

A close-up photograph of a fluffy white pup, likely an Arctic fox, peering out from a hole in a large, white, textured block of ice. The pup's face is the central focus, showing its dark eyes, black nose, and thick white fur. The background is a vast, flat expanse of ice under a pale sky.

Changing climate and the Baltic region biota

Antti Halkka
Helsinki 2020

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Cover photo of a ringed seal pup, Gulf of Riga by Seppo Keränen

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III

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IV

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Contributions

The following table shows the contributions of authors to the original articles:

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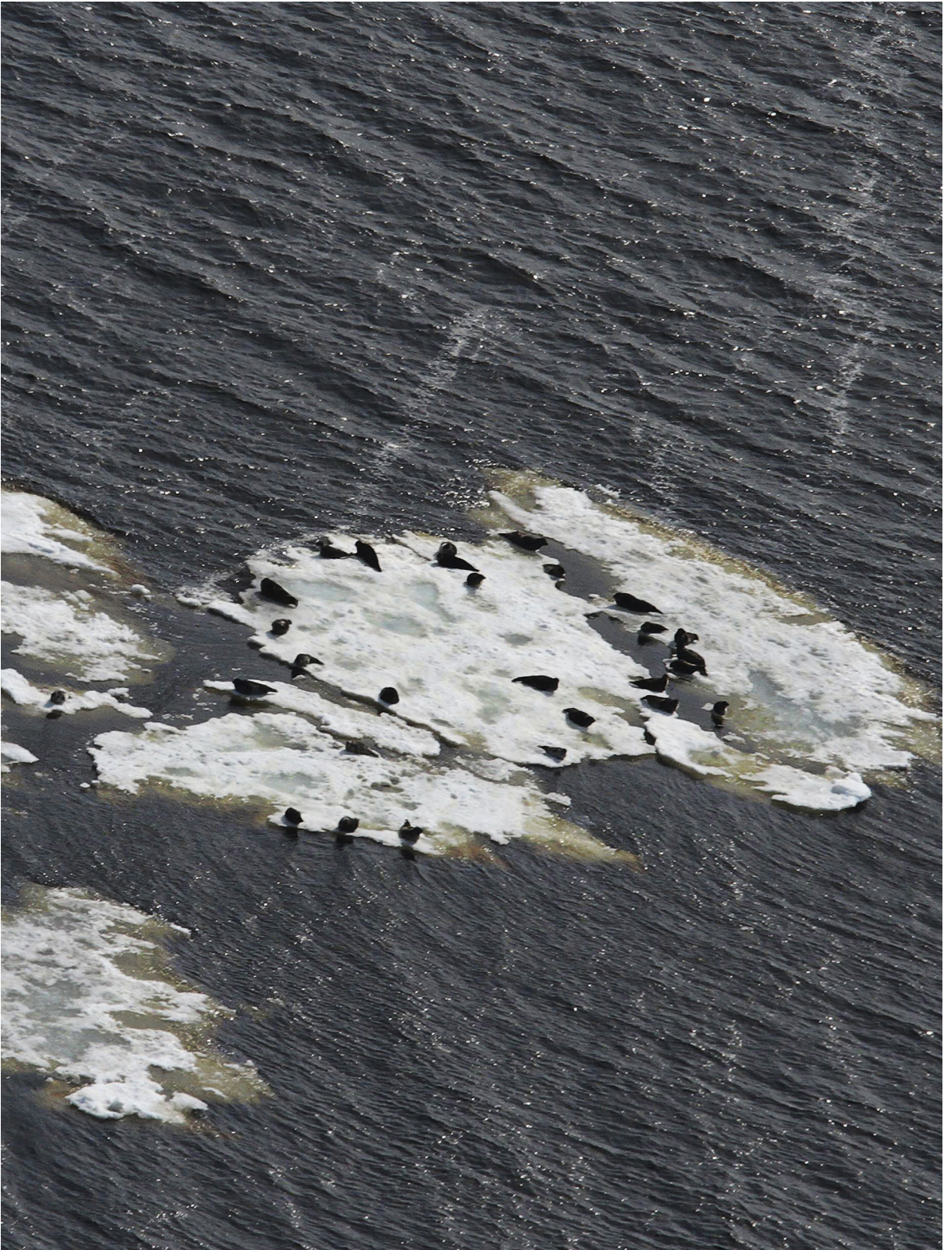
ABSTRACT

The Baltic region is characterised by a strong seasonal climate. Climate change may bring profound ecological changes to the region. These ecological responses to a changing climate can be better understood if the effects of recent yearly variations are known. Other ways to explore possible consequences of future climate change are by using climate models and by looking at the response of species to warm climate phases of the past millennia. This thesis utilizes these methods including a range of study species: a mammal, migratory birds, and an insect.

The mammalian species studied is the Baltic ringed seal (*Pusa hispida botnica*), a subspecies of the ringed seal. Ringed seals need ice as a substrate for breeding, including the construction of a breeding lair. It is shown (study I) that the projected changes in the ice climate for 2071–2100 in the southern breeding areas of the Baltic ringed seal (the Gulf of Finland, the Archipelago Sea and the Gulf of Riga) are so large, that for most years successful breeding is unlikely. In the northernmost parts of the Bothnian Bay, the ice climate is still projected to be suitable for breeding for most years. By the end of this century the Bothnian Bay could be the only remaining breeding area for the Baltic ringed seal. Based on an extensive material of subfossil seal finds, study (II) suggests that ringed seals have probably lived continuously in the Baltic Sea for more than 10,000 years, even surviving the Holocene Thermal Maximum (a several millennia-long warm period). As the warm winters of the Holocene probably weren't as warm as the temperatures projected for the final decades of this century, the survival prospects of the ringed seal in the Baltic will probably be reduced in a way unprecedented in the history of the subspecies.

The bird study (III) adds to the growing evidence that temperatures along migration routes have an effect on arrival times. We found negative correlations between temperature and arrival times in several of the ten studied long-distance Finnish migrants, indicating that birds arrive earlier when the temperature is higher along the migration route. Temperature data used in studies of bird spring migration phenology often comes from the breeding grounds. As the correlation between the timing of migration and temperature, in this and other studies, is often located along the migration route (several hundreds of kilometres away from the breeding grounds), the responsiveness of bird spring migration timing to temperature change may be underestimated. The possibility of long-distance migrants using temperature to predict yearly variations in the advancement of spring in the breeding area and the relationships of changes between distribution and phenology are discussed.

The dominating source of large-scale climate variability in Europe, the North Atlantic Oscillation (NAO), had an impact on the population dynamics of the meadow spittlebug (*Philaeus spumarius*), a common insect (study IV). We show that winter NAO affects nymph mortality in the Tvärminne study area of Southern Finland. A relatively stationary lagged effect of winter NAO on the April temperature was found in the Baltic area. As the lagged effect of winter NAO on spring temperature in Northern Europe is well documented in meteorological literature, I propose that such lagged effects of winter NAO can, in many cases, be behind the associations found between winter NAO and spring migration phenology of long-distance bird migrants in Europe.



Ringed seals on ice. Bothnian Bay, May 2015. Photo by Antti Halkka.

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1. INTRODUCTION

Climate change (IPCC 2013, 2018, Trenberth and Hurrell 2019) has brought a lot of new interest in ecological studies on the impacts of climate variation and climate change on ecosystems and species (Parmesan and Yohe 2003, Bellard et al. 2012). Projected future global effects of climate change are authoritatively reviewed in IPCC-reports (IPCC 2013, 2014, 2018, 2019). Such effects include surface temperature rise in all assessed scenarios, warming and acidifying oceans, global sea level rise, decreases in area of near-surface permafrost, increased extinction risk for a large fraction of species, and problems for species to shift their ranges rapidly enough to keep pace with the changing conditions (IPCC 2014).

The profound shifts in temperature regimes are projected to lead to considerable changes in species distribution (Huntley 2019) and the composition of species assemblages or communities (Brotons et al. 2019). For species to be able to cope with these pressures, phenotypic plasticity and in many cases evolutionary changes are needed (Nussey et al. 2007, Merilä and Hendry 2014). The velocity of climate change is high, as has been demonstrated with the high speed of change in the locations of isotherms (Loarie et al. 2009, Burrows et al. 2011).

1.1. Future climate change in Europe

In Europe, regional warming is projected to exceed global averages (van Oldenborgh et al. 2014, Vautard et al. 2014), and this is also the

case for most of Africa (Nikulin et al. 2018). The entire Afro-Paleartic migration system of birds (the subject of **III**) is projected to have a drastically changed climate in the future.

Future changes of climate are most often studied with modelling. These studies make use of climate projections based on the IPCC SRES emission scenarios (Nakićenović 2000) or the more recent representative common pathways or RCPs (Moss et al. 2010, Meinshausen et al. 2011, van Vuuren et al. 2011). Each RCP scenario consists of a specific radiative forcing projection near the year 2100. For example, RCP4.5 is a pathway that involves a reduction of global CO₂-emissions after the 2040s, and forms a "common platform for climate models to explore the climate system response to stabilizing the anthropogenic components of radiative forcing" (Hughen et al. 2004). Climate models are forced with SRES and RCP-scenarios, and the results can then be used to assess ecological effects by looking at relevant variables, such as temperature, precipitation, and ice cover.

RCP4.5 is often used together with RCP8.5, which represents a pathway with very high greenhouse gas emissions (Riahi et al. 2011). In RCP8.5, CO₂ emissions continue to rise until the end of this century, and it has been criticised as being a "return to coal" -scenario (Ritchie and Dowlatabadi 2017). RCP8.5 is, however, still deemed possible, although RCP8.5 can only "emerge under relatively narrow circumstances" (Riahi et al. 2017). Warming will continue be-

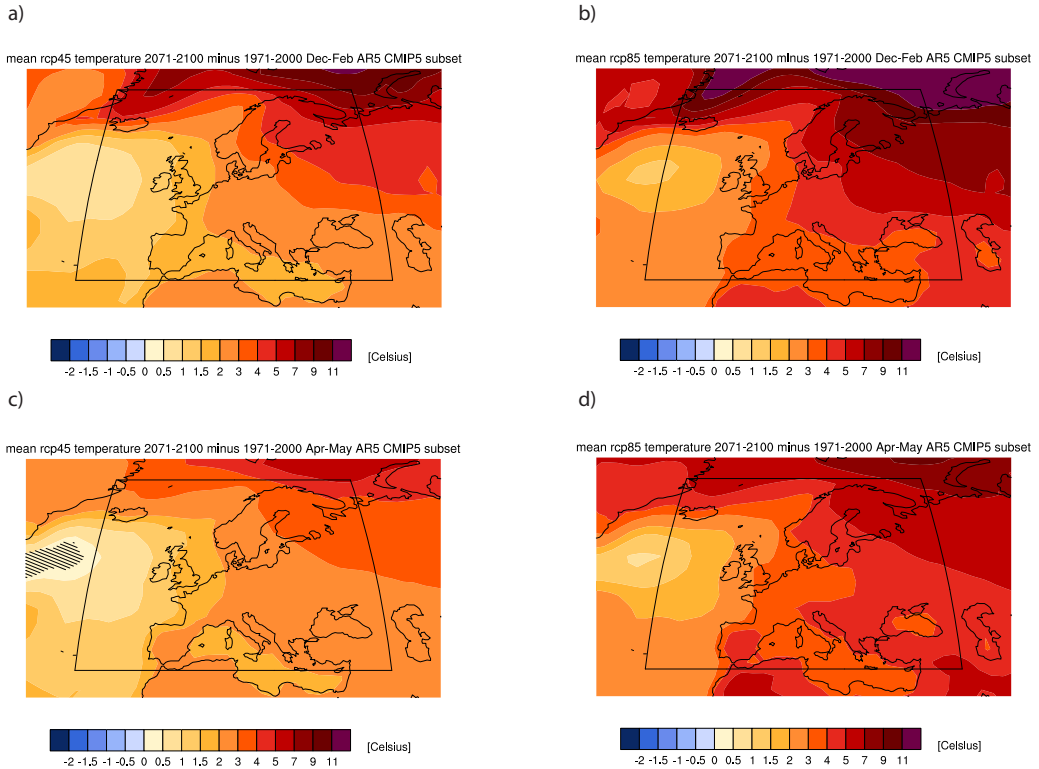


Fig. 1. Projected December–February (top) and April–May (bottom) temperature changes in Europe under the IPCC scenarios RCP4.5 (a, c) and RCP8.5 (b, d) between 1971–2000 and 2071–2100. The plots were produced with the KNMI Climate Explorer extension of the IPCC WG1 AR5 Annex I Atlas (van Oldenborgh et al. 2014), as spring months are not included in the published version. Source: <https://climexp.knmi.nl/help/atlas.shtml>

yond the year 2100 under all RCP-scenarios except RCP2.6 (IPCC 2014). Projected changes in mean winter and April–May temperature in Europe are shown in **Fig. 1**.

Climate change is also altering current patterns of seasonality. The average onset of the growing season in Europe is projected to advance by at least two weeks (RCP4.5) from 1971–2000 to 2070–2099 (Ruosteenoja et al. 2016a). Large-scale environmental shifts and changes in climatic zones in Europe are expected (Metzger et al. 2008, Jylhä et al. 2010, Breuer et al. 2018). This involves considerable drying of large parts of middle and southern Europe (Fabian and Matyasovszky 2010, Breuer et al. 2018). Results of wind regime changes are more varied in the climate model future scenarios than temperature changes (Ruosteenoja et al. 2019). In spring (Mar–May), north–westerly winds are

projected to increase over the majority of Europe, but southerly to easterly winds will be more likely in the Mediterranean area in spring (Ruosteenoja et al. 2019).

Projected changes in temperature lead to a considerable reduction of the sea ice cover in the Baltic (Haapala et al. 2001, Meier 2006, Jylhä et al. 2008, Meier et al. 2011, Luomaranta et al. 2014, Meier 2015). The most recent study (Luomaranta et al. 2014) sums up the estimates of percentage change in the annual maximum ice extent of the Baltic Sea (MIB) by late 21st century (2080s). The projected reduction in MIB in typical ice years is 58% in SRES B2 and RCP4.5, 70% in SRES A2, and 74% in RCP8.5. In scenarios involving very large emissions, sporadic future winters without ice are possible in the end of this century (Omstedt et al. 2000, Meier 2006). Large changes in snow climate are al-

so expected (Jylhä et al. 2008). Projected Baltic water temperature increase (volume averaged) is 1.6°C (RCP4.5) and 2.7°C (RCP 8.5) from 1976–2005 to 2069–2098 (Saraiva et al. 2019).

The leading pattern of atmospheric variability in Europe is the North Atlantic Oscillation (NAO). Alternations in the NAO-pattern result in large changes in the mean wind speed and direction over the North Atlantic (Hurrell et al. 2003, Trenberth and Hurrell 2019). The traditional NAO-index is based on pressure differences between the Arctic Subpolar Low (Iceland) and subtropical Atlantic (Azores) High. A positive value of the index is connected to westerly winds that bring warm, moist air to northern Europe with large effects on temperature and precipitation in the region (Hurrell 1995, Hurrell et al. 2003). There has been much research on the ecological effects of the NAO (Ottersen et al. 2001). These studies include impacts on Baltic ice (Jevrejeva 2002, Yu Karpechko et al. 2015) and bird migration (Vähätalo et al. 2004, Stervander et al. 2005, Haest et al. 2018a).

1.2. Recent change in climate in Europe and the Baltic region

Global surface temperature has been warming at a rate of about 0.17°C per decade since the 1970s (Hansen et al. 2010). Europe has been warming more rapidly than most climate models have projected (van Oldenborgh et al. 2009).

A clear anthropogenic warming signal is now seen in Europe (Kjellström et al. 2013) and in the Baltic Sea area (Barkhordarian et al. 2016). The rapid warming in Europe can be seen as a result of greenhouse gas forcing, reduction of aerosols, and changes in the North Atlantic Oscillation. According to a recent assessment, the declining aerosol trend contributed to 23% of the reanalysis driven simulated surface warming in Europe (35–55°N) in 1980–2012 (Nabat et al. 2014).

A shift towards accelerating warming can be seen in Europe in the 1970s (SW-part) and 1980s, (main part) (Miranda and Tomé 2009). Miranda and Tomé (2009) showed that different areas are characterised by what they call break-

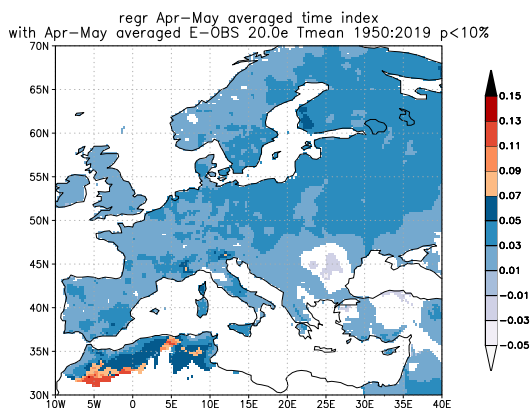


Fig. 2. Spring (April–May) temperature trend in Europe between 1950 and 2019. Gridded E-OBS-data (Cornes et al. 2018) was used in Climate Explorer to generate the picture. The scale is in degrees per year. In much of Europe, the trend is between 0.1 and 0.5 degrees per decade. An area that has not been warming (a “warming hole”) can be seen in the southeastern part. For data I acknowledge the E-OBS dataset from the EU-FP6 project UERRA (<http://www.uerra.eu>) and the data providers in the ECA&D project (<https://www.ecad.eu>).

points in temperature change. For example in Scandinavia, such a breakpoint can be placed in the 1980s (Miranda and Tomé 2009), when the temperature started to warm rapidly. This was a bit later than the global start of a rapid warming in the 1970s (Cahill et al. 2015).

This recent period of rapid warming in Europe has formed a good basis for ecologists that started to focus on the impacts of climate change on biodiversity, species, and ecosystems in the 1990s. Europe’s warming trend since the 1970s has been involved in a plethora of phenological and other ecological climate change studies, as can be seen in the timeframe of the studies in a recent review (Cohen et al. 2018, their tables S1 and S2).

There are significant spatial differences in the timing and magnitude of the regional temperature change globally and in Europe between 1950 and 2019. **Fig. 2** shows the temperature trend of April–May temperature. It can be seen that the warming of these spring months has been most rapid in the northern parts of Europe, and that an area west and south of the Black Sea has not warmed in this period.

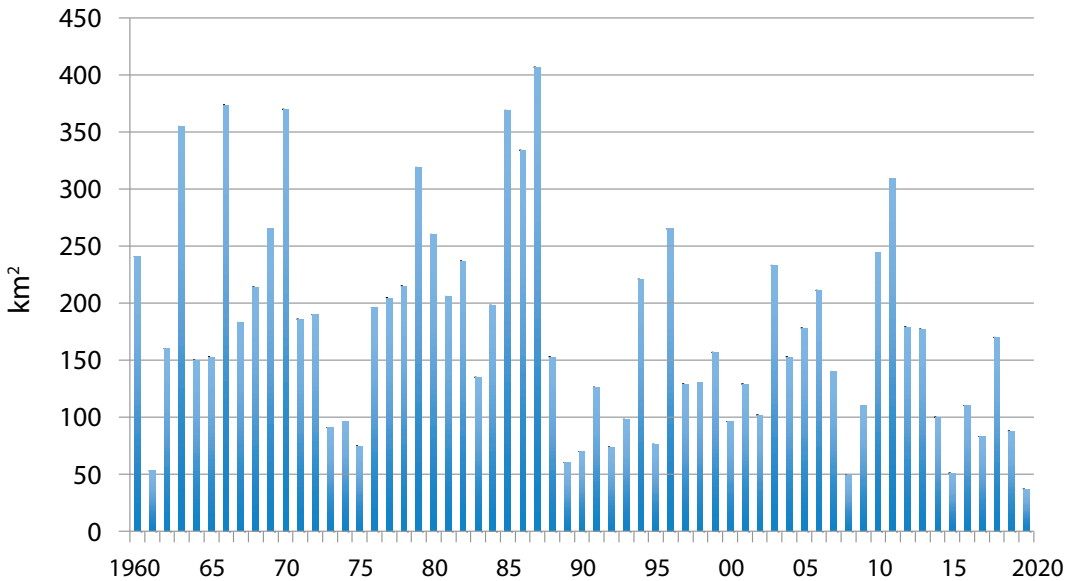


Fig. 3. Baltic maximum annual ice extent in 1960–2020. Data courtesy of Finnish Meteorological Institute (FMI). Recently, the ice years 2007–2008, 2014–2015, and 2019–2020, were exceptionally mild. A new unprecedentedly low maximum ice cover was observed in 2019–2020 (37,000 km²) (Vainio, 2020).

The most rapid changes in temperature have occurred during winter and spring seasons (relevant in studies **I**, **II**, **III** and **IV**). Between 1959 and 2008, springs were warming in Finland, 0.29°C per decade, and winter warming was even greater (0.69°C/decade) (Tietäväinen et al. 2010). These results with highest increases in winter and spring temperatures within the last 40 years were confirmed in a later study (Mikkonen et al. 2015). Spring has warmed also in the Baltic region (Rutgersson et al. 2015). A trend study of the years 1961–2014 found that spring snow depth had decreased and that snowmelt occurs earlier in Finland (Luomaranta et al. 2019).

The long time-series of the maximum annual ice extent in the Baltic Sea ice (MIB) is the most widely used indicator of large-scale change of ice climate in the Baltic Sea (Jylhä et al. 2008, Haapala et al. 2015). The NAO has a considerable influence on MIB (Omstedt and Chen 2001, Vihma and Haapala 2009). The 20th century was probably the warmest century with the least MIB for the last 500 years (Hansson and Omstedt 2008). The mildest ice winters observed are 2007/2008 and 2014/2015 (Uotila et

al. 2015, Ronkainen et al. 2018). According to Uotila et al. (2015), a MIB lower than 60,000 km² had occurred only once (1929/1930) in the period 1720–1985 before these exceptional recent winters.

The most conspicuous finding of the last 30 years is the occurrence of such extremely mild winters, and that only the winter 2010–2011 had a MIB of more than 300,000 km² (**Fig. 3**). A declining trend in MIB has been found in several studies (Vihma and Haapala 2009, Haapala et al. 2015), but is sensitive to the selection of the time period (Luomaranta et al. 2014). Also ice-season length in the Baltic has decreased rapidly (Jevrejeva et al. 2004), as can be seen in the most recent trend calculations. The 100-yr-trend has been a 18 day decrease in Kemi, and a 41 day decrease in Loviisa (Haapala et al. 2015).

1.3. Past climate change in the Holocene

Holocene climate changes in the Baltic region have been reviewed in several studies (Hammarlund et al. 2003, Seppä et al. 2005, Björck 2008, Wanner et al. 2008, Seppä et al. 2009, Borzenk-

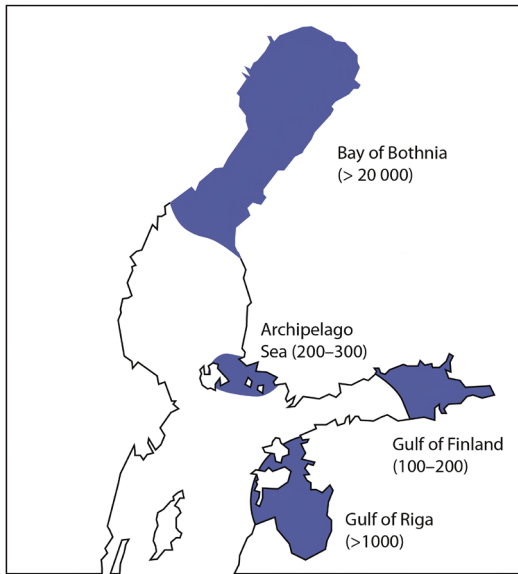


Fig 4. The Baltic Sea, and the four breeding populations of the ringed seal. The sizes of the populations are adapted from Helcom (2018).

ova et al. 2015, Zhang et al. 2017). Solar orbital changes have strongly influenced the energy balance of the area. It can be calculated that summer solar insolation was strongest 7000–6000 years ago (Borzenkova et al. 2015).

The orbital forcings are the main reason behind a long warm phase in the Holocene, the Holocene thermal maximum, after which a gradual cooling phase followed (Wanner et al. 2008, Seppä et al. 2009, Borzenkova et al. 2015). Temperatures around the Baltic Sea were highest between 8000 and 4500 years ago (Borzenkova et al. 2015). During this phase, the yearly mean temperature was about 1.0–3.5° higher than at the end of the 20th century (Borzenkova et al. 2015). This phase had anomalously high positive temperature anomalies in the North-Atlantic–Fennoscandian region compared to the global mean (Sejrup et al. 2016).

Proxy records are mostly suitable for the reconstruction of yearly or summer temperatures, but middle Holocene winter climate relevant to sea ice (I, II) is not as well known (Giesecke et al. 2008). The winter temperature and humidity in the area are strictly connected to the strength of westerly wind and transport of heat from the At-

lantic (Hurrell et al. 2003, Seppä et al. 2005), and therefore difficult to model. If only orbital forcing is taken into account, winters could have been cool, but if changes in heat stored in oceans and circulation changes are included in models, also winter warming is evident (Zhang et al. 2010). A warming of the winter climate in the Baltic region has been proposed with proxy studies (Iversen 1944, Giesecke et al. 2008, Wanner et al. 2008, Borzenkova et al. 2015) with highest winter temperatures between 7000 and 6000 years BP.

1.4. Climate and the ringed seal

As an Arctic species, the ringed seal (*Pusa hispida*) is heavily dependent on ice and snow. The ringed seal is inhabiting water bodies where periodical ice cover lasts at least several months (Reeves 1998, Lowry 2016). Ringed seals use ice as a platform for resting, breeding and moulting, and they are completely dependent on ice and snow for breeding (McLaren 1958, Helle 1980, Kelly et al. 2010, Niemi et al. 2019). Ice climate suitable for the species can be found in the Arctic (subspecies *P. h. hispida*), in the Sea of Okhotsk (*P. h. ochotensis*, and in the Baltic Sea (*P. h. botnica*) and the nearby lakes Saimaa (*P. h. saimensis*) and Ladoga (*P. h. ladogensis*) (Reeves 1998, Lowry 2016). In the Baltic, the ice winter length is at maximum ca. 6 months, but in the Arctic, annual ice cover period in ringed seal habitats can last up to 10–11 months (Yurkowski et al. 2016).

Ringed seals have four breeding areas in the Baltic Sea (Fig. 4): the Bothnian Bay, the Archipelago Sea, the Gulf of Finland and the Gulf of Riga. Breeding areas are located in the parts of the Baltic that have the most severe ice climate. The current population is concentrated in the Bothnian Bay, and it is estimated that it harbours at least 80 per cent of the total Baltic population of more than 20,000 ringed seals (Helcom 2018). In the Gulf of Finland, the current population is as low as 100–200 and in the Archipelago Sea 200–300. The Gulf of Riga has the second largest breeding population with more than a thousand ringed seals. Adult male ringed seals are thought to be territorial in winter (Smith and Hammill 1981, Kelly et al. 2010), and indica-

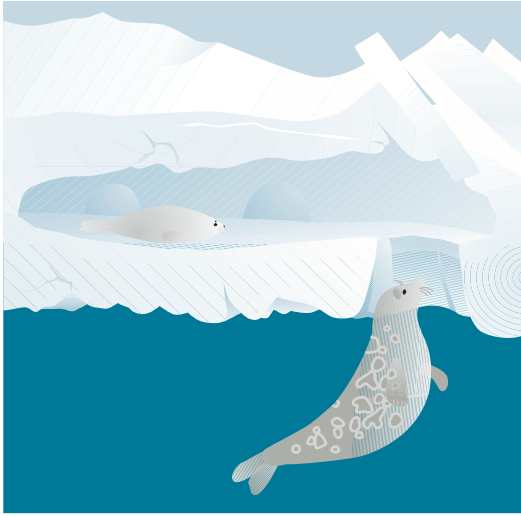


Fig. 5. Breeding lair of the ringed seal. The only entrance to the lair is from below. Adapted after Smith and Stirling (1975). Graphics by Vesa Pynnöniemi.

tions of territoriality has recently been shown in females (Niemi et al. 2019).

Grey seals (*Halichoerus grypus*) breed on land and on drift-ice, but ringed seals are adapted to an ice environment with pack-ice or shore-fast ice (Reeves 1998, Lowry 2016). Ringed seal life history is well adapted to a stable winter ice-environment (Stirling 2005, Kelly et al. 2010, Lowry 2016). Ringed seal populations that breed on land do not exist anywhere in their distribution area (McLaren 1958, Lydersen et al. 2017).

Ringed seals are most dependent on ice and snow during the breeding season. The lactation period of the species – 6–9 weeks – is one of the longest in pinnipeds, and longest in the Phocinae. After breeding, ringed seals moult, or renew their hair. This is done preferably on ice (Stirling 2005), but in any case on a dry substrate where their skin is not in constant contact with water with a detrimental cooling effect (Feltz and Fay 1966). In the Baltic, moulting can continue on land after the disappearance of ice (Härkönen et al. 1998). Hauling out of ringed seals on land is common in the Baltic, and was recently documented also in Svalbard (Lydersen et al. 2017).

Ringed seals breed in a specifically built breeding cavity, subnivean lair (Fig. 5), which is important for thermoregulation and for shel-

tering the seals from predators (McLaren 1958, Smith and Stirling 1975, Kelly and Quakenbush 1990, Smith et al. 1991), most notably polar bears (*Ursus maritimus*) and arctic foxes (*Vulpes lagopus*) but also large birds such as gulls (*Larus* sp.) and ravens (*Corvus corax*) (Lowry 2016). In the Baltic Sea the white-tailed eagle (*Haliaeetus albicilla*) is probably the most notable predator for pups (Härkönen 2015), but also red foxes (*Vulpes vulpes*) are common in archipelago habitats (Jüssi 2012). A Saimaa ringed seal pup killed by red fox was documented in the mild winter of 2015 (Auttila 2015).

The lair provides insulation and protection from harsh weather conditions. Ringed seals have large quantities of brown adipose tissue at birth but are born without subcutaneous blubber (Lydersen and Hammill 1993), and the metabolic rates of pups increase dramatically if they are wet (Smith et al. 1991). Lairs are built into snow structures and ridged ice cavities.

As the lair has to be built before giving birth to the pup, an early start of the ice season is important for also snow accumulation. In areas where polar bears are abundant, snow is considered necessary for population viability. For lair formation, a minimum snow depth on level ice is considered to be about 20–30 cm (Hezel et al. 2012, Iacozza and Ferguson 2014). In a recent Canadian model study, pup mortality was set to 100% if April snow depth did not exceed 20 cm (Reimer et al. 2019).

Recent studies have found that snow depth on ice has been decreasing rapidly in the Arctic (Webster et al. 2014), although generally the data base of snow trends on ice is considered to be of low quality (IPCC 2019). In the Baltic context, snow depth has not been considered to be of the same importance as in the Arctic. Baltic ringed seal lairs are often found in ridged ice where suitable cavities can be found (Sundqvist et al. 2012). Most importantly, polar bear and arctic fox predation is absent in the Baltic. In the Baltic, ringed seals are forced to breed on open ice in poor ice winters (Fig. 6).

Projected future ice development in the Arctic is now recognised as a major threat to the ma-



Fig. 6. Ringed seals with their pups on open ice. Top: Archipelago Sea, March 2005. Photo by Seppo Keränen. Bottom: Archipelago Sea, NE Aland Islands, 26.2. 2006. Photo by Monica Stjernberg.

rine mammals in the Arctic (Laidre et al. 2015), including the ringed seal (Kelly 2001, Hezel et al. 2012, Kovacs et al. 2012). Climate change is seen as a threat to ringed seals mainly because of alternation and reduction of suitable ice and snow habitat (Kelly 2001, Laidre et al. 2008, Hezel et al. 2012, Sundqvist et al. 2012, Laidre et al. 2015, Reimer et al. 2019).

The breeding areas of the Baltic ringed seal are in the parts of the Baltic where breeding time ice cover is most probable also in mild winters (Fig. 7).

It was suggested already in the 1950s, that the mild Baltic Sea ice winters in the 1930s had caused problems for ringed seal reproduction and a decline of the population in the Archipelago Sea and in parts of the Swedish east coast (Bergman 1958). In this thesis, future ice climate in the breeding areas is investigated.

1.5. Climate and bird migration

A growing literature is showing that climate change is altering the breeding, staging and wintering habitats of birds (Dunn and Møller 2019), and driving a general poleward shift in the species distributions (Brommer 2004, Parmesan 2006, Chen et al. 2011, Virkkala et al. 2013). Also, the abundances of birds, measured as weighted centre points, are generally shifting polewards (Lehikoinen and Virkkala 2016, Välimäki et al. 2016, Virkkala and Lehikoinen 2017).

The impacts of climate change on bird species richness, distribution and community composition are projected to be large, and are already occurring (Jetz et al. 2007, Huntley et al. 2008, Virkkala et al. 2013, Brotons et al. 2019, Huntley 2019). It has been estimated (Pacifiçi et al. 2017) that "23.4% of threatened birds (out of 1,272 species) may have already been negatively impacted by climate change in at least part of their distribution".

Community changes have been studied with the help of community temperature index (CTI). This index gets different values, based on the relative abundance of individuals of species from different temperature regimes (Devictor et al. 2012, Lindström et al. 2013, Stephens et al.

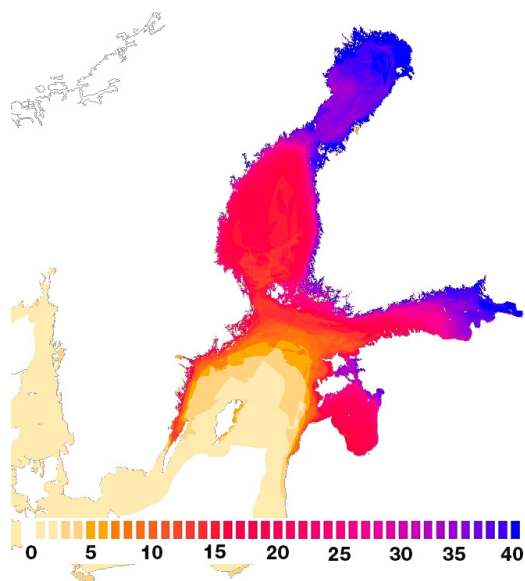


Fig. 7. Frequency of ice cover in the Baltic on the 21st of February 1968–2007. The map shows the number of winters with ice; the maximum consists of all the 40 years between 1968–2007. The selected date serves as a proxy of ice habitat availability in the breeding time of the ringed seal. Source: Antti Halkka and Kaisa Annala (unpublished).

2016, Santangeli and Lehikoinen 2017). Relatively rapid changes in species assemblages have been detected, with the proportion of cold-adapted species generally decreasing, and that of warm-adapted species increasing (Stephens et al. 2016, Brotons et al. 2019).

An important research question is whether the changes in distribution, community composition, and phenology can keep pace with the environmental change. Lags in the response are often found. Such lags include lags in the change of community composition to suit new temperature regimes (Devictor et al. 2008, Bertrand et al. 2011, Devictor et al. 2012, Lindström et al. 2013, Nieto-Sánchez et al. 2015, Santangeli et al. 2017, Burrows et al. 2019), changes in the distribution of species (Pöyry et al. 2009, Pinsky et al. 2013, Lehikoinen and Virkkala 2016, Pinsky et al. 2019) and the connected species richness (Virkkala and Lehikoinen 2017, Blowes et al. 2019).

Lags can in some cases be explained by local thermal refugia, which allow species to persist

in remaining patches of suitable habitat (Potter et al. 2013, Lima et al. 2016, Pinsky et al. 2019).

Migrating birds have to adapt to changes in habitats, and shifts in the phenology of the habitats, reflected in the seasonal availability of food items such as insects and plants. Such adaptations can involve changes in breeding and wintering areas, migration routes and migration phenology.

Bird migration itself is an evolutionary adaptation to the climatic seasonality on our planet (Newton 2007); most bird species that live in seasonal environments migrate. Migration is physiologically demanding for birds, and the yearly schedule of migrating birds involves many phases where accurate timing of phases is important (Newton 2007).

Spring migration and especially the timing of arrival to the breeding areas is the most studied of these events (Knudsen et al. 2011). This reflects the importance of the timing of arrival for migrating birds, but also a general geographic bias in published studies. Breeding areas of migratory birds are often located in Europe and North America, which are over-represented in ecological literature (Culumber et al. 2019), and long time series of bird migration phenology have been predominantly collected in Europe and North America (Knudsen et al. 2011).

The timing of bird spring migration is intimately tied to survival (Newton 2007). Too early arrivals can result in a costly loss of resources needed in breeding. The availability of food can still be scarce in spring, and such shortages can in exceptional cases result in mortality of early-arriving individuals (Brown and Brown 2000, Moreno and Møller 2011). A recent study based on ringing results (Lerche-Jørgensen et al. 2018) found that survival decreases with date in short-distance migrants, as migrants returning early to the breeding grounds had the best survival prospects. A different survival distribution was found in long-distance migrants (Lerche-Jørgensen et al. 2018): survival was highest in birds arriving slightly later than the average for the species (Lerche-Jørgensen, et al. 2018).

1.5.1. The mismatch hypothesis

Birds have been shown to be able to adjust the timing of their spring migration, so that they are arriving earlier in earlier springs (e.g. (Huin and Sparks 2000, Jonzén et al. 2006, Rubolini et al. 2007, Lehikoinen et al. 2010, Visser et al. 2012, Bitterlin and Van Buskirk 2014, Lehikoinen et al. 2019)). For example, high latitude geese species track a green wave of fresh vegetation along their migration to the Arctic breeding areas (Drent et al. 2003, Drent et al. 2006, van der Graaf et al. 2006, Van Der Jeugd et al. 2009). Too late arriving birds can miss the peaks of ecological productivity, and a too late arrival can mean that the best territories are already occupied. It has been repeatedly shown that migratory birds try to time their arrival to the breeding grounds in a rather narrow time window, which is also theoretically expected (Kokko 1999).

Long-distance migrants breeding in high latitudes, and overwintering in the tropics and subtropics, are not supposed to have any reliable cues of the advancement of phenology in their breeding area (Both and Visser 2001, Ambrosini et al. 2019). Projected and already occurring changes in temperature are most profound outside the tropics and subtropics. It has been suggested that this can lead to a mismatch with resources as long-distance migrants could not match their arrival with the earlier springs brought by the warming climate (Both and Visser 2001, Both et al. 2006, Both et al. 2010). This constrains the ability of long-distance migrants to adapt to changes in the breeding grounds (Ockendon et al. 2012). Such a mismatch can have population and ecosystem level consequences (Jones and Cresswell 2009, Beard et al. 2019). Birds have been repeatedly shown to lag behind the phenology of the environment, although the degree of possible mismatch differs between species (Both et al. 2006, Both et al. 2010, Clausen and Clausen 2013, Radchuk et al. 2019). Evidence of population consequences of mismatch have been difficult to find despite much research on the subject (Visser and Gienapp 2019).

According to a recent meta-analysis, compared to other groups, birds are slow in their phenological response to temperature changes (Cohen et al. 2018). As expected, the phenology of invertebrates, butterflies and amphibians, and generally ectotherms, reacted more strongly to increases in temperature than the phenology of birds and mammals (Cohen et al. 2018). An earlier study found the phenological temperature sensitivity to be largest in fishes, insects, plants and crustaceans (Thackeray et al. 2016).

The differences between the responses of birds and plants are interesting because such differences are thought to be contributing to possible mismatches between different trophic levels. In a pioneering study, Marra et al. (2005) found that lilac (*Syringa vulgaris*) budburst advanced about three days per one degree increase in temperature when the corresponding advancement across several species of birds was one day per one degree. The authors suggested that the "impact of temperature on plant phenology is three times greater than on bird phenology".

Later studies have shown that the difference proposed by Marra et al. (2005) largely holds. A recent meta-analysis assessed that the average temperature sensitivity of bird spring migration is about one day per one degree Celsius (Usui et al. 2017), which was also the conclusion of a study with a 183 year dataset from Central Europe (Kolarova et al. 2017). In plants, spring leafing and flowering advances typically several days per one degree (Celsius) increase in temperature: recent studies indicate a 2–4 day response in Europe (Wang et al. 2014) and China (Wang et al. 2015). In some regions and species the advancement per one degree can be as strong as 5–6 days (Wolkovich et al. 2012), or 5–8 days (Tansey et al. 2017).

In laying dates, the temperature response is steeper than that found in migration studies. The estimate of extensive meta analyses was, that laying had advanced by about 2 days per 1 degree increase in ambient temperature (Dunn and Møller 2014). A recent detailed study found an advance of 2–5 days per °C in the first lay date of four bird species in Britain, and concluded that

the study species, including the pied flycatcher, could be sufficiently plastic to track temperature-mediated variation in the optimum laying date (Phillimore et al. 2016). Breeding time has advanced with increasing spring temperature also in Finland (Kluen et al. 2017). It is important to remember that temperature responses can have individual differences (Brommer et al. 2008).

1.6. Climate and insects

The dependence of insects of abiotic factors (Harrison 2012) has been recognised for a long time. Insects are ectotherms, and thus more dependent on ambient temperature and sunlight than endothermic animals. Temperature is the dominant abiotic factor affecting populations of herbivorous insects (Bale et al. 2002).

Studies of insects and climate change have gained popularity only recently. In the 2010s, up to 200 studies have been published annually; in the 1990s only a handful of studies were recorded yearly (Andrew et al. 2013). Lepidoptera, Diptera and Coleoptera are the most studied groups. The order Hemiptera (where *Philaenus* belongs) places fourth. However, a lower percentage of papers studying the responses to climate change relative to the number of species identified is found in this order, as in the other species rich groups Coleoptera and Hymenoptera.

Of climate variables, temperature has dominated insect studies, and has been involved in 40% of the studies (Andrew et al. 2013). The effects of climate change on insects are increasingly studied with natural history collections (Kharouba et al. 2019), or experimental warming (Pelini et al. 2014).

Insect phenology has been one of the most active study fields. An early study found that a warming of one degrees Celsius could advance first and peak appearance of British butterflies by 2–10 days (Roy and Sparks 2000). In a pioneering insect study, positive NAO values were connected with increases in migration of Lepidoptera in Britain (Sparks et al. 2005b). Many studies have found a general advancement of

phenology with increasing temperatures. For example, it was found that winter and spring temperature affect the spring phenology of the orange tip butterfly (*Anocharis cardamines*) (Stålhandske et al. 2015). The lack of time-series data is a problem in insect phenology. There are for example very few studies of soil invertebrate phenology despite their importance in ecosystems (Eisenhauer et al. 2018).

Insect abundance (IV) has been most commonly studied with pest insects. These are in many cases thought to benefit from a warmer climate. For example, a shorter generation time, and higher fecundity, is generally expected for herbivorous forest insect pests in a warmer climate (Jactel et al. 2019). Climate driven population cycles were recently reviewed (Lancaster and Downes 2018), and found to be in many cases driven by variations in the quality of food plants.

Possible links between insect declines and climate change have been discussed, but other factors such as pesticides and habitat changes have been found to be the most prominent causes of the observed declines (Sanchez-Bayo and Wyckhuys 2019). For instance, a recent study from Germany from standardized inventories between 2008 and 2017 showed that species abundances declined dramatically in grasslands, but no connection to changes in climate was found (Seibold et al. 2019). Tropical arthropods may be particularly vulnerable to climate warming (Lister and Garcia 2018).

1.7. Aims of the thesis

My thesis includes studies of climate variability and change and their effects on the ecology of seals, birds and the meadow spittlebug. The pinned studies (I, II) concern the past history and future challenges of the Baltic ringed seal. In paper I the future ice climate of the Baltic breeding areas of the ringed seal are studied. Paper II deals with the history of the ringed seal in the Baltic. Our extensive study (III) adds 36 radiocarbon dates, and analyses also the existing 11 published dates, and covers the entire Holocene history of the species in the Baltic Sea, not achie-

vable with the scarce material available in earlier studies (Ukkonen 2002, Schmölcke 2008).

Climatic niche is involved in all the study papers included in the thesis. Basic ecological requirements of species are reflected in their climatic niches (Hutchinson 1957, Chase and Leibold 2003), which define the range of temperatures, rainfall and humidity and other factors that a species can tolerate to successfully perform the different phases of its lifecycle. These requirements can also be mediated via other species in the food web.

In the ecology of the ringed seals (I, II), a cold winter climate is crucial for the occurrence of ice cover during the breeding period of this strictly pagophilous, or ice dependent, Arctic mammal (see section 1.4.). Breeding time ice cover is a sensitive phase, with specific climatic niche, in the life-cycle of the ringed seal. Projected future changes in ice cover are large, and climate change is a new emerging threat to the Baltic ringed seal (Dippner et al. 2008). A degradation of the breeding habitat combined with less snow on the sea-ice may lead to population declines and threaten the future of Baltic ringed seals. Poor ice winters have already become increasingly common in the Baltic (Jevrejeva et al. 2004, Vihma and Haapala 2009, Luomajaranta et al. 2014). The availability of exceptionally long-time and detailed ice data and climate historic data provides a good background for climate sensitivity studies in the Baltic region (Omstedt et al. 2004).

A climate sensitive phase in the yearly life-cycle of migrating birds (III) is the match of arrival and breeding to the seasonality of resources (Kokko 1999). In paper III I study the still partly controversial ability of long-distance migratory birds to time their arrival to the breeding grounds by tracking yearly variations of climate along their migration route. The ability of birds to predict temperature or the advancement of spring of the migration route ahead, and ultimately also the predictability of the yearly phenology of breeding area (III) is based on spatial autocorrelation of temperature (Hansen and Lebedeff 1987, Rigor et al. 2000, North et al.

2011). Spatial autocorrelation is a central theme in **III**, and interestingly, model results show that climate change might result in increased spatial and temporal autocorrelation of temperature (Di Cecco and Gouhier 2018).

For spittlebugs (**IV**), humidity during the spittle phase is of great concern, and this phase is clearly a sensitive part of the life-cycle, as these

small insects have to complete their univoltine lifecycle on plants that can be easily desiccated. The spittlebug study investigates the climate factors affecting the population sizes of the insect in small island populations and discusses the effects of the NAO, the dominating large-scale climate index in Europe.

2. MATERIALS AND METHODS

2.1. Study locations

All the study sites are located in the Baltic Sea region. Future ice cover scenarios were modelled for the Gulf of Finland, the Gulf of Riga, the Archipelago Sea and the Bothnian Bay breeding areas of the Baltic ringed seal (I). Ringed seal Holocene history was investigated for the entire basin (II). Bird migration data is from the Hanko bird observatory at the entrance of the Gulf of Finland. Island populations of spittlebugs were studied in Tvärminne Zoological Station, Hanko (IV).

The migration of long-distance migrants was studied in the European part of their migration route (III). Large-scale spatial climate data was used in (III) and (IV). A large-scale climate index, the NAO, is a central climate variable involved in the spittlebug study (IV).

2.2. Modelling of ice conditions (I)

This modelling study of ice-winter development is based on the atmosphere-ice-ocean-land-surface model (RCAO) developed at the Rossby Centre in the Swedish Meteorological and Hydrological Institute (SMHI). Two control simulations (1961–1990) and four scenario simulations representing the late 21st century (2071–2100) climate were produced. The scenario simulations represent two global driving models and two IPCC scenarios, A2, B2, which belong to the IPCC SRES scenarios (Nakićenović 2000).

Sections from the Bothnian Bay, the Gulf of Finland, the Archipelago Sea and the Gulf of Ri-

ga were chosen to represent the breeding areas of Baltic ringed seals. We then studied the scenario ice climate in these areas focussing on the lengths of the ice season (measured in days) and ice cover percentages in the selected areas.

The simulations were performed with Cray T3E-600 at the Swedish National Supercomputing Centre. As modelling needs much computational power, the number of driving global models is restricted in comparison to statistical approaches, which can use a larger range of global models (Luomaranta et al. 2014).

2.3. Historical ringed seal records and climate (II)

Nearly 50 radiocarbon-dated geological and archaeological subfossil ringed seal remains from the Baltic Sea area including the Danish straits form the basis of the analysis. Because of land uplift in the northern Baltic, many of the ringed seal remains have been found in the Gulf of Bothnia region. In the south-western parts of the area, the finds originate predominately from shell middens (heaps of mussels). Of the 47 dated finds, 11 were obtained from published studies, and 36 were radiocarbon-dated in Helsinki and Lund. All dates were calibrated with OxCal 4.1. software (Ramsey 2009), and special care was taken to account for specific Baltic reservoir ages as deviations from global marine reservoir ages.

The dated finds were then related to known Holocene climate variability in the Baltic region

(Hammarlund et al. 2003, Björck 2008, Borzenkova et al. 2015).

The reasoning in papers **I** and **II** is based on the assumption that ringed seals are completely ice-dependent during breeding time. In a recent modelling study of ringed seals and climate change (Reimer et al. 2019), pup mortality was assumed to be 100% if ice breakup preceded the assumed birth date of pups.

2.4. Migration data of birds and related climate data (III)

We used spring arrival dates of ten Finnish long-distance migrants observed at the Hanko Bird Observatory from 1979 to 2010. Years with <20 observation days (the springs 1989, 1990, and 1993) were excluded from the analysis. We used daily numbers of staging individuals for nocturnal migrants, and observed migrants for the only diurnal migrant included (Lesser black-backed gull, *Larus fuscus*). Data of the 5th and 50th percentiles of arrivals were used. The use of percentiles, means or medians is considered to be a better proxy for the timing of overall migration timing than the often used first arrival dates (FADs) (Goodenough et al. 2015).

Ring encounters used in the assessments of the possible migration routes were obtained from the Ringing Centre at the Finnish Museum of Natural History. The ring encounters were plotted with Mapinfo Professional 9.5.1. As temperature data, we used gridded mean monthly temperatures of the Global Historical Climatology Network and the Climate Anomaly Monitoring System (GH-CN/CAMS) (Fan and van den Dool 2008).

We correlated the detrended migration time series spatially with the detrended temperature grid-cells of gridded monthly mean temperatures. Correlations were computed separately in each cell in the (0.5°, 9600 cells) GH-CN/CAMS temperature (Fan and van den Dool 2008) grid. The significance of the correlations was evaluated using a two-tailed t-test. Climate Explorer of the Royal Netherlands Meteorological Institute was used in the spatial correlation analysis (van Oldenborgh et al. 2009, Trouet and van Oldenborgh 2013).

We used the correlation length scale (CLS) of monthly Helsinki April and May temperatures as the criteria for the distance where the spatial autocorrelation ends (Hansen and Lebedeff 1987, Rigor et al. 2000, North et al. 2011). CLS is defined as $1/e \sim 0.37$.

2.5. Spittlebug data (IV)

The paper is based on meadow spittlebug abundances on three island populations in Tvärminne in the years 1970–2005. Sizes of sweep net samples were used as proxies of population sizes (see methods in **IV**). As candidate climate variables, we used January–February and January–March North Atlantic Oscillation (NAO) and variables from winter and April–May climate. Two local winter proxies were used: the mean temperature of the coldest month and the length of the snowy season of the preceding winter. Spring–early summer variables included monthly (April, May, June) and bimonthly (April–May) temperatures, and a meadow humidity index, MHI. MHI consists of the precipitation sum in millimetres from which the temperature sum (daily sum of mean temperature in degrees) is subtracted.

Weather data was obtained from the Finnish Meteorological Institute (FMI), the Nordklim data set, and NCEP/NCAR gridded temperature data (Kalnay et al. 1996). We used the NAO-index of the Climate Research Unit of the University of East Anglia (<http://www.cru.uea.ac.uk>).

We used a set of candidate linear first order autoregressive models of climate effects on spittlebug abundance, and selected the most parsimonious models on the basis of the Akaike information criterion corrected for small sample size (AICc) (Burnham and Anderson 2004). We also studied the effects of climate proxies (length of the snowy season, humidity, temperature, and NAO) on the mortality of nymphs in 1969–1978. A set of candidate models was also used to investigate nymph survival. The mortality data was obtained with the minicage-method; in this method the spittle mass with nymphs is enclosed in a small box, and the mortality of nymphs is registered (see Methods in **IV**). Year was included in models when a significant trend was detect-

ed. Collinearity was tested with the variance inflation factor (VIF), and models with collinearity (VIF>10) between variables were not used. Statistical analysis was performed with R software (version 2.1.1.).

2.6. Common aspects of statistical methods

The number of time-steps (years) included in the time-series studies (**III**, **IV**) was mostly >30 thus being large enough (>20 steps) for the analyses (Lehikoinen et al. 2010, Van de Pol and Bailey 2019). We used detrending before analysis in **III** and **IV**. As detrending methods, and to deal with serial autocorrelation, we used autoregressive modelling (**IV**), inclusion of year in the analysis (**IV**), adjusting the degrees of freedom (**II**), linear detrending (**III**) and difference-detrending (**IV**). All of these are common methods to deal with possible serial autocorrelation, and with the possibility that shared trends result in associations between variables without a causal link (Lehikoinen et al. 2010, Brown et al. 2016).

It has been suggested that in studies of the plasticity of responses to climate change, detrending is to be preferred (Iler et al. 2017). A recent study found that 22 of the 35 bird studies that reported correlations between the NAO and spring phenology "might have suffered from spurious correlations due to not taking account the presence of a deterministic or stochastic trend in both time series" (Haest et al. 2018a). Detrending in time series analysis has been suggested for a long time (Royama 1992). Detrending may however, reduce the possibilities to detect real relationships (Brown et al. 2016).

2.7. Methods of graphs with ice-data

Figs 10,12, and **13** are produced with data of Finnish Institute of Marine Research (currently Finnish Meteorological institute) ice charts. The charts were scanned or obtained directly in a digital form, and the ice areas were digitised with ArcGis ESRI 9.0 software. Borders of sea areas used to calculate ice extents in **Fig. 13** are those of SMHI, Sweden.

3. RESULTS AND DISCUSSION

3.1. Projected changes in ice-climate and ringed seal (I)

Baltic ice cover is projected to decrease in the future, as seen from the modelled mean maximum ice cover in 2071–2100 (I) (Fig. 8). According to our modelling, the length of the ice-covered period, measured in ice days, will be drastically reduced in all breeding areas in the future scenario years 2071–2100: in the Gulf of Finland (GF), the Gulf of Riga (GR), Archipelago Sea (AS) and the Bothnian Bay (BB).

According to our results (I) the ice cover period in 2071–2100 is still sufficiently long to allow for a successful breeding of ringed seals in the northern Bothnian Bay (mean of all four scenario combinations or the *ensemble mean* of 123 days). In the southern breeding areas the ensemble mean number of ice days is only 18 (AS), 20 (GR) and 48 (GF) days, indicating that ice is not available for most of the ringed seal breeding time (Fig. 9). In the ensemble mean scenario climates of 2071–2100, the breeding habitat of the Gulf of Finland has still more than 60 ice days in 35% of the winters, and therefore it also has better ice habitat prospects than the Archipelago Sea (4%>60 days) or the Gulf of Riga (9%>60 days). In the northernmost part of the Bothnian Bay, ice climate is still suitable for breeding in most years (99% of winters with more than 60 ice days).

From a conservation viewpoint, our results show that climate change is emerging as a new threat factor for the southern (AS, GR, GF) ringed seal breeding populations. As these populations are currently not growing, an addition-

al, and increasing, projected burden of worsening breeding habitat is bad news for the already small breeding populations, and other possible threats should be mitigated where possible. The ice habitat in the Gulf of Finland is projected to survive better than in the Gulf of Riga and Archipelago Sea.

A modelling study (Sundqvist et al. 2012) using the SRES scenario A1B1 resulted in an increase in Gulf of Finland population towards the end of this century. The Gulf of Finland is a special case as probably more than 50% of

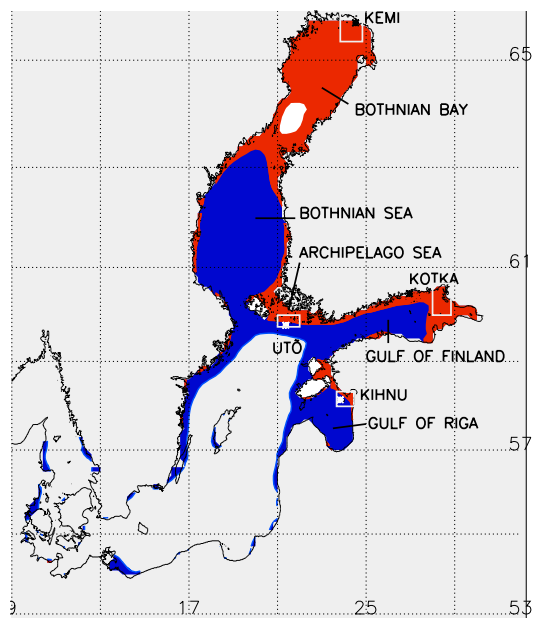


Fig. 8. Ensemble mean (of 2 models in control, four in scenario climate) mean maximum ice-cover in control 1961–1990 (blue) and scenario 2071–2100 simulations (red). Ringed seal climate study sites are shown as squares. (I)

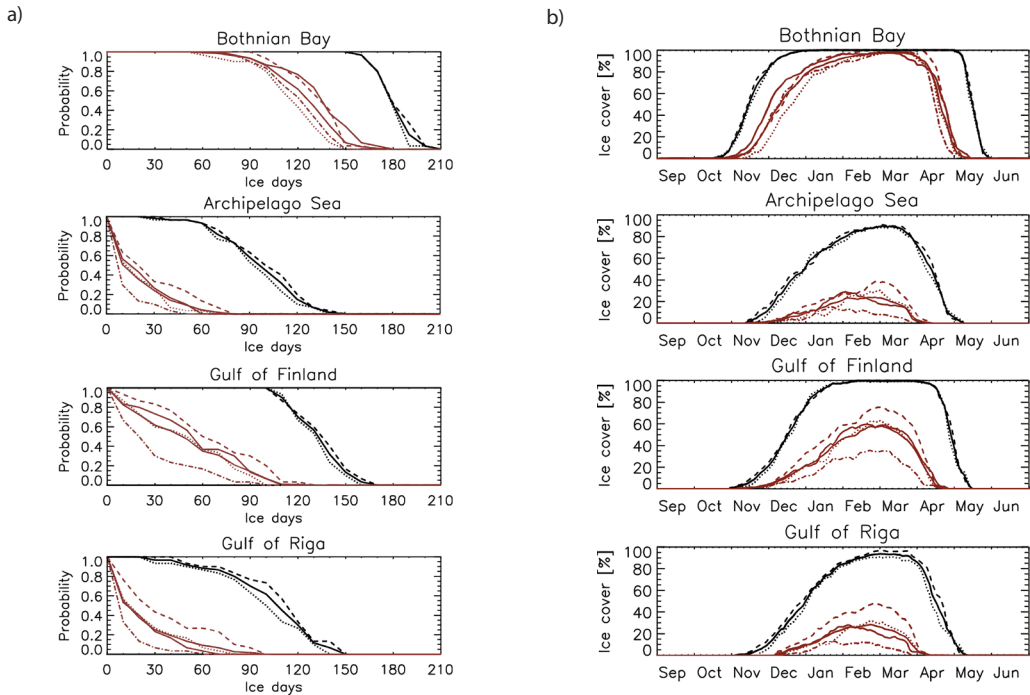


Fig. 9. a) Cumulative probability of ice winters with more than x ice days and (b) mean seasonal ice cover in the four study sites. Control runs shown are RAO-H, Hadley centre HadCM2 (Black dotted line) and RAO-E, Mac Planck Institute ECHAM4/OPYC3 (black dashed line), and control mean (black solid line). Scenarios are shown in red: scenario mean (red solid line), RAO-H/A2 (red dotted line), RAO-H/B2 (red dashed line), RAO-E/A2 (red dash-dotted line), RAO-E/B2 (red dash-triple dotted line). (I)

the ringed seal stock there died of an unknown cause in 1991–1992 (Härkönen et al. 1998), and the population has not recovered despite several good ice winters. A recent Helcom indicator report states that the population has decreased, and that the current size of the survey population may be as low as 100 individuals (Helcom 2018).

Thus, even if the ice of the Gulf of Finland in the end of this century is projected in I and in Sundqvist et al. (2012) to be more suitable as a breeding habitat than in the other southern breeding populations, additional factors are affecting this population severely. The worsening ice habitat concerns a population that is already very small, and not recovering. Therefore I argue that a drastically worsening ice climate in this century, projected in all ice model studies, would probably result in a negative growth rate also in the Gulf of Finland.

In the Gulf of Riga, also Sundqvist et al.

(2012) project a population collapse. Archipelago Sea was not included in their modelling. As the authors note, ice season break up was not taken into account in their approach (Sundqvist et al. 2012). Early break up of ice has earlier been linked to probable interrupted lactation of pups and reduced pup survival or condition (Harwood et al. 2000, Stirling 2005). The length of the ice season is central in (I) and (with snow) the main pup survival effect incorporated in a recent model study of climate change and ringed seals (Reimer et al. 2019).

Our modelled Bothnian Bay breeding area is in most years still suitable for breeding. As our results are from the northern end of the basin, the results do not show as good prospects for the entire Bothnian Bay. The projected ice season length is considerably reduced near the year 2100 (Fig. 10). The stability of the Bothnian Bay ice is also being impacted as the bay is not freezing over entirely in every year.

A partly open basin can lead to possible storm damages to breeding structures, and a reduced survival of pups. The winter 2014–2015 was documented as the first year when the Bothnian Bay remained partly open during the entire ice winter, and such years can be relatively common towards the end of this century (Uotila et al. 2015). Less ice can also lead to increased competition between seal species. Kauhala et al. (2019) propose, that milder ice winters in the Bothnian Bay might already have led to an increased presence of grey seals there, and that this could be one factor behind the declining nutritional status of the ringed seals in the area.

If the ringed seal survives only in the Bothnian Bay, the subspecies consisting of only one subpopulation would be more vulnerable to, for example, possible epidemics, than a population consisting of several relatively distinct breeding populations (IUCN 2014).

In the Archipelago Sea, and to a lesser extent in the Gulf of Riga and the Gulf of Finland, large archipelagos might in some cases allow for the continuation of lactation on land, and increasing attempts of land breeding are probable. In a larger context, islands may be considered as refugia, much as the thermal refugia (Potter et al. 2013) increasingly discussed in distributional change contexts. Islands are clearly suboptimal as a breeding habitat, as ringed seals always prefer ice, and land breeding populations do not exist. I propose that archipelago environments may allow for population persistence for a longer time than in an uniform ice environment. This is because of the probable but still not sufficiently documented possibility of breeding and completing lactation on land, and because islands generate spatial variability in ice winter duration with patches of persistent ice found in sheltered locations between islands.

In the southern breeding areas, the annual variation in the severity of winters results in exceptional years that are ice-free, but also allows for some years with an ice period exceeding one month or so. This variability, shown here for recent winters in selected Archipelago sea FMI stations (Fig. 11) might allow the seals in the

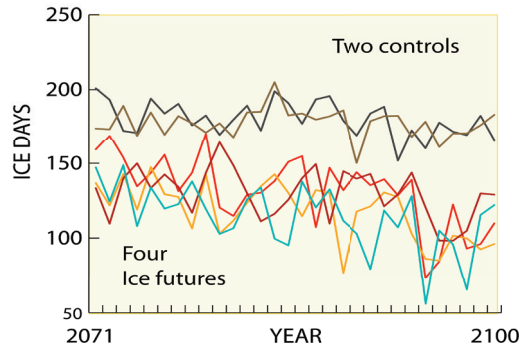


Fig. 10. Ice winter length (as ice days) in the Bothnian Bay model area in the control simulations and in the four modelled future scenarios. Data from (I), courtesy of Markus Meier, SMHI.

southern breeding areas have breeding habitat of moderate quality in some years in the studied 30-year period 2071–2100. The effects of yearly habitat quality variation to populations should be modelled to investigate this possible rescue effect of varying breeding habitat.

Ringed seal pups have been encountered on land in a handful of cases in Finland, Estonia and Latvia. These pups may have been born on land or, if in a good condition, the female seal may have continued lactation on land after the break up of ice. Predation risk on land can be high as the pups are vulnerable to white-tailed eagles and medium sized carnivores such as red fox on land or open ice (Auttila 2015). The possibility of the pup and female to escape into water from land is proba-

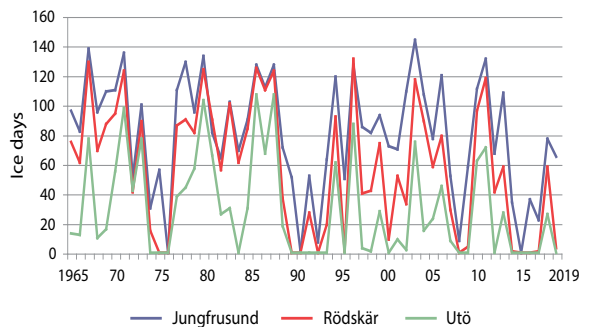


Fig. 11. Ice winter severity measured as the number of ice days in 1964–2019 at selected stations in the Archipelago Sea: Utö, 59°46.9' 21°22.4'; Rödkär 60°07.1' 21°18.6'; Jungfrusund 59°59.0' 22°23. Finnish Meteorological Institute (FMI) data.

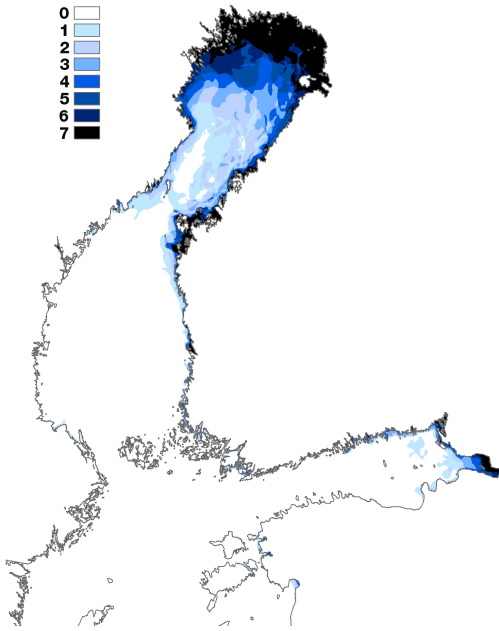


Fig. 12. Ice cover of the Baltic Sea between February 1st and April 1st in 2008, the second mildest ice winter known for the Baltic Sea. Ice charts were digitised in 11-day intervals. This resulted in seven snapshot days of ice cover. The figure shows in how many of those seven days ice has been present. FMI ice chart data, Halkka and Annala unpublished.

bly more limited than from ice. It might be possible that emergency breeding on land is possible for individuals occasionally, but I assume that pup survival is not high, and that land breeding may not have a large positive effect for population growth rate.

A Finnish modelling study (Jylhä et al. 2008) suggests that in the period 2071–2100, most of the winters could be unprecedentedly mild (with a MIB under 52,000 km²) under the SRES A2 scenario, and up to half of the winters could be unprecedentedly mild under the SRES B2 scenario. This indicates, that the winter 2007–2008 with a MIB of 49 000 km² might be a suitable example of possible future average winters.

In the winter 2007–2008, ice was concentrated in the Bothnian Bay (Fig. 12). The dominance of Bothnian Bay ice area as breeding habitat in 2008 is also very clear if presented as areal extent (Fig. 13).

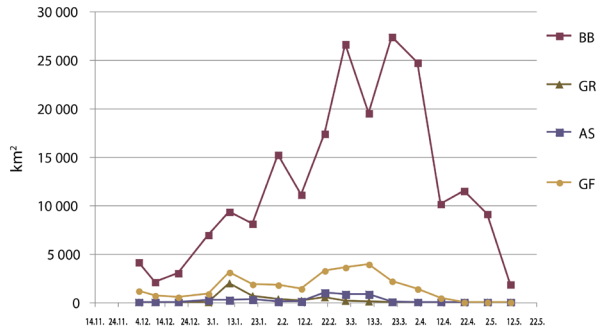


Fig. 13. Development of ice cover area (km²) from November to May in the Bothnian Bay (BB), the Gulf of Finland (GF), the Archipelago Sea (AS) and the Gulf of Riga (GR) in the mild winter 2008. Source: FMI ice chart data, Halkka and Annala, unpublished.

In the breeding period of ringed seals (from mid-February to March) the southern breeding areas were mostly ice-free in 2008. In the Archipelago Sea, a pup was found on an island, and had very probably been born there (Fig. 14a). In the Gulf of Finland, ice was found in the bays of Vyborg and St. Petersburg, where ship traffic and other human presence may stress the seals. In the Gulf of Riga, the only remaining ice was in the Pärnu Bay, where we observed about 50 ringed seals, many of these female seals with pups, on ice with about the same number of white-tailed eagles (Jüssi 2012). In the Gulf of Riga, three stranded ringed seal pups were found in Latvia and taken to Riga Zoo but none of these seals survived (Fig. 14b).

Another example of unprecedentedly mild winters is the most recent one, 2019–2020, a record mild year (Vainio 2020). In 2020, the only available breeding ice in the Gulf of Finland was found very near Saint Petersburg. Seven Baltic ringed seal pups were found and taken to the seal rehabilitation centre there, and at least one dead stranded ringed seal pup was found (data communicated by zoologist Elena Andrievskaya from the Marine Mammals Research and Conservation Centre / "The Baltic Ringed Seal Fund").

It is currently not known how demographically separate the four breeding populations are, and neither is it known if adult seals can start to abandon areas if good breeding habitat is no longer available. Bergmann (1958) suggested



Fig. 14. Ringed seals pups in 2008. Left (a): A pup born on land in the Archipelago Sea. Photographed in Gärskär, Vänö 20.2.2008. Right (b) : A pup found stranded in Latvia 12.3.2008. Photos courtesy of Tommy Arfman and Riga Zoo.

that ringed seals might have abandoned breeding areas in the warm winters of the 1930s. Ringed seals can move large distances in the open-water season, and movements between distinct areas in the Baltic have been documented during open water season (Oksanen et al. 2015). Satellite tracking has shown that Baltic ringed seals mostly stay in a feeding area specific to a breeding population (Härkönen et al. 2008), but can occasionally move large distances. In the recent satellite-tagging study (Oksanen et al. 2015), two adult female seals marked in the Bothnian Bay migrated to the Gulf of Riga presumably to breed. The authors of this study (Oksanen et al. 2015) suggest breeding area conservatism based on earlier studies.

3.2. Historical occurrence of ringed seals in relation climate fluctuations (II)

Paper II presents the Holocene history of the ringed seal in the Baltic basin, and is with almost 40 dated seal finds the most complete study in the area (Fig. 15). Two seals from the entrance of the Baltic were older than 45,000 cal. BP. The seal collagen $\delta^{13}\text{C}$ values found reflect salinity changes of the Baltic Sea, corroborating salinity reconstructions (Willumsen et al. 2013).

Two Finnish finds from the Gulf of Bothnia are from the Ancylus stage (10,700–10,200 cal. BP). As this was a freshwater stage, ringed seals were feeding on freshwater fish. The Saimaa and Ladoga seals are feeding exclusively on fresh-

water fish (Sipilä and Hyvärinen 1998, Kunnasranta et al. 1999, Auttila et al. 2015), and freshwater species (e.g. whitefish, *Coregonus* sp.) are common in the current diet of Baltic ringed seal (Stenman and Pöyhönen 2005, Mehtonen 2019).

The ringed seal has probably existed in the Baltic basin continuously for the entire Holocene history of the sea (>10,000 years). As the ringed seal needs ice for breeding, an obvious conclusion is that winter ice has been present in the Baltic for the entire time period. This includes the warm Mid-Holocene phase, which has been well documented in the region (Borzenkova et al. 2015). Ringed seal also coexisted with the

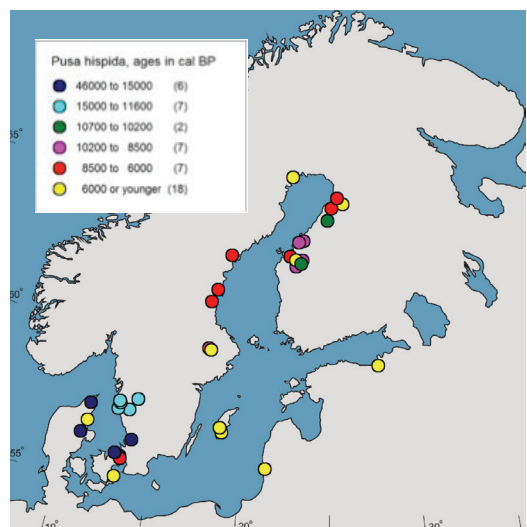


Fig. 15. Radiocarbon-dated subfossil ringed seal finds from the Baltic Sea. (II)

harp seal (*Phoca groenlandica*) for several millennia. Ringed seals are more coastal than harp seals, and this might have mitigated possible competition between the species.

The results indicate, that in early and mid Holocene, ringed seals had at least periodically a more southern distribution than now. The archaeological finds from Stora Förvar cave from Stora Karlsö (latitude 57°N), Gotland include bones of newborn ringed seal pups (Lindqvist and Posnert 1997), which are dated to 9,200–8,000 cal. BP. The finds from the mid-Holocene Littorina stage from Kõnnu site in Estonia (Lõugas 1997), dated at 7000 cal. BP, and young ringed seal bone material finds from other western Estonian sites from this period are of special interest as they are from the warm Holocene Thermal Maximum part of the Holocene. This warm period is placed at 8,000–4,500 cal. BP, (Borzenkova et al. 2015), with maximum temperatures probably around 8,000–6,000 cal. BP (Seppä et al. 2005).

January temperature during the Holocene Thermal Maximum may, however, have been generally about 2–3 degrees warmer than modern temperatures (Giesecke et al. 2008, Brown et al. 2012). This is less than the increase in Baltic winter (December–February) temperature in the IPCC SRES scenarios used in paper I for the end of this century.

The projected RCP4.5 temperature increase from 1981–2010 to 2070–2099 is 4.3°C in winter (December–February) and nearly 5°C in January in Finland (Ruosteenoja et al. 2016b). The RCP4.5 also results in average winter temperatures above 0°C in western Estonia (Sepp et al. 2018). A 3–8°C winter temperature change is currently projected in the region (Ruosteenoja et al. 2007, Christensen et al. 2015, Ruosteenoja et al. 2016a). As the now often used RCP4.5 is a mitigation and stabilization scenario (Thomson et al. 2011) with emissions and projected temperature increases below those of SRES A2 and B2 (Rogelj et al. 2012), the projected winter warming in also this scenario probably exceeds that suggested for the Holocene thermal maximum.

The results of paper II thus in no way suggest that the Holocene history of ringed seals in the

Baltic might indicate good survival prospects for the subspecies in the projected future ice climate of the southern breeding areas. It cannot, however, be excluded that Holocene Thermal Maximum winters may have periodically restricted the breeding distribution of the ringed seal to the northern parts of the Baltic sea with most predictable ice in the Bothnian Bay area.

3.3. Spring migration of birds and temperature (III)

3.3.1. Bird migration and temperature along the migration route

Paper III uses the Hanko Bird Observatory data to investigate if the timing of the arrival of long-distance migrants is connected to temperatures en route. Our hypothesis was that a negative correlation was expected if the birds were adjusting their migration speed according to ambient temperatures en route (Huin and Sparks 1998, 2000, Hüppop and Hüppop 2003, Ahola et al. 2004, Hüppop and Winkel 2006, Lehtikoinen et al. 2010).

The spatial CLS-autocorrelation (methods) of southern Finland monthly temperature with gridded April and May temperatures stretched to northern central Europe, > 1000 km from southern Finland (Fig. 16). Most of the study species showed a significant negative correlation pat-

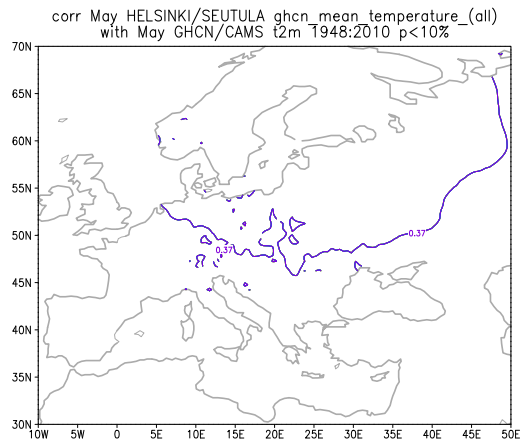


Fig. 16. The CLS-distance of Helsinki mean May temperature with mean May temperature in Europe in 1948–2010. (III)

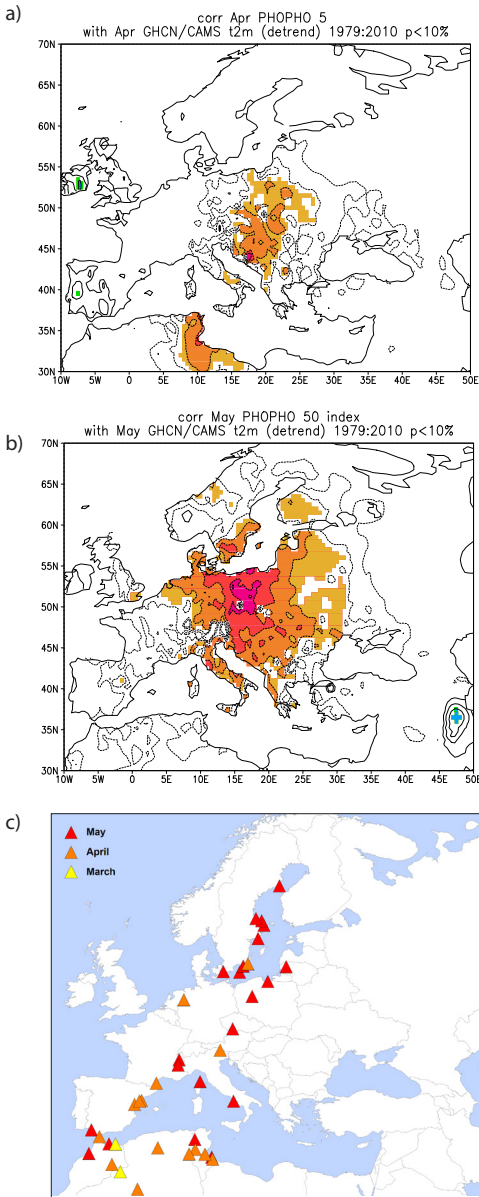


Fig. 17. Correlations of Hanko common redstart migration timing with European temperatures. (a) 5% and April, (b) 50% and May, (c) Finnish redstart ring encounters in spring. (III)

tern along the assumed migration route in the 5th percentile (5%) and/or 50% arrival dates. This indicates that the studied birds migrated faster when temperatures were high. Off-route positive correlations were also found; these result from chance or are demonstrations of teleconnections (Nigam and Baxter 2015) that can

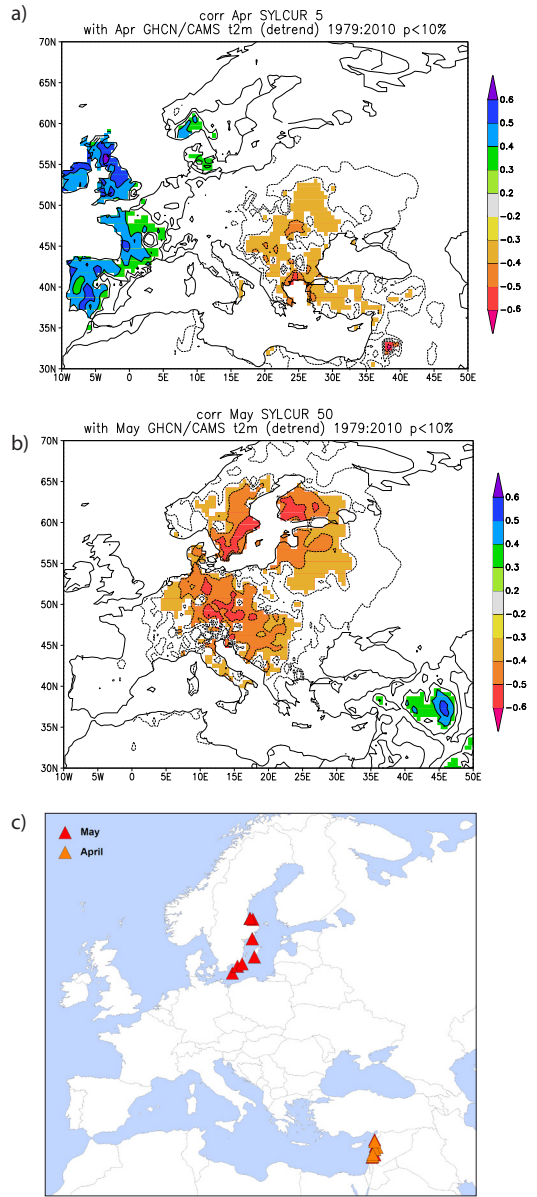


Fig. 18. Correlations of Hanko lesser whitethroat migration timing with European temperatures. (a) 5% and April, (b) 50% and May, (c) Finnish lesser whitethroat ring encounters in spring. (III)

link variability of temperature in non-contiguous regions. The presumed direction of the flyway used by the species (the general direction of migration) was reflected in the correlation patterns. Species that have been shown to use an eastern migration route (Fransson et al. 2005, Zduñiak et al. 2013, Valkama 2014, Aloni et al.

2017) that passes east of the Mediterranean Sea or over the eastern parts of it, showed temperature correlations in south-easterly direction. Such results include chiffchaff (*Phylloscopus collybita*) (5% and 50%), blackcap (*Sylvia atricapilla*) (50%), lesser whitethroat (*Sylvia curruca*) (5%) and lesser black-backed gull (*Larus fuscus*) (5% and 50%).

Could the birds use the temperature cues to adjust the timing of migration to yearly variations in the advancement of spring in the breeding area? For some species such as common redstart (*Phoenicurus phoenicurus*) (Fig. 17), spotted flycatcher (*Muscicapa striata*), and the lesser whitethroat (*Sylvia curruca*) (Fig. 18) the answer is possibly yes, as the correlations are near enough Finland for spatial autocorrelation of climate to give reliable information of the yearly variation in the target area. In pied flycatcher (*Ficedula hypoleuca*), the correlation pattern was placed much eastwards of the route proposed by ring encounters and newer geolocator data (Ouwehand et al. 2016). Baltic region April temperatures have been later shown to be correlated with the timing of arrival of common redstart in North Karelia (Valtonen et al. 2017), in line with our results.

In willow warbler and lesser black-backed gull, the correlations were placed in the right direction but at a distance of more than a thousand kilometres from Hanko observatory. At such a distance, the spatial autocorrelation of temperature with Hanko is weak or non-existent. Such a result was hypothesised to result from chance, or real ecological effects not linked to adjusting migration to yearly variation in breeding area temperatures. We did not find any significant *positive* temperature–arrival time correlations along the migration routes of the 10 study species, i.e. warmer temperatures were not delaying migration anywhere along the migration routes.

Negative correlations outside the CLS-distance are open to explanations. Why should higher temperatures lead to speeding up migration even when it does to suit to yearly variations in the target area? In III we suggest that better feeding opportunities associated with warm-

er temperatures might be the proximate cause. In any case, speeding up of migration with increasing temperatures along the migration route affects the arrival timing of birds. As spatial differences in temperature increase in Europe are of temporary nature, and even the known "warming holes" in northern Australia and central North America are not projected to persist in the future (Grose et al. 2017), such a response may be of help in matching arrival timing with the developing phenology of the environment. In some cases a response outside the CLS-distance would, however, possibly lead to too early arrivals.

New geolocator studies provide insights on the abilities of birds to respond to temperature changes along the migration route. Some studies have shown that birds can accelerate or slow down their migration speed according to yearly variations in climate. Semi-collared flycatchers (*Ficedula semitorquata*) breeding in Bulgaria slowed down their migration speed in the last leg of the migration in a cold year (Briedis et al. 2017). They advanced their migration in the warm spring of 2014, and migrated slower in the following cold spring (Briedis et al. 2017). Another geolocator study with collared flycatchers *Ficedula albicollis* from Czech republic (Briedis et al. 2018) proposes that cues about the phenology at the destination "can be obtained only after crossing the Sahara Desert (and possibly Mediterranean Sea)", and that "acceleration of migration speed through the last leg of the journey may play an important role ... in adjusting migration timing in accordance with phenology" (Briedis et al. 2018).

Birds species and populations of the same species may, however, have different migration strategies (Newton 2008). Geolocator studies have also shown evidence of a weak or non-existent reaction to conditions en route. Recently, Ouwehand and Both (2017) suggested that African departure dates strongly affect spring arrival timing of pied flycatchers in a population in the Netherlands. Ouwehand and Both (2017) state that "variation in arrival dates to breeding sites in 2014 was caused by variation in departure date from Sub-Saharan Africa, and not by

environmental conditions encountered en route.” The last leg of spring migration was completed with such a speed that there was not much possibility to adjust to yearly phenology (Ouwehand and Both 2017). Pied flycatcher might not, however, be a typical migrant. In a large compilation of spring migration speeds of songbirds (in Schmaljohann 2019), it had the highest total speed of migration among palearctic migrants, 316 km/day (Ouwehand et al. 2016). In other studies environmental conditions en route have been shown to affect the timing in the species (Ahola et al. 2004, Hüppop and Winkel 2006).

A correlation between departure and arrival has been found also in two recent meta-analyses of long-distance migrants. The study of Schmaljohann (Schmaljohann 2019) involved data of spring migration of more than 20 species, and both short- and long-distance migrants. A one-day change in the start of bird migration led to a 0.4–0.6 day change in their arrival. Another study (Briedis et al. 2019) included 350 migration tracks of 14 species of trans-Saharan migrants. These results do not, however, exclude the possibility of adjusting migration speed en route, but the relationship between departure and arrival times may set constraints on the scale of possible adjustments, and remind of the fact that migration data consists of individual migration schedules (Both et al. 2016).

Correlations of the African part of the migration route were excluded from our analysis. It is well known that climate (such as temperature and precipitation, and linked productivity) can affect the timing of migration before the birds reach the Mediterranean area (Tøttrup et al. 2008, Robson and Barriocanal 2011). For example, conditions in the Sahel area south of the Sahara have been shown to influence passage date of trans-Saharan migrants in the western Mediterranean area (Robson and Barriocanal 2011); birds migrated later in years with high primary production. In addition, drought episodes can delay migration considerably, as shown for red-backed shrike (*Lanius collurio*) and thrush nightingale (*Luscinia luscinia*) during the eastern African drought of 2011 (Tøttrup et al. 2012).

3.3.2. Where to measure temperature, and in what time window?

One important question arising from our map-based approach is where the relationship between temperature and arrival time should be measured. The question has been discussed earlier (Lehikoinen et al. 2010), but spatial correlations remind of its importance. In bird migration phenology, the temperature used in correlative studies is very often sought near the observation point or in the case of FADs from meteorological stations representing a country or region. A recent extensive meta-analytical study of bird migration and climate (Cohen et al. 2018) made a deliberate choice to use nearest location data from a database of monthly meteorological observational data also in cases when the included study had used data from the migration route.

As shown in **III** and in other studies (Ahola et al. 2004, Marra et al. 2005, Hüppop and Winkel 2006), using breeding area temperatures can result in weak or absent correlations between timing and temperature. If studies using breeding area temperatures are then used in meta-analyses and reviews, the results may underestimate the relationship between ambient temperature and the timing of arrival.

As the speed of migration has been shown to depend largely on stopover duration (Schmaljohann and Both 2017, Lindström et al. 2019), the correlations might indicate possible stopover areas of the study species. The Mediterranean correlations found in some species in our study are interesting as possible indications of stopovers in the area. Studies with geolocators have found that passerines overwintering in Africa have spring stopovers in Mediterranean Africa and in Europe. Common redstarts migrating from the Sahel region to Denmark had their first stopovers in Morocco, Algeria, Spain or France, and a second and final set of stopovers mostly in France (Kristensen et al. 2013). Also Swedish northern wheatears (*Oenanthe oenanthe*) had stopovers in south and north sides of the Mediterranean (Arlt et al. 2015). It is interesting, that for common whitethroat (*Sylvia communis*), our 50% correlation shows a patch of significant ar-

ea in the Central Mediterranean. In the garden warbler (*Sylvia borin*), a Mediterranean correlation area is found in both the 5% and 50% cases.

The timing of breeding is often not studied together with the timing of arrival (Dunn and Winkler 2010, Dunn and Møller 2019). This is a drawback because the mismatch hypothesis also concerns the synchronisation of breeding with the resource peak of the environment. A handful of studies that have included timing of both arrival and breeding have obtained contrasting results. In a Finnish study (Ahola et al. 2004), pied flycatchers arrived earlier, but no change was found in their breeding time. In the Netherlands, arrival had not advanced, but breeding had advanced (Both and Visser 2001). A shortened interval between arrival and appearance of juveniles was also found in a study of mid- and long-distance migrants in Pennsylvania (McDermott and DeGroot 2017). In that study, the timing of arrival had no effect on the breeding onset in 12 of the 17 study species (McDermott and DeGroot 2017). The relationship between arrival and breeding is complicated, as has been shown with modelling (Kristensen et al. 2015) and in recent field studies with e.g. northern wheatears (Low et al. 2019).

Wind was not included in our study of climate and migration timing. Many studies have shown, that wind speed and direction influence spring migration phenology (Sinelschikova et al. 2007, Haest et al. 2018b), but wind is rarely included in passerine phenology studies (Lehikoinen et al. 2010). Wind data is increasingly available with the help of software such as RNCEP (Kemp et al. 2012), and should be more routinely used in arrival time analysis.

Wind and temperature effects are difficult to disentangle from each other (Lehikoinen et al. 2010), and the correlations in our study can include contributions of wind effects. One possibility to discern wind from temperature in future studies could be to assess the length of the significant temperature window found. Geolocator studies, and earlier ringing studies of long-distance migrants, are proposing a temporally relatively short migration leg in e.g., Eu-

rope, including pied flycatcher (Ouwehand et al. 2016) and redstart (Kristensen et al. 2013).

The length of temperature response could be studied with the sliding window -approach that has been increasingly suggested as a method for climatic sensitivity studies (Phillimore et al. 2016, Haest et al. 2018b, Samplonius et al. 2018, Van de Pol and Bailey 2019). In this method all possible (realistic) time-windows are tested as separate regression models, and the best period is then chosen, with a careful consideration of the possibility of spurious results (Van de Pol and Bailey 2019). The length of the period of the significant temperature response is also important as long responses can be proxies of the general development of spring, which is often assessed with growing degree days (GDD). Their use in migration phenology has been mostly restricted to geese studies, where GDD is a routinely used proxy (Bauer et al. 2008, Eichhorn et al. 2009, Lameris et al. 2017). Testing the effects of GDD in passerine spring migration phenology could help us to better conceive if birds are adjusting their arrival to the general advancement of spring or for shorter temperature or wind windows.

3.3.3. Data quality issues, and possible connections between phenological response and distributional shifts

Phenological responses, range shifts and changes in bird community composition are all demonstrations of thermal niche tracking (Socolar et al. 2017). As all of these are changing simultaneously, it is tempting to think of possibilities of studying these together. Space-for-time substitution has been traditionally used in the analysis of temporal trends such as succession, and is also involved in the modelling of distributions (Pickett 1989, Elith and Leathwick 2009, Blois et al. 2013). In phenology, geographic variation in the timing of phenological events has been used to project possible long-term temporal responses to climate change (Phillimore et al. 2010, Phillimore et al. 2016). Range shift effects have been discussed in the context of migration distances (Potvin et al. 2016), and wintering range shifts towards breeding have been suggested to lead

to an advancement of migration (Lehikoinen et al. 2010).

Geographic patterns in bird migration phenology have not been studied systematically in the climate change context, but yearly schedules of arrival have long known to be dependent on latitude. For example, classic studies from the 1930s show that redstarts arrive at their northernmost European breeding grounds about two months later than to Mediterranean Europe (Newton 2007). As each degree of latitude is about 111 kilometres further than the previous one, the two month difference in redstart first appearance dates (Newton 2008) between southern Italy (40°N) and northern Fennoscandia (70°N) is about 60 days per 3300 kilometres or ~0.5 day per 100 kilometres. More recent studies verify such a connection between breeding arrival and latitude (Huin and Sparks 1998, Sparks et al. 2005a, Both and te Marvelde 2007, Hurlbert and Liang 2012).

Only a handful of studies have reconstructed migration timing of different latitudinal populations at a certain point along the migration route of a species, as in a pioneering study of *Sylvia* warblers (Fransson 1995), and in a study of pied flycatchers (Both and te Marvelde 2007, Both 2010). In a smaller geographical scale of hundreds of kilometres, a large effect of latitude to timing does not, however, always hold for long-distance migrants (Kullberg et al. 2015).

The above studies indicate that a change of average distribution northwards would, in a stable climate, probably involve a delay in spring migration in at least the European part of the migration schedule of long-distance migrants. If bird ranges and abundance centres are generally moving northwards as modelled (Huntley et al. 2008, Barbet-Massin et al. 2012, Huntley 2019) and observed (Auer and King 2014, Virkkala and Lehikoinen 2014, Gillings et al. 2015, Lehikoinen and Virkkala 2016, Välimäki et al. 2016, Virkkala et al. 2018), the spatial shift could be reflected in a temporal shift in some types of time-series data used in bird migration phenology, such as some observatory data. Range changes could thus in some cases counteract the pres-

sure for an earlier spring migration phenology; if the distributional changes follow the temperature change, the needed changes in arrival timing are not as large as in a population staying in a certain location.

Also data quality issues should always be addressed. The quality of bird migration data is often discussed (Lehikoinen et al. 2010, Møller and Hochachka 2019), but the interpretation of temperature-phenology relationship may also depend strongly on the choice of temperature data. It has been suggested, that the representativeness of temperature metrics can be a general problem in phenological studies (Keenan et al. 2019). The importance of the choice of temperature data is related to the general problem of uncertainty in predictors, which is due to proxy choices bringing noisiness and measurement error to the model (Keenan et al. 2019), resulting in regression dilution (attenuation bias), which typically leads to an underestimate of the true slope value (Macmahon et al. 1990, McArdle 2003, Berglund 2012, Halsey and Perna 2019).

As both the spatial (location of temperature data used) and temporal (chosen time window of temperature data) quality of temperature proxies in bird migration phenology can in many cases not be optimal, I propose that true slope values of the temperature-phenology relationship might be in many cases underestimated, and the capability of the phenology of birds to react to climate change may be better than has been thought.

3.4. Spittlebug populations and climate variability (IV)

The study of NAO and spittlebug populations (IV) is one of the first of studies of the effect of large-scale climate variability on insects, and has been followed by numerous other attempts to relate large-scale indices to insect population dynamics (Boggs and Inouye 2012, Roland and Matter 2013, Pardikes et al. 2015, Lancaster and Downes 2018, Pak et al. 2019).

Significant spatial synchrony between the populations at lag 0 was found, and the NAO probably contributed to this. Such synchronising effects have been shown also in caribou in



Fig. 19. Spittlebug spittle mass on meadowsweet (*Filipendula ulmaria*). Spittlebug nymphs are sensitive to desiccation of plants and the spittle mass. Photo by Antti Halkka.

Greenland (Post and Forchhammer 2002), and great cormorant (*Phacrocorax carbo sinensis*) in Europe (Engen et al. 2005). NAO also contributes to synchronising e.g. aphid population parameters (Saldana et al. 2007), and aphid flight phenology (Sheppard et al. 2016). Synchronisation of nearby populations by shared climate effects have been known for a long time (Moran 1953). Synchrony can generally increase the extinction probability in a set of populations (Heino et al. 1997).

The NAO and local climate variables had an effect on spittlebug population sizes in Tvärminne. The most supported models explaining the population dynamics of spittlebug abundance included January–February or January–March NAO and variables from winter and April–May climate. A negative effect of positive NAO on population sizes was supported in all three populations in Tvärminne. The only variables that entered the best model in all three populations were NAO and the autoregressive population size of the previous year. Other supported climate variables differed in the three populations with the mean temperature of the coldest month getting support in Stora Västra Långrundet and Gulkobben, and April–May temperature in Rovholmen.

In addition to population dynamics, we studied spittlebug survival in a critical life-phase,

where nymphs are sensitive to desiccation (Fig. 19). We found evidence of drought effects using May temperature and precipitation as a proxy of drought. Top models of nymph survival from the third instar to adult also supported a NAO effect on nymph mortality, where a positive NAO reduces survival. Climate variables entering the survival modelling included May–June humidity, length of the snow season, and the mean temperature of the coldest month.

The results indicate, that the NAO integrates climate phenomena, that may be difficult to find by using only local variables (Forchhammer et al. 2002). The negative impacts of a positive NAO on spittlebug population sizes and growth rates found in our study were probably partly related to desiccation. A positive NAO is connected to a decrease in snow cover in southern Finland, and snow is important for the spring humidity of the meadows.

We found a notable lagged correlation between variations of winter NAO, and spring temperatures in the Baltic area. In addition, it was shown with a long time series that this effect has been relatively stationary for at least 100 years in the northern Baltic Sea area. The lagged effect of a the winter NAO on spring temperatures possibly also contributed to the general NAO effect. Such effects of winter NAO on spring climate are rarely mentioned in the ecological and phenological literature. Several studies show that a lagged effect of NAO or the related Arctic Oscillation exist, and these studies also discuss the climate memory and circulation changes responsible for the time-lag (Kryjov 2002, Rigor et al. 2002, Bamzai 2003, Blender et al. 2003, Buermann et al. 2003, Ogi et al. 2003, Schaefer et al. 2004, Gormsen et al. 2005, Schaefer et al. 2005, Gouveia et al. 2008, Tedesco et al. 2009, Cho et al. 2014, Li et al. 2016).

We also suggested (IV) that the association between winter NAO and spring temperatures might be behind the effects of winter NAO on long-distance (late spring) migrants, a lagged effect that has puzzled ornithologists in some North European studies. For example, a Swedish study found it "remarkable" that NAO affect-

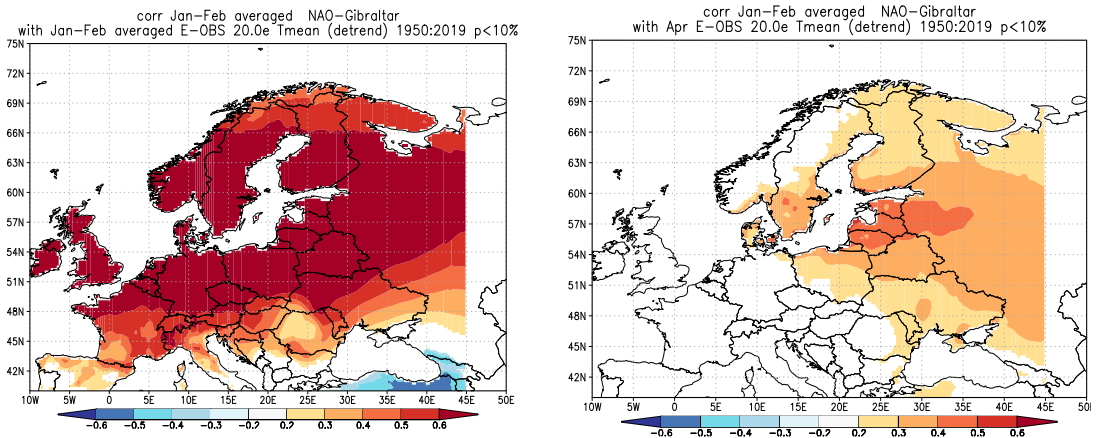


Fig. 20. Detrended correlation of January–February NAO (Jones et al. 1997) with January–February (left) and April (right) temperature in Europe in 1950–2019 plotted with Climate Explorer (Trouet and Van Oldenborgh 2013). In April the correlation extends from Black Sea to northern Russia and the Baltic Sea area. E-Obs data.

ed long-distance migratory birds which migrated ”through Europe weeks to months later than the winter NAO index was measured” (Stervander et al. 2005).

The lagged effect of the NAO in spring is most notable in April (**Fig. 20**) and around the Baltic Sea. In May the effect is not as stationary, and is mostly restricted to coastal western Europe (not shown). In areas where lagged correlations are found, winter NAO probably has a much greater influence on the ecology of species than can be expected solely based on the direct winter influence of NAO.

The effect of the NAO can be also mediated via the effects on winter climate on spring

plant phenology, as has been proposed (Hüppop and Hüppop 2003). In this respect, the lead times of the temperature response of plant phenology are interesting, as long lead times might indicate connections with winter climate forced by NAO (**IV**). The lead times in temperature on spring plant phenology vary between early and late flowering plants. Fitter and Fitter (2002) found that deviations in the timing of plant species flowering in May in Britain was connected to February temperature, as was the deviation of flowering in species that flower in March. April flowering had the strongest relationship with March temperature (Fitter and Fitter 2002).

4. CONCLUSIONS

4.1. Baltic ringed seal and climate change

Climate change is projected to have severe impacts on the southern breeding areas of the Baltic ringed seal. Scenario changes of ice climate of Gulf of Finland, Archipelago Sea and Gulf of Riga for 2071–2100 are so large that successful breeding is probably not possible in most years (I). The reduction of ice season length is more drastic in scenarios involving SRES scenarios A2 (a scenario with large emissions) than in scenario B2 (less emissions). An A2-world would probably include the extirpation of all southern Baltic ringed seal breeding populations. Also under SRES scenario B2 ice habitat is so substantially reduced that the extinction of the southern breeding populations is probable. In the scenario climates of 2071–2100, the breeding habitat of the Gulf of Finland still has more than 60 ice days in 35% of the winters, and therefore better ice habitat prospects than the Archipelago Sea (4%) or the Gulf of Riga (9%). In the Gulf of Finland, also other factors than the worsening ice habitat are currently affecting the population negatively. Identifying these factors, and acting on them would be important. The importance and viability of Baltic ringed seal land breeding in archipelago environments should be assessed.

In the northern part of the Bothnian Bay, the Baltic Sea can probably maintain a ringed seal breeding population also as ice winters become much milder the future. This area harbours al-

ready more than 80 per cent of the entire population of the Baltic subspecies.

Baltic ringed seals have had a challenging prehistory related to climate changes. Our results indicate that ringed seals can have lived continuously in the Baltic Sea for more than 10,000 years (II). A continuous presence would include that ringed seals have survived the Holocene Thermal Maximum, during which summer temperatures and probably also winter temperatures were substantially higher than in the modern history of the species. Possible ringed seal breeding in the Gulf of Riga during the Holocene Thermal Maximum may be an indication of at least periodically cold winters during the period.

Winters during the Holocene Thermal Maximum were, however, not as warm as the scenario futures A2 and B2, and the results in II do not show that ringed seal can survive the projected climate change.

4.2. What does the relationship between migration timing of birds and temperature along the migration route mean?

Our results add to the growing evidence that temperatures along the migration route have an effect on arrival times. We found negative correlations between temperature and arrival times in the majority of the studied 10 Finnish long-distance migrants, and in three selected species from Helgoland, Moravia and Kazan. The correlations are in many cases, but not always,

placed close enough of the observation point to be informative of breeding area temperatures. In those cases, the results indicate that birds may use temperature or related cues to predict yearly variations in advancement of spring in the breeding area. The European correlations both close enough and outside the predictive distance were always negative: higher temperatures invariably tended to speed up spring migration.

Our results and published literature indicates that negative correlations prevail in studies of long-distance spring migration phenology. I argue that any negative association between temperature along the migration route and arrival time is usually beneficial for birds in adjusting to climate change, as all areas will eventually becoming warmer, and spring will advance everywhere. This is irrespective of any proximate factors behind the tendency of birds to adjust migration timing to temperatures along the migration route. The possible harmful effects of reacting strongly to temperatures outside of CLS-distance probably depend on the scale of the response.

4.3. Spittlebugs and climate, and general conclusions

The dominating large-scale climate variation in Europe, the NAO, had an impact on population sizes of the meadow spittlebug *Philaenus spumarius*, a very common insect. The study shows that a positive winter NAO leads to reduced population sizes, and also affects negatively nymph

mortality in the Tvärminne study area in spring and early summer. We demonstrate that winter NAO has a lagged effect on Baltic area spring temperature. As the lagged effect of winter NAO on spring (especially April) temperatures are previously well validated in the meteorological literature, the lagged effects of winter NAO on spring temperatures can be behind many of the associations found between winter NAO and spring migration of long-distance migratory birds, and possibly other spring phenomena associated with winter NAO.

The effects of climate variation and climate change to spittlebug populations were probably largely mediated via survival in the nymph life-phase with a narrow climatic niche. Such sensitive life-phases might be common, and important to identify in the climate change context. In ringed seal ecology, such a phase is the breeding time with its specific habitat requirements. In migratory birds the match of arrival and breeding time to seasonal resource peak has been proposed as a sensitive phase of the lifecycle, but more research is needed to confirm this.

The effects of climate variation and change should be studied with an integrative approach. As, for example, latitude is involved in both the phenology of bird arrivals and distributional changes in birds, changes in phenology and range changes should be seen as responses that can be modelled together when studying the total response of migratory birds to climate change.

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Ringed seals in the Archipelago sea are quite commonly seen in groups. Photo by Seppo Keränen.

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