsson G, Sigurdsson BD, Hrafnkelsdóttir B, Oddsdóttir E, Eggertsson O & Ólafsson E 2013.** New arthropod herbivores on trees and shrubs in Iceland and changes in pest dynamics: A review. *Icelandic Agricultural Sciences* (26): 69-84.
- Hermes DA 2004.** Using degree-days and plant phenology to predict pest activity. In Krischikand V & Davidson J(eds). IPM (integrated pest management) of midwest landscapes. Minnesota Agricultural Experiment Station Publication, St. Paul MN, pp 49-59
- Hill J, Thomas C & Huntley B 2003.** Modeling present and potential future ranges of European butterflies using climate response surfaces. In: Boggs CL, Watt WB & Ehrlich PR (eds). *Butterflies*. University of Chicago Press, pp. 149-168.
- Hodgson JA, Thomas CD, Oliver TH, Anderson BJ, Brereton T & Crone E 2011.** Predicting insect phenology across space and time. *Global Change Biology* 17(3): 1289-1300.  
DOI: [10.1111/j.1365-2486.2010.02308.x](https://doi.org/10.1111/j.1365-2486.2010.02308.x)
- Hokkanen H 1993.** Overwintering survival and spring emergence in *Meligethes aeneus*: effects of body weight, crowding, and soil treatment with *Beauveria bassiana*. *Entomologia experimentalis et applicata* 67(3): 241-246.  
DOI: [10.1111/j.1570-7458.1993.tb01674.x](https://doi.org/10.1111/j.1570-7458.1993.tb01674.x)
- Hrafnkelsdóttir B & Oddsdóttir E 2010.** Ertuygla [Broom moth]. Ársrit Skógræktar ríkisins 2009: 18-19 [In Icelandic].
- Hrafnkelsdóttir B, Oddsdóttir E, Halldórsson G & Sverrisson H 2012.** Varnir gegn ertuyglu [Management of the broom moth]. Ársrit Skógræktar ríkisins 2011: 13-15 [In Icelandic].
- Hrafnkelsdóttir B, Sigurdsson BD, Oddsdóttir ES, Sverrisson H & Halldórsson G 2020.** The effect

- of insect herbivory on seed production of *Lupinus nootkatensis*, an introduced species in Iceland. *Agricultural and Forest Entomology* 22: 136-145. DOI: [10.1111/afe.12368](https://doi.org/10.1111/afe.12368)
- Hrafnkelsdóttir B, Sigurdsson BD, Oddsdóttir E, Sverrisson H & Halldórsson G 2019.** Winter survival of *Ceramica pisi* (Lepidoptera: Noctuidae) in Iceland. *Agricultural and Forest Entomology* 21: 219-226. DOI: [10.1111/afe.12323](https://doi.org/10.1111/afe.12323)
- Hrafnkelsdóttir B 2020.** The interaction between native insect herbivores, introduced plant species and climate change in Iceland. PhD thesis at The Agricultural University of Iceland, p. 70.
- Jepson JU, Biuw M, Ims RA, Kapari L, Schott T, Vindstad OPL & Hagen SB 2013.** Ecosystem impacts of a range expanding forest defoliator at the forest-tundra ecotone. *Ecosystems* 16: 561-575. DOI: [10.1007/s10021-012-9629-9](https://doi.org/10.1007/s10021-012-9629-9)
- Keena MA & Moore PM 2010.** Effects of Temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) Larvae and Pupae. *Environmental Entomology* 39(4): 1323-1335. DOI: [10.1603/EN09369](https://doi.org/10.1603/EN09369)
- Kristinsson H 2010.** Flowering plants and ferns of Iceland( 3<sup>rd</sup>. edition). Mál og menning, Reykjavík bls 368.
- Liu Z, Gong P, Wu K, Wei W, Sun J & Li D 2007.** Effects of larval host plants on over-wintering preparedness and survival of the cotton bollworm, *Helicoverpa armigera* (Hübner)(Lepidoptera: Noctuidae). *Journal of Insect Physiology* 53(10): 1016-1026. DOI:[10.1016/j.jinsphys.2007.05.005](https://doi.org/10.1016/j.jinsphys.2007.05.005)
- Logan JA, Régnière J & Powell JA 2003.** Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1(3): 130-137. DOI: [10.1890/1540-9295\(2003\)001\[0130:ATIOGW\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2)
- Luoto M, Heikkinen R, Pöyry J & Saarinen K 2006.** Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography* 33(10): 1764-1778. DOI :[10.1111/j.1365-2699.2005.01395.x](https://doi.org/10.1111/j.1365-2699.2005.01395.x)
- Magnússon B 2010.** NOBANIS—invasive alien species fact sheet—*Lupinus nootkatensis*. [From: Online Database of the European Network on Invasive Alien Species] URL: [http://www.nobanis.org/files/factsheets/Lupinus\\_nootkatensis](http://www.nobanis.org/files/factsheets/Lupinus_nootkatensis). pdf: 11.
- Murray M 2008.** Using degree days to time treatments for insect pests. Utah State University Extension, IPM-05-08, Logan, UT.
- Ólafsson E 2009.** Ertuygla (*Ceramica pisi*)[website], <https://www.ni.is/is/biota/animalia/arthropoda/hexapoda/insecta/lepidoptera/noctuidae/ertuygla-ceramica-pisi> accessed 23 January, 2023 [In Icelandic].
- Ólafsson E & Björnsson H 1997.** Fiðrildi á Íslandi 1995 [Butterflies in Iceland 1995], p. 135, Náttúrufræðistofnun Íslands Reykjavík [In Icelandic].
- Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J & Tammaru T 1999.** Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399(6736): 579-583. DOI: [10.1038/21181](https://doi.org/10.1038/21181)
- Pureswaran DS, Roques A & Battisti A 2018.** Forest Insects and Climate Change. *Current Forestry Reports* 4(2): 35-50. DOI: [10.1007/s40725-018-0075-6](https://doi.org/10.1007/s40725-018-0075-6)
- Schierbeck HJG 1886.** Skýrsla um nokkrar tilraunir til jurtaræktunar á Íslandi [Report on several plant cultivation experiments in Iceland]. *Tímarit hins íslenska bókmenntafélags* 7: 1-66 [In Icelandic].
- Sigurðsson BD, Halldórsson G & Heiðarsson L 2003.** Ertuygla. „Nýr” vágstur í skógrækt í nánd við lúpínubreiður. [Broom moth causes problems on afforestation sites in S and SE Iceland]. *Skógræktarritið 2003* (1): 87-92 [In Icelandic].
- Sinclair BJ, Vernon P, Klok CJ & Chown SL 2003.** Insects at low temperatures: an ecological perspective. *Trends in Ecology & Evolution* 18(5): 257-262. DOI: [10.1016/S0169-5347\(03\)00014-4](https://doi.org/10.1016/S0169-5347(03)00014-4)
- Svavarsdóttir K, von Schmalensee M, Aradóttir ÁL & Stefánsson RA 2016.** Áhrif sláttar og eitrunar á lúpínubreiður og gróðurfar [A comparison of two eradication methods for the invasive species *Lupinus nootkatensis* in Iceland - English summary]. *Náttúrufræðingurinn* 86 (1–2): 5–18 [In Icelandic].
- Systat Software I 2008.** SigmaPlot for Windows, version 11.0, Systat Software, Inc San Jose, California.

**Ungerer MJ, Ayres MP & Lombardero MJ 1999.** Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography* 26(6): 1133-1145.

DOI: [10.1046/j.1365-2699.1999.00363.x](https://doi.org/10.1046/j.1365-2699.1999.00363.x)

**Wolff NL 1971.** The Zoology of Iceland, p. 193, Munksgaard, Copenhagen.

**Zalom FG & Wilson T 1982.** Degree-days in relation to an integrated pest management program, Cooperative Extension, University of California.

Received: 10.7.2023

Accepted 24.10.2023