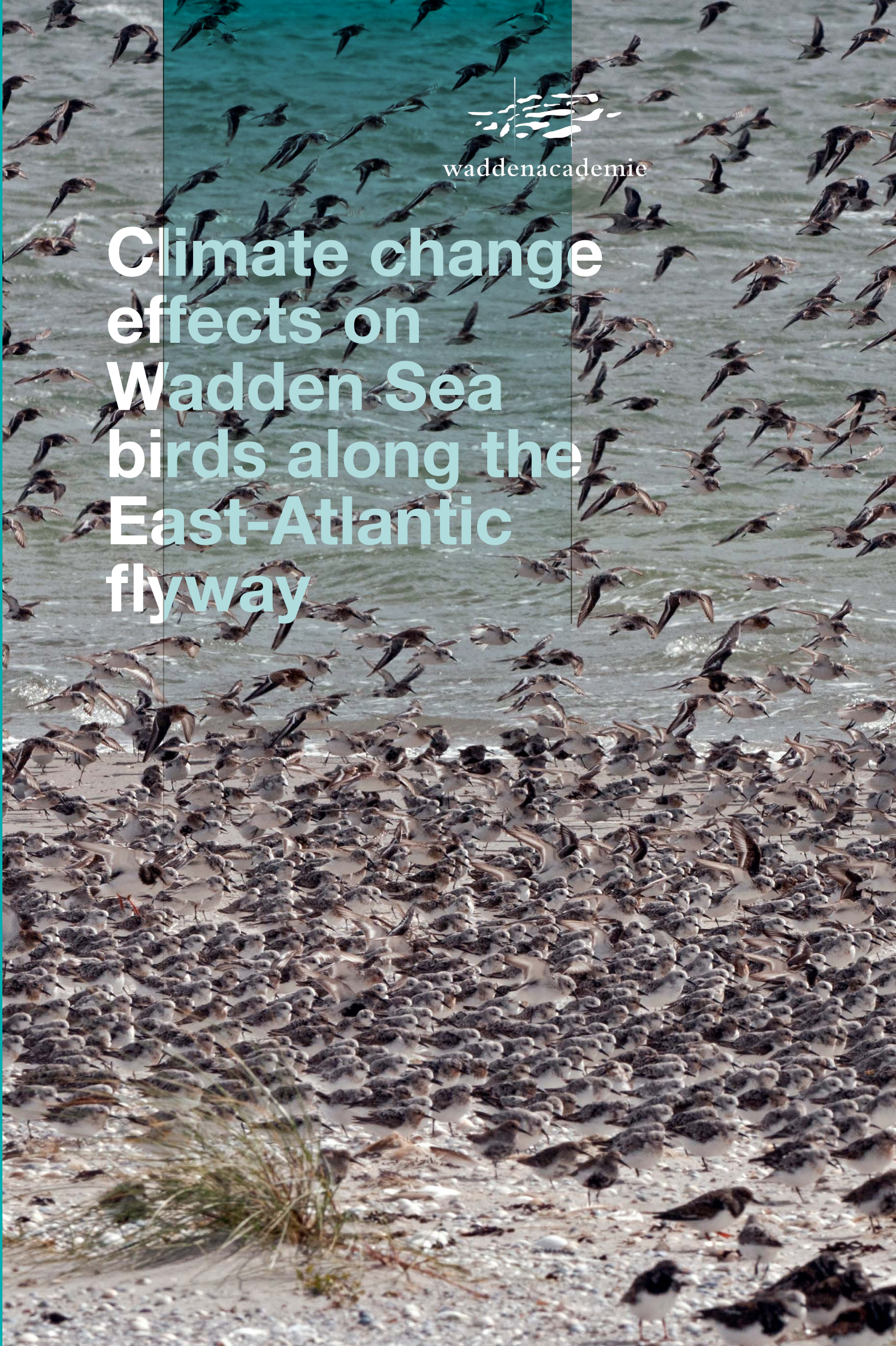# Climate change effects on Wadden Sea birds along the East-Atlantic flyway

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Climate change effects on Wadden Sea birds along the East-Atlantic flyway

Position Paper

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FOREWORD

The Programme Towards a Rich Wadden Sea (PRW) is working to achieve a resilient and sustainable Wadden Sea Region with the Wadden Sea Region's prospects in the year 2050 as a distant speck on the horizon. The programme covers eight different themes: Climate Change, Natural Dynamics, Marine Wildlife, Birds, Fishing, Accessibility and Mobility, Edges of Tidal Flats, and Enhancing the Outstanding Universal Values of the World Heritage Site. These themes are clustered into two pillars: *Improving nature for a resilient ecosystem*, and *Transitions to sustainable shared (economic) use.*

For birds, the Wadden Sea is an important staging site in the habitat that stretches from wintering zones along the coast of West Africa to nesting zones in Siberia.

Within the context of its Birds theme, PRW is developing climate change management measures in addition to its international flyway monitoring work. Climate change is having a significant impact on the Wadden Sea and consequently on the birds that live there. To respond proactively to these changes, we must develop an early-warning system and take the necessary management measures so as to offer birds the healthiest and safest possible habitat in the Wadden Sea. The first step in these efforts is to assess the likely impacts of climate change on birds in the Wadden Sea.

PRW asked the Wadden Academy to carry out a literature review and, on that basis, assess what climate change will mean for birds using the East Atlantic Flyway and for their habitats. The focus is on geese and long-legged waders, covering most of the species typical of the Wadden Sea. The study also identifies major gaps in our knowledge.

The Wadden Academy assists in the sustainable development of the Wadden Sea Region by concentrating relevant knowledge, making it accessible and applying it in practical terms. Jeroen Reneerkens, an expert on the impact of climate change on migratory birds, was asked to prepare this report. The Wadden Academy was responsible for quality control and process supervision.

Based on this report, *Effecten van klimaatverandering op vogels in het Waddengebied*, PRW has now taken steps to work with policymakers, management bodies and stakeholder authorities in the Wadden Sea Region to develop a dedicated package of measures in 2020.

Leeuwarden, 26 March 2020

H.J. Venema
Programme Towards a Rich Wadden Sea

Prof. J. van Dijk
Wadden Academy

CONTENTS

EXECUTIVE SUMMARY

The Wadden Sea is an essential node for many thousands of birds that migrate twice a year between their Arctic/sub-Arctic nesting zones (in northeastern Canada, Greenland, Fennoscandia and Russian Siberia) and their winter habitats along the Northwest European (including the Wadden Sea) and West African coasts. In West Africa, the Banc d'Arguin National Park in Mauritania and the Bissagos Islands of Guinea-Bissau are crucial wintering zones for water birds. The three countries bordering the Wadden Sea are responsible for protecting its ecosystem, to which birds are essential.

According to all the scenarios for greenhouse gas emissions assessed by the Intergovernmental Panel on Climate Change (IPCC), the surface temperature of the Earth will continue to rise in the twenty-first century. There is abundant evidence that, in addition to many other ongoing human threats, climate change may jeopardise the survival and quality of natural resources at all critical sites along the East Atlantic Flyway, in which the Wadden Sea plays a vital role.

This report, produced by the Wadden Academy at the request of the Programme Towards a Rich Wadden Sea (PRW), is a literature review assessing what this means for birds using the East Atlantic Flyway. In view of existing or anticipated effects, the aim is to assess whether and how we can prevent or mitigate potential population decline. The focus in this report is on geese and long-legged waders, the most numerous wading birds about which we also know the most.

Climate change along the East Atlantic Flyway – Arctic nesting zones have become 0.75°C warmer In the past decade (2000-2019), a much faster rate than global warming on average. With global temperature rises still heading towards 2°C, temperatures in the Arctic could rise by an average of 4°C, and even 7°C in winter.

The Wadden Sea is adjacent to the North Sea, which saw the second-highest rise in temperature of all the world's major marine ecosystems. In the Wadden Sea, the average year-round atmospheric temperature rose by 1.8 °C between 1901 and 2013 and is expected to rise by a further 1.0 to 2.3 °C by 2050. The Dutch Wadden Sea is forecast

to experience an annual increase in rainfall of 5% between 2030 and 2035, a further 4% increase by 2050, and an additional increase of 5–7% by the year 2100. This additional rainfall will occur mainly in winter, while summers are expected to become drier. An increase in rainfall will lead to an average decline in the salinity of the Dutch sector of the Wadden Sea. Between 1890 and 2014, the sea level there rose steadily at a rate of 1.86 ±0.15 mm annually. Extreme projections by the Danish Meteorological Institute (DMI) show a sea-level rise of 34 to 61 cm in 2071-2100 compared to 1986-2005, but other projections are even more extreme.

Temperatures in West Africa are forecast to be 3 to 6°C higher at the end of the twenty-first century than they were at the end of the twentieth. West Africa is expected to undergo changes in precipitation and accelerated global warming is likely to lead to more frequent dry periods and less frequent wet periods. This applies to scenarios projecting temperature increases of both 1.5 °C and 2 °C. Such changes in the climate could in turn lead to changes in river discharge and affect estuaries used by birds migrating from the Wadden Sea. Alongside projected trends in average weather conditions, there will also be significant variability from the mean, leading to an increase in extreme weather events.

Impact of climate change on birds in the Wadden Sea – The climate is an important influence on the way ecosystems function. Local and widespread changes in temperature, sea level, wind patterns and rainfall will affect birds in the Wadden Sea and their habitats along the East Atlantic Flyway. The size of the suitable Arctic nesting zone is expected to shrink at an alarming rate. Climate change is also impacting wading birds in these Arctic nesting zones because it is altering interactions within the food web and increasing the frequency and intensity of extreme weather events. The predation of chicks is expected to increase due to lemming cycle collapse, although long-term monitoring programmes have not (as yet) provided compelling evidence for this collapse. Chick growth and survival are adversely impacted by climate change, leading to asynchrony between their growth period and the period of peak food availability. Evidence

confirming these two threats remains tentative, however, in part because of geographical variation and because certain species (and individuals within species) respond differently to such effects. The same goes for the impact of these threats on the fitness of these populations and the implications for population size. Even if there is clear evidence that certain threats are impacting fitness, we often do not know whether and to what extent this translates into changes in population size. Such uncertainty makes it difficult to forecast how different climate change scenarios might impact bird populations in the Wadden Sea significantly.

The main (investigated) threat to birds in the Wadden Sea appears to be sea-level rise. Depending largely on the speed and scale at which it occurs, sea-level rise will lead to the loss of dry tidal flats in the Wadden Sea, which are an essential foraging area for large numbers of birds. More frequent and more severe floods also threaten birds that breed on salt marshes, such as oystercatchers and redshanks. There is also clear evidence that more frequent and intense heat waves can lead to mass mortality of shellfish, which are an essential food source for birds foraging in the Wadden Sea. While sea-level rise is a serious threat on a time scale of decades, more frequent and longer heat waves may be a more immediate threat to birds in the Wadden Sea.

We are much less knowledgeable about the impact of climate change on African coastal areas along the East Atlantic Flyway, the winter habitats of many birds originating in the Wadden Sea. Rises in atmospheric temperature, however, and particularly the projected increase in the frequency and duration of heat waves, are likely to have a greater (adverse) impact on the survival of birds' benthic invertebrate prey than in temperate regions. This is because the temperature band within which tropical benthic species can survive is narrower. Alteration of wind regimes may also significantly increase the cost of migratory flight from West Africa, in turn increasing the risk of mortality during migration. It is difficult to forecast how wind patterns will change, however.

Effects on populations and bird adaptive capacity – There is consensus that climate change will impact the reproduction and/or survival of birds (including in the Wadden Sea), likely leading to changes in bird population size. One of the biggest challenges for ecologists today, however, is to forecast how many and which populations will change as a result. Despite major gaps in our knowledge and uncertainties in climate projections and, more importantly, in their ecological and demographic implications for wading birds, all studies clearly indicate that aspects of ongoing climate change are expected to have adverse impacts. These threats are currently being studied in isolation, but they will have a cumulative impact on wading birds along their migratory route. In other words, the combined impacts of climate change are likely to be more significant than we now know. This is worrying, given that birds may not be able to adapt sufficiently to the many and rapid changes that climate change is bringing about in their habitats.

Mitigating the impacts of climate change in the Wadden Sea – There is an urgent need for nature conservationists, landowners and politicians to prepare for a situation in which it becomes increasingly difficult to protect nature in the Wadden Sea as undertaken. We cannot stop climate change immediately but only reduce its speed and intensity, leading to challenging and far-reaching socioeconomic changes worldwide. Since many wading bird populations are already declining, the need to mitigate the impact of climate change by eliminating persistent, proven threats to birds in the Wadden Sea cannot be emphasised enough. A sound knowledge of ecology can make such mitigation efforts more effective. It is clear that a healthy Wadden Sea ecosystem will make it easier for birds there to adapt to constant changes. This means: no more overfishing of shellfish, shrimp, lugworms and fish, no hunting, no gas extraction or salt mining, and maximum restrictions on human disturbance of birds, especially at high-tide roosting sites. If there is a significant likelihood of losing tidal flats to sea-level rise (depending on the rate of such a rise in the near future), we must explore whether it would be effective to give the Wadden Sea room inside the dykes while keeping the human population safe from flooding (e.g. by using flood defences such as those in the Eastern Scheldt estuary).

INTRODUCTION

Climate is a key factor that determines the composition and functioning of ecosystems, driving many aspects of species' ecology (Forsman and Mönkkönen 2003, Thomas *et al.* 2006, Meltofte *et al.* 2007). There is overwhelming evidence that the global climate is warming and that this has important consequences for all living organisms on Earth (Root *et al.* 2003, Stocker *et al.* 2013). Humans significantly contribute to global warming by the emission of greenhouse gases, with CO_2 emissions from fossil fuel use continuing to grow by over 1% annually and reaching a new high with 2% in 2018 (World Meteorological Organization (WMO), UN Environment (UNEP) and Change (IPCC), Global Carbon Project, Future Earth, Earth League 2019). Observations of increases in air and ocean temperatures, the widespread melting of snow and ice and rising global average sea levels and ocean acidification all clearly highlight that the climate on our planet is changing at an unprecedented rate. Although especially the effects of climate change on ecosystem functioning are difficult to predict, there is a general consensus that climate change will largely influence the functioning of Earth's ecosystems (Travis 2003, Thomas *et al.* 2004)with stronger and faster species extinction rates and changes in community structure (Pimm 2009). In fact, there is a growing realisation that climate impacts are larger and happen sooner than climate assessments indicated even a decade ago (World Meteorological Organization (WMO), UN Environment (UNEP) and Change (IPCC), Global Carbon Project, Future Earth, Earth League 2019). It is believed that we are now facing a serious risk of crossing critical tipping points which will have a very large and widespread impacts and lead to long-term irreversible changes (Lenton *et al.* 2019). Acknowledging this, it can hardly be surprising that climate change is one of the most significant threats to global ecosystems and biodiversity (Stocker *et al.* 2013, Ripple *et al.* 2019).

Climate change affects all ecosystems, but coastal areas and areas at high northern latitudes seem particularly affected (Walther *et al.* 2002, Parmesan and Yohe 2003). Within those ecosystems migratory animals seem to especially have difficulties to cope with the environmental changes in the habitats they inhabit year-round (Wilcove

and Wikelski 2008, Knudsen *et al.* 2011). We may thus expect that the ongoing climate change will have an impact on coastal birds breeding at high northern latitudes. This includes the many thousands of shorebirds and geese that rely on the Wadden Sea to spend the winter and/or prepare for migration northwards to their low and high Arctic breeding grounds or southward to other coastal areas along the East Atlantic Flyway (van de Kam *et al.* 2004). The effects of climate change will need to be considered in the conservation of (migratory) birds that use the Wadden Sea (referred to as "Wadden Sea birds" from here onwards), together with other anthropogenic threats to these birds. The Netherlands, Germany and Denmark have an obligation to safeguard the well-being of Wadden Sea bird populations and their environment (Boere and Piersma 2012). Most Wadden Sea birds are migratory and use different parts of the world during different parts of their annual cycle. In all these areas different climate change effects may play a role and come on top of other ongoing threats, such as the destruction of habitat.

Climate changes unpredictably in direction, speed and intensity both across Earth's different climate zones (Pithan and Mauritsen 2014) and regionally, between local marine environments (Pimm 2009). This likely complicates the adaptability of migratory Wadden Sea birds to the changing environment along their migratory flyways (Senner *et al.* 2018). The effects of climate change are multi-faceted; they can be direct effects of changed weather on birds, or indirect effects such as results in loss of suitable feeding habitat due to sea level rise, loss of suitable breeding habitat due to changes in vegetation and altered trophic interactions (e.g. increased predation pressure and changes in food availability). All these factors may result in poorer survival and/or reproduction for individuals and could eventually lead to smaller populations of Wadden Sea birds. The challenge is to disentangle what relative effect of each possible climate change effect is compared to other threats and how these might be mitigated.

Here, I review the existing scientific literature on climate change effects on Wadden Sea birds and address important gaps in our current knowledge on these matters. I focus on geese and shorebirds using

the Wadden Sea which encompass most Wadden Sea birds (van de Kam *et al.* 2004). Although the Wadden Sea clearly is an important area for bird groups other than geese and shorebirds, most scientific literature exists on these two species groups. Thus, in this article, "Wadden Sea birds" are mainly shorebirds and geese that rely on the Wadden Sea during some critical moments in their annual cycles, although I occasionally will refer to scientific studies on Wadden Sea ducks and Spoonbills *Platalea leucorodia.* In this literature review, I have also summarised literature about climate change effects on Arctic geese and shorebirds from other flyways than those that use the Wadden Sea, when I believed they represent general findings that may apply to Wadden Sea birds as well.

1. KEY SITES ALONG THE EAST ATLANTIC FLYWAY FOR WADDEN SEA BIRDS

The Wadden Sea is an essential intertidal area within the East Atlantic Flyway; the coastal area used by shorebirds and geese that reproduce in North-east Canada, Greenland, Svalbard, sub- and low-Arctic Fennoscandia and a large part of Siberia. Birds from this huge (sub-)Arctic area migrate via the Wadden Sea to and from their non-breeding sites. Some of them spend the winter in the Wadden Sea, while others use the Wadden Sea to moult their feathers and/or as a staging site during their annual migrations (Boere 1976, van de Kam *et al.* 2004, Reneerkens *et al.* 2005). The Dutch and German parts of the Wadden Sea became UNESCO World Heritage in 2009, the Danish part in 2014, which encourages national governments to appropriately conserve and maintain its natural values. Previously, the Wadden Sea was already assigned as a Ramsar site, a Natura-2000 site, an Important Bird Area, and a Man and Biosphere Reserve based on the global importance of the area within the East Atlantic flyway. The international importance of the Wadden Sea as an essential coastal area for millions of migratory waterbirds was an essential factor in obtaining these statuses (Boere and Piersma 2012) .

The Wadden Sea is such an important area for many birds because of its flora and fauna on the intertidal mudflats and salt marshes which form a rich food source. The intertidal mudflats are above water level at low tide and underwater at high tide, intersected by subtidal gullies which are covered by water at all states of the tide. Migratory birds that use the Wadden Sea as a staging site during migration, winter elsewhere (mostly south and to a lesser extent west of the Wadden Sea) along the west coasts of Europe and Africa (van de Kam *et al.* 2004, Reneerkens *et al.* 2005, Buiter *et al.* 2016).

A few essential, large estuarine areas which harbour a large fraction of these Wadden Sea birds are some estuaries in France or in the Mediterranean region, such as the Tagos estuary in Portugal. In Africa, the Banc d'Arguin in Mauritania, the Bijagós archipellago in Guinea-Bissau and Walvis Bay in Namibia are three key sites for non-breeding Wadden Sea birds.

In this review, I focus on climate change effects in three large regional areas: the (Low and High)

Arctic, north-west Europe (i.e. the Wadden Sea) and West Africa, where the two most important wetlands for Wadden Sea shorebirds to spend the non-breeding period are located: the Banc d'Arguin in Mauritania and the Bíjagos archipello in Guinea-Bissau (van de Kam *et al.* 2004). I have not distinguished between staging areas and wintering areas because most sites along the East Atlantic Flyway, including the Wadden Sea itself, are used both for staging and wintering.

1.1 Description of sites

Wadden Sea – The Wadden Sea's coastline has been subject to heavy human modification with extensive systems of dikes which makes it among the most human-altered on Earth (Hogan 2011). Within the Netherlands, part of the Wadden Sea (the previous Zuiderzee) was closed off by the Afsluitdijk and turned into the freshwater IJsselmeer. In 1969, the previous Lauwerszee was closed off from the Wadden Sea. The closure of the Zuiderzee by the Afsluitdijk has had large geomorphological consequences. The western part of the Dutch Wadden Sea is still heavily dictated by adapting to the closure (Elias and van der Spek 2006), with extensive sedimentation in the distal parts of the former access channels to the Zuiderzee and rapid accretion on the shoal areas along the Frisian coasts (Elias *et al.* 2012).

Despite its national and international recognition as an important nature area crucial for many thousands of waterbirds, the Wadden Sea has been, and still is, subject to human exploitation that is harmful to its natural values (Reneerkens *et al.* 2005). These threats include harvesting of shellfish (Piersma *et al.* 2001), shrimps *Crangon crangon* (Lotze 2007), lugworm *Arenicola marina* (Beukema 1995), hunting of birds (Ekroos *et al.* 2012, Tjørnløv *et al.* 2019) as well as the extraction of gas and salt (Dijkema 1997, Duijns *et al.* 2013).

Bijagós archipelago – This archipelago consists of a group of 48 islands and islets off the coasts of Guinea-Bissau. There are numerous intertidal flats

of muddy sand surrounded by mangroves which host one of the largest populations of migratory shorebirds in the world, the majority of which are birds that use the Wadden Sea during migration to and from the (sub)Arctic breeding grounds (Zwarts 1988, Salvig *et al.* 1994). The system depends both on upwelling and estuarine input.

Banc d'Arguin – The Banc d'Arguin is a nationally protected shallow gulf of > 10,000 km² between the Sahara and the Canary upwelling system off the Mauritanian coast. The 500 km² intertidal mudflats are essential habitat for thousands of Wadden Sea shorebirds. Benthic invertebrates form the food base for these shorebirds. Although the biomass of benthic invertebrates is relatively low (Wolff *et al.* 1993a), it supports a very high density of consuming birds (Zwarts *et al.* 1990), among others because the fraction of benthic invertebrates that is harvestable by shorebirds is relatively high (Piersma *et al.* 1993) and possibly because of high production of benthic invertebrates (Zwarts *et al.* 1990). It has been suggested that the ecosystem is fuelled by nutrients and organic matter from the Canary upwelling system (Wolff *et al.* 1993b), which for the benthic invertebrates in the north-western part of the intertidal area turned out to be the case. However, phytoplankton from the upwelling does not support the intertidal benthic community in the south-east of the Banc d'Arguin (Carlier *et al.* 2015). The food web of the south-eastern intertidal flats is mainly supported by local benthic primary production (Carlier *et al.* 2015)and thus seems independent of the Canary upwelling and any (potential) changes in the upwelling due to climate change.

The entire area of the Banc d'Arguin, including all mudflats, channels and islands, is protected but threats to the natural ecosystem are offshore oil and gas extraction in the same area where hundreds of international fishing trawlers are active, which is fairly close to the western border of the national park (Araujo and Campredon 2016, Environmental Justice Atlas 2017). The recent discovery of large amounts of offshore gas in Mauritania by British Petrol may become a near-future threat (Offshore Energy Today.com 2019). These threats highlight the difficulties of (inter)national nature conservation in countries whose resources attract the attention

of powerful international stakeholders (Magrin *et al.* 2011). While the ecosystem is claimed to be impacted by the effects of climate change with expected changes in species composition and richness (Araujo and Campredon 2016), this is, to the best of our knowledge, not backed up with scientific data.

Arctic tundra – The majority of Wadden Sea birds breed in the Low or High Arctic (van de Kam *et al.* 2004) as defined in the Arctic Biodiversity Assessment (CAFF 2013), with some also breeding in the sub-Arctic, which is not part of the Arctic (Meltofte 2017). Of 200 Arctic bird species, 59 are shorebirds of which 41 are largely confined to the Arctic for reproduction (CAFF 2013). The Arctic vegetated lowland, usually referred to as tundra, is where the Low Arctic has more lush vegetation than the High Arctic, where almost no vegetation may be present in some large lowland areas. The vegetation in the Low Arctic is often knee-high with meter-high bushes, in the High Arctic the vegetation is only ankle-high (Meltofte 2017). Plant growth is limited by the short growing seasons, low temperatures and slow nutrient cycles. The area is characterised by low temperatures, short summers with continuous daylight and winters with complete darkness. The relatively few species that inhabit the Arctic are all adapted to live in extreme environments, and their populations are capable to deal with strong environmental variation. Nevertheless, the current rate of climate change in the Arctic is unprecedented and is believed to be the largest current threat (Post *et al.* 2009, CAFF 2013).

Clearly, migratory birds are affected by a variety of different climate change aspects at the various locations used during an annual cycle. It should be noted that global warming is most pronounced at more northern latitudes, where many Wadden Sea birds breed, but that anticipated changes in weather may have impacts on each part of the ecosystems used by Wadden Sea birds year-round.
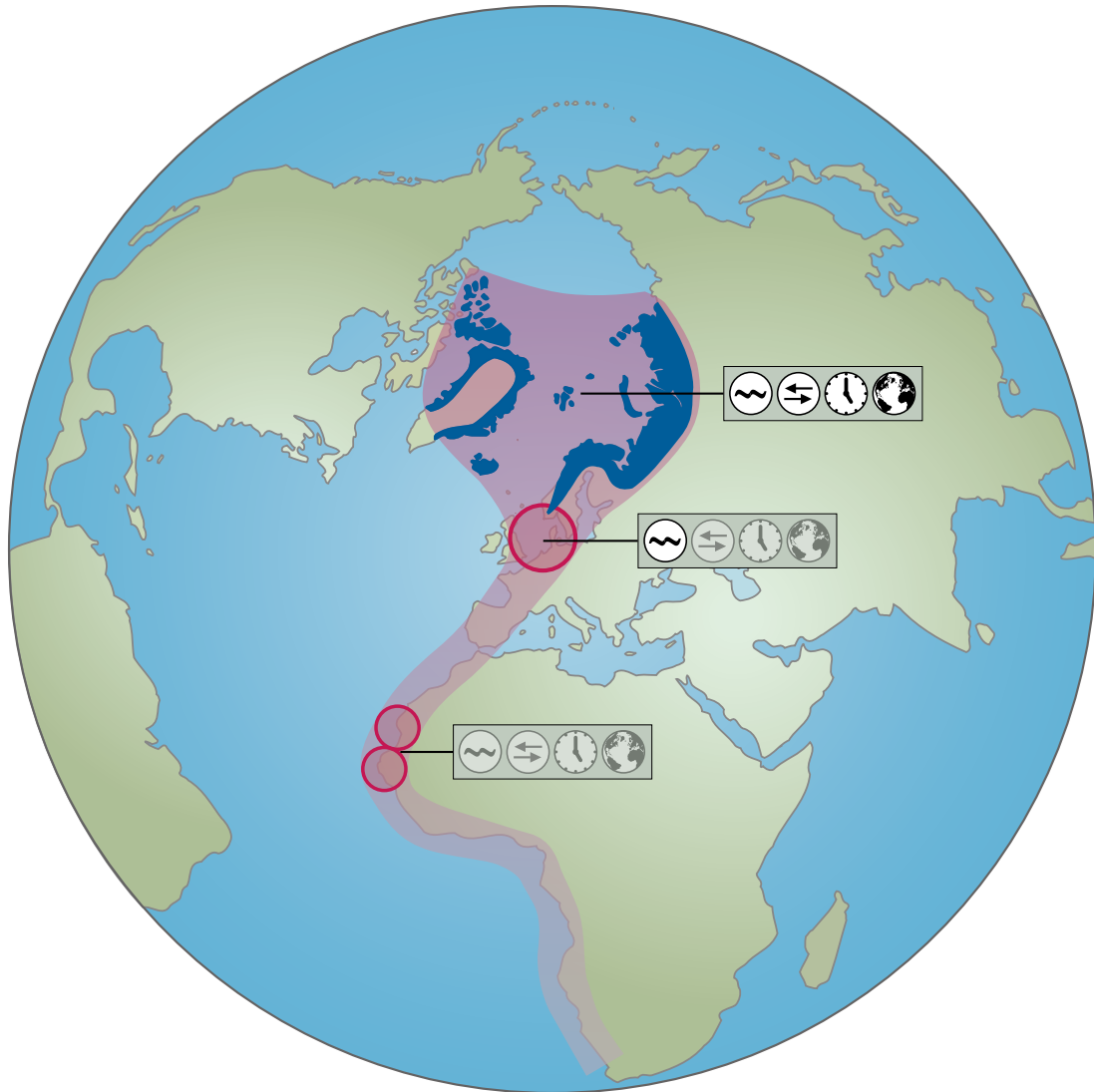
Fig. 1. *The Wadden Sea (large red circle within Europe) lies on a crucial crossroad of migration routes (red shade) of waterbirds that breed in the Arctic region (blue surface) and spend the non-breeding period along multiple coastal sites in Europe and the west coast of Africa (small red circles: Banc d'Arguin in Mauritania in the north, and Bijagós archipelago in the south). For the Arctic area, the Wadden Sea and the West-African a box indicates whether there are indications (bold symbols), or we currently lack knowledge of (non-bold symbols) for disappearing suitable habitat (waves), changed ecological interactions (arrows), changes in phenology (clock) or changes in distribution (globe).*

2. DOCUMENTED AND PROJECTED CHANGES IN CLIMATE

2.1 Global

The global average temperature is rising at an unprecedented rate with each recent year showing a new record; the latest five years (2015-2019) will almost certainly become the warmest 5-year period ever recorded (World Meteorological Organization (WMO), UN Environment (UNEP) and Change (IPCC), Global Carbon Project, Future Earth, Earth League 2019). Earth's land and ocean surface temperatures have increased by 0.87°C between 1850-2015 (Høye *et al.* 2007, Post *et al.* 2009, Gilg *et al.* 2012, CAFF 2013, Schmidt *et al.* 2019) with the last three decades to be the warmest over the last 1400 years for the Northern hemisphere (Arneth *et al.* 2019). The surface temperature is projected to rise over the 21st century under all assessed emission scenarios by the Intergovernmental Panel on Climate Change (IPCC) (Arneth *et al.* 2019). Global temperature increases come with changes in weather patterns (i.e. climate; the average weather over 30 years). Global effects of climate change are amongst others increased water and air temperatures, higher sea levels, acidification of sea water, coastal erosion and changed sedimentation (Change 2014). The IPCC (Arneth *et al.* 2019) reports that "It is very likely that heat waves will occur more often and last longer, and that extreme precipitation events will become more intense and frequent in many regions. The ocean will continue to warm and acidify, and global mean sea level to rise." Although all projections come with uncertainty about the magnitude of each effect, it can be safely concluded that global climate change will have far-reaching consequences for ecosystems and that they will last for millennia (Clark *et al.* 2016).

The global sea level is expected to rise due to the expansion of sea water when it is warmer and due to melt of ice sheets and glaciers, especially the Greenland ice sheet (World Meteorological Organization (WMO), UN Environment (UNEP) and Change (IPCC), Global Carbon Project, Future Earth, Earth League 2019), but the melting of Antarctic land ice may have an additional large effect on sea levels (DeConto and Pollard 2016).

Using climate projection models that include time series and concentrations of greenhouse gas emissions, as well as land use and land cover, the IPCC projects that for the period 2081–2100, compared to 1986–2005, global mean sea level rise is likely to be in the 5 to 95% range of projections from process-based models, which give 0.26-0.55 m, 0.32-0.63 m, 0.33-0.63 m, and 0.45-0.82 m for different climate scenarios (Collins *et al.* 2013). For the most extreme scenario considered by the IPCC, the sea level will have risen 0.52-0.98 m by 2100, with a rate of 8-16 mm yr^{-1} during 2081–2100 (Church *et al.* 2013), while new observations and models indicate that the ice dynamics of Antarctic, and to a lesser degree the Greenland ice sheet, may importantly lead to non-linear increases in sea level rise (summarised by (Oost P. *et al.* 2017)), which will then become considerably more and earlier than the most extreme scenario considered by the IPCC (Church *et al.* 2013).

A changing climate does not only entail an increase in averages of weather variables (such as temperature and wind force) but also in the variability of these. Both the frequency and the magnitude of extreme weather events are observed (Krasting *et al.* 2013, Bintanja and Andry 2017)and predicted (IPCC 2014). The occurrence of extreme weather events is however difficult to predict, and their ecological consequences even more so (Oost P. *et al.* 2017, Ripple *et al.* 2019). An increase in the frequency of extreme weather events could have profound consequences for the viability of Wadden Sea bird populations if they happen at large spatial scales (Schmidt *et al.* 2019).
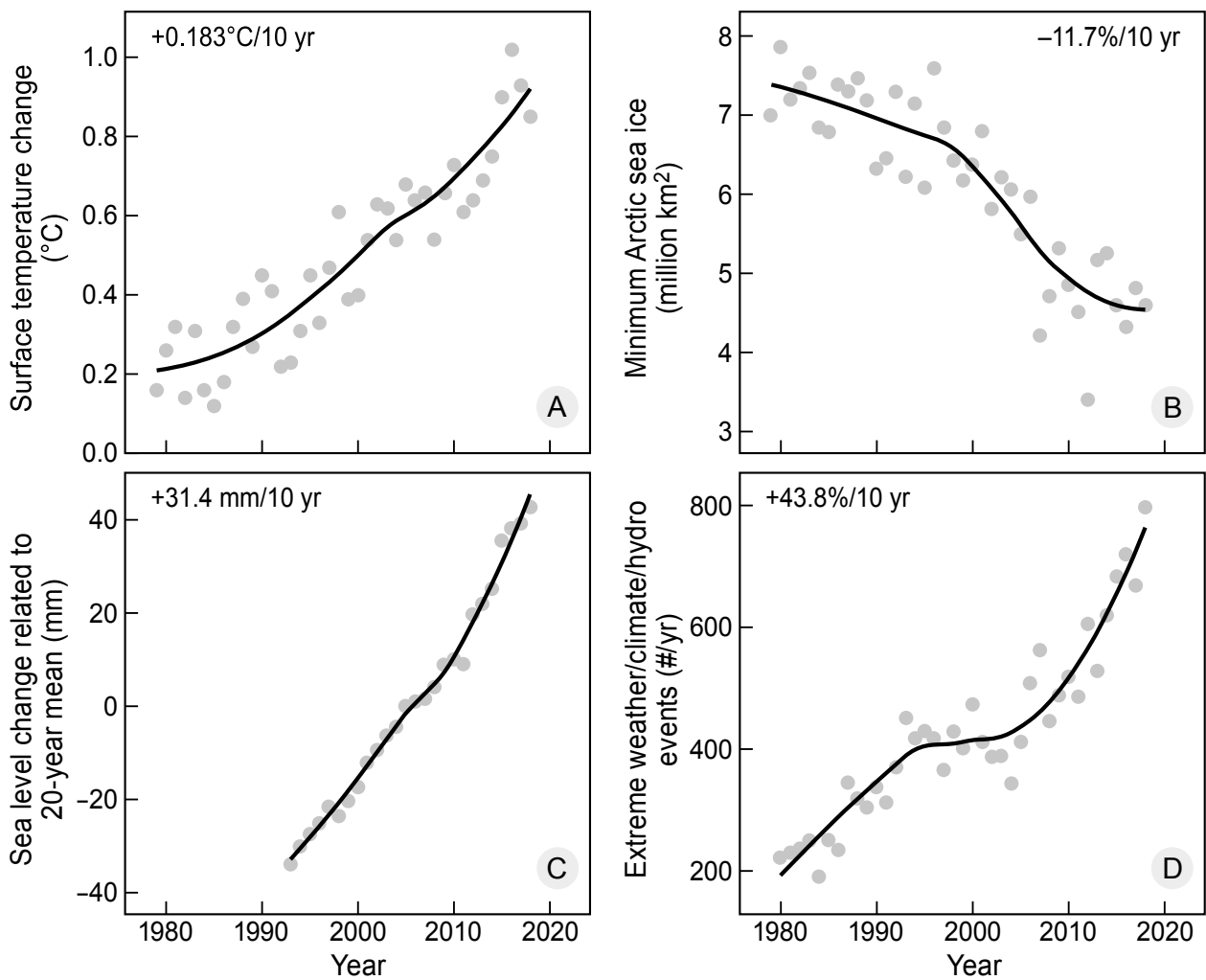
Fig. 2 *Time series of (a) surface temperature change, (b) Arctic sea ice extent, (c) change in sea level and (d) the occurrence of extreme weather events from 1979 until recent. The rates shown in the panels are the decadal change rates for the entire ranges of the time series as additive changes in (a) and (c) and in percentage terms in (b) and (d).The grey dots are annual data and the black lines the local regression smooth trend lines. Reprinted from (Ripple et al. 2019) where sources and additional details can be found in the supplementary material.*

2.2 West Africa

The climatic sub-regions in West Africa where the Banc d'Arguin and the Bíjagos archipelago are located are the Sahara and the Soudano–Sahel (sub-humid) region which have different climatic conditions (IPCC 2013). Depending on the emission scenario, temperature projections over West Africa for the end of the 21st century range between increases of 3 and 6 °C from the late 20th century baseline (IPCC 2013, Riede *et al.* 2016). The IPCC has "medium confidence" about the prediction that African ocean ecosystems will be affected by changes in ocean upwellings (Agyekum *et al.* 2018, which affect both the Banc d'Arguin and the Bijgós archipelago. Despite lack of historical data, most regions within Africa for which data are available have recorded an increase in extreme temperatures (Niang *et al.* 2014). West Africa is projected to experience changes in rainfall regime and enhanced warming is projected to lead to an increase in dry spells and a reduction of the wet spells under both 1.5 and 2 global warming level (Seneviratne *et al.* 2012). This may lead to changes in river run-off and affect estuaries used by Wadden Sea birds.

Red Knots feeding on bivalves on the tropical mudflats of the Banc d'Arguin, Mauritania. For Red Knots, and many other tropical wintering shorebirds, the Wadden Sea is an essential staging site

2.3 Wadden Sea

The Wadden Sea is formed over a period of more than 7000 years under a temperate climate, rising sea level, and, especially during the last century, human interventions and has throughout its recent history been capable of keeping up with relative sea level rise (Elias *et al.* 2012). Temperature regimes are largely affected by the low tidal range. The mudflats are exposed to direct sunlight during low tide during the day.

Oost *et al.* (2017) summarised the forecasted atmospheric temperature, sea surface temperature, precipitation, wind and sea level rise for different parts of the Wadden Sea in 2030-2035, 2050 and 2100 based on the projections by the IPCC as reported in its fifth assessment report (AR5) (IPCC 2014). The IPCC is currently in its sixth assessment cycle (AR6), during which amongst others reports of the three working groups will be, and already have been, published. As the AR6 has not been finalised yet (Arneth *et al.* 2019), I here mainly relied on Oost *et al.* (2017) and references therein, who summarised the translations of local climate scenarios in the AR5 to the Wadden Sea specifically. Here, I focus on projections for the Dutch Wadden Sea, and refer to Oost *et al.* (2017) and references therein for projections for the German and Danish Wadden Sea. Where applicable, I added additional references to specific studies. It is important to realise that reported uncertainties for projections of precipitation, wind and sea-level rise are (much) larger than for temperature changes.

Air temperatures
Average year-round air temperature increased between 1901 and 2013 with 1.8 °C. During this period, the number of days with a minimum temperature below 0 °C decreased. The number of days with a maximum temperature higher than 20 °C increased. It is projected that the average annual air temperatures will rise between 1.0 − 2.3 °C by 2050, relative to the average temperature over the period 1981-2010. For the end of the century, these temperatures are projected to increase between 1.2 − 3.7 °C. The temperature of the coldest days in winter and the warmest days in summer are expected to increase between 2071-2100. The

number of days with frost in the Wadden Sea area, might decrease by a projected 35-80 % relative to 1981-2010, while maximum temperatures above 40 °C at the end of 2100 inland in the Netherlands are expected, although probably less prominent in the cooler Wadden Sea region.

Sea surface temperatures
In the western part in the Dutch Marsdiep tidal inlet, sea surface temperatures are measured since 1860. During the first 30 years the annual average temperature continually decreased by 1.5 °C. Since about 1890 up until 1990, average temperature varied without a clear trend. Only the last 25 years showed a warming of about 1.5 °C (Philippart C.H.M. *et al.* 2017), in line with current increases of air temperatures. Water temperature varies spatially within the Wadden Sea area where winters in north-eastern part (towards Denmark) are generally colder than the southwestern part (towards the Netherlands). The land-locked or semi-enclosed seas of the North Sea, Baltic Sea and Wadden Sea represent showed the most rapid warming of sea surface temperatures with sea surface temperatures increasing between 1982-2006 at a rate three times as fast as the global rate. Indeed, the Wadden Sea, situated between the North Sea and the Baltic Sea, was one of the two fastest warming large marine ecosystems worldwide (Belkin 2009).

Precipitation
Most scenarios project an increase of precipitation, but there is a large uncertainty around these estimates. For the Dutch Wadden Sea a 5% increase in annual mean precipitation is expected around 2030-2035, a 4% increase towards 2050 and a 5-7% increase towards 2100. The increase will mainly take place in the winter, while summer are expected to become dryer. Such increases will lead to an average decrease in salinity of the Wadden Sea. Extreme amounts of precipitation are expected to increase within north-western Europe throughout the year (Oost P. *et al.* 2017). This will result in changes in riverine run-off. This likely affects the input of freshwater into marine intertidal systems and may affect exchange of suspended sediments and organic matter between the North Sea and the Wadden Sea. Consequently, primary productivity

of the Wadden Sea can be influenced if changing precipitation patterns result in changes in river outflows (Burchard *et al.* 2010, Flöser *et al.* 2011, Van Beusekom *et al.* 2012, Jung *et al.* 2017).

Sea level rise

Dutch sea-level has been rising steadily at a rate of 1.86 ± 0.15 mm per year (± 2 σ limits) between 1890-2014, which is similar to the global estimate over the overlapping period 1900-2009 of about 17 cm. The most extreme projections predict a sea-level rise in 2071-2100 relative to 1986-2005 of 34 cm (10 to 60 cm) to 61 cm (30 to 90 cm). However, even more extreme projections exist too. Later studies indicate that due to the contribution of faster melting of Antarctic land ice, maximum sea-level rise may be 1.8 m or more by 2100 (Jevrejeva *et al.* 2006, Hansen *et al.* 2013, Hansen 2016, DeConto and Pollard 2016) which is considerably more than projected in AR5 by the IPCC, and will possibly happen earlier than projected too (DeConto and Pollard 2016). Although it should be noted that these projections are to be considered preliminary, it will have serious consequences for the Wadden Sea area already before 2100, if they turn out to be realistic (van der Spek 2018).

2.4 Low and High Arctic tundra

The Earth does not homogeneously warm up with climate change. Due to several positive feedbacks the regional warming in the Arctic region is considerably faster compared with other regions on Earth (McBean *et al.* 2005, Pithan and Mauritsen 2014, Post *et al.* 2018). Over the past decade, the Arctic has warmed by 0.75°C, far outpacing the global average. With global temperature increases approaching 2°C warming, the Arctic may reach 4°C mean annual warming, and even 7°C winter warming (Post *et al.* 2019). Given its relatively fast warming, the ecological consequences of climate-induced impacts on species are expected to be most pronounced in the High Arctic (Post *et al.* 2009, Gilg *et al.* 2012). With an increased temperature, also precipitation is predicted to drastically increase in the Arctic (Bintanja and Selten 2014, Schmidt *et al.* 2019). The witnessed increasing air temperatures

and precipitation are drivers of major changes in various components of the Arctic system, which is getting into an unprecedented state with major implications for both the Arctic ecosystem and beyond (Box *et al.* 2019).

The Arctic climate exhibits strong natural variability, both from year to year but also on longer timescales. The magnitude of this variability will also change with climate warming. For example, the warmest midwinter temperatures at the North Pole have been increasing at a rate that is twice as large as that for mean midwinter temperatures at the pole (Moore 2016). Although Wadden Sea birds do not occur in the Arctic during midwinter, extreme weather events during the non-breeding season in the Arctic affect the Arctic food-web (Post *et al.* 2009, Schmidt *et al.* 2017a, Berger *et al.* 2018) and may eventually affect reproduction and survival of Arctic-breeding Wadden Sea birds (Schmidt *et al.* 2019). With less sea ice in the Arctic, we can expect more and more variable amounts of snow in the future (Liu *et al.* 2012, IPCC 2014). Snowfall will especially increase in the colder locations, years and seasons of the Arctic, but in the more temperate locations and periods snowfall is likely to decrease because warmer air will result in more rain instead of snow (Krasting *et al.* 2013, Bintanja and Andry 2017). More rain-on-snow events are projected to occur in the Arctic (Moore 2016) negatively affecting Arctic mammals (Rennert *et al.* 2009, Berger *et al.* 2018) with cascading effects on both population productivity and population size of Wadden Sea birds (Nolet *et al.* 2013).
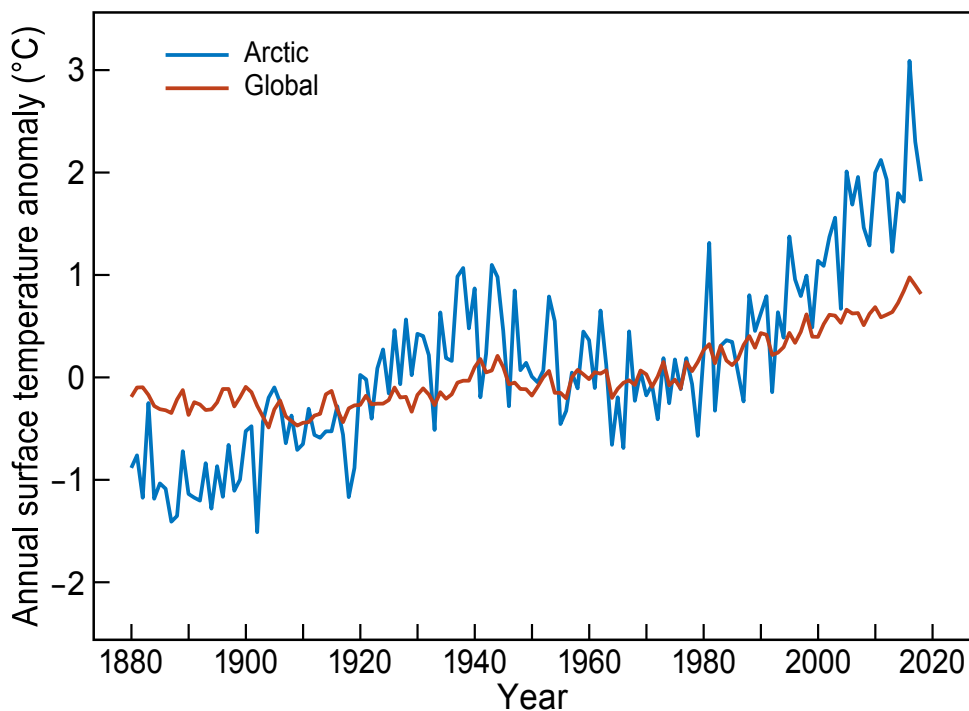
Fig. 3. *The surface temperatures in the Arctic have changed considerably faster compared to the global temperature change. Annual mean anomalies of the combined Land-Ocean Temperature Index (L-OTI) for the Arctic (64°N to 90°N), and globe between 1880 and 2018 (zonal data bins defined by data acquired at https://data. giss.nasa.gov relative to the mean period 1951–1980). Based on Post et al. 2019.*

Predictions of how the Arctic ecosystem will change with climate remain speculative given our limited knowledge and the complexity of all the interacting processes that are involved. There is even some doubt about the widespread claim that Arctic species are more sensitive to climate change impacts than other species; it has been suggested that they might actually be more resilient to climate change, based on the fact that they have already undergone more dramatic changes in the recent past than species from other biomes (Beaumont *et al.* 2011).

In 2018, the major part of the Arctic breeding grounds of Wadden Sea birds experienced an unusual amount of snow which resulted in a reproductive failure across the entire ecosystem in North-east Greenland (Schmidt *et al.* 2019).

If – as predicted (Arneth *et al.* 2019) – the frequency of extreme weather events will increase, this may have drastic consequences for the Arctic ecosystem as well as for Wadden Sea bird populations, but the extent to which populations will be affected is very hard to predict. Given the large area within the Arctic region over which so much snow fell, a reduction in reproductive output for many Arctic-breeding Wadden Sea birds is to be expected. However, reproduction of Arctic-breeding birds at the level of the population is difficult to monitor, and we thus lack the possibility to detect the potential population-scale effects of extreme weather events, even if they are of the magnitude as reported by (Schmidt *et al.* 2019).

Mudflats of the Banc d'Arguin in Mauritania are covered by seagrass. Many Wadden Sea shorebirds winter in the Banc d'Arguin. Not much is currently known about the effects of climate change on the functioning of tropical coastal ecosystems. Photo by Jeroen Reneerkens

3. DESCRIPTION OF CLIMATE CHANGE EFFECTS ON WADDEN SEA BIRDS – INTRODUCTION

Climate change can impact individual behaviour and physiology and eventually the survival probabilities and (lifetime) reproductive output, which may impact population sizes. Together, such individual changes may result in altered distributions of animals, changes in timing of annual life history events (e.g. the timing of reproduction or moult), which may be adaptive responses to an environment in a changed climate. If the timing of annual life history events (phenology) differs between interacting species (e.g. predators and prey), such 'phenological mismatches' often affects interacting species differently. For example, in case the interaction is antagonistic an increased phenological mismatch will be negative for a predator, but beneficial for its prey. Also, climate change effects on some organisms may cascade through a food web and affect other linked populations of species.

In this section I describe the proven and expected consequences of climate change effects on Wadden Sea birds for each geographical area along the East Atlantic Flyway, where such published information existed. Knowledge gaps are indicated and – when no published information was found – we speculate about the potential of the existence and consequences of climate change effects based on circumstantial evidence.

4. EFFECTS OF TEMPERATURE ON ENERGY EXPENDITURE AND SURVIVAL

4.1 Effects of weather variables on benthic invertebrates

Water and air temperatures have an impact on the distribution, survival and reproduction of benthic invertebrates in the Wadden Sea, upon which Wadden Sea birds prey. For example, when intertidal areas freeze, polychaetes may become less available for wintering waders. Some populations of benthic invertebrates are increasingly more abundant in areas with milder temperatures (Wiersma and Piersma 1994a). For example, there is a significantly positive relationship between winter temperature and number of sites were the polychaete worms *Lanice conchilega* and *Nephtys hombergii* were found (Beukema and Dekker 2011). On the other hand, increasing mean winter temperatures can negatively affect other benthic species. For example, after several consecutive mild winters, repeated recruitment failure was observed in mussels *Mytilus edulis* and cockles *Cerastoderma edule* (Beukema *et al.* 2009). Both mussels and cockles are an important food source for bivalve eating shorebirds, such as Oystercatchers and for Eiders *Somateria mollissima*.

Thermal stress can be particularly severe to intertidal invertebrate organisms, which are out of water at regular intervals (e.g. during low tide), where they are exposed to desiccation and temperature extremes. Some species may cope temporarily with such stressors by burrowing, but such behavioural responses are inadequate when temperature approaches critical values, causing severe physiological stress and eventually mortality (Gosling 2004).

Compared with tropical areas, organisms living in temperate areas, such as the Wadden Sea, are exposed to a greater variation in temperatures. As such, temperate benthic invertebrates are expected to have larger lethal thermal limits compared with tropical species. Indeed, benthic invertebrates from the Wadden Sea have a thermal tolerance window that is ca. 7 °C greater than that of tropical species and are thus expected to survive across a wider range of temperatures. The tropical shellfish species could survive higher temperatures in their upper lethal thermal limits than the temperate species, while the temperate Wadden Sea species survived cooler

temperatures than the tropical species (Compton *et al.* 2007). In a warmer climate, Wadden Sea shellfish will not benefit from their higher freeze tolerance.

Interestingly, tropical shellfish also live closer to their maximum habitat temperature (ca. 4.6 °C) than the temperate species (ca. 7.8 °C; Compton *et al.* 2007). Thus, there is no reason to suspect that tropical invertebrates are better adapted to increasingly warm environments. In fact, because tropical invertebrates are relatively sensitive to temperature changes and already live close to their thermal optimum, the small temperature increase is expected to have even more deleterious effects compared with invertebrates at higher latitudes (Beukema *et al.* 2009). Consequently, the largest negative impacts of climate warming on population growth rates in ectotherms are expected in the tropics (Deutsch *et al.* 2008), which may diminish the food availability for tropical wintering Wadden Sea birds even more (Deutsch *et al.* 2008) with presumed negative consequences for their migratory performance and survival (Rakhimberdiev *et al.* 2018, 1990, Reneerkens *et al.* 2020).

Still, during two exceptionally warm summers in 2018-2019, cockles *Cerestoderma edule* in the Wadden Sea showed mass mortality on the exposed cockle beds in the Wadden Sea (Philippart unpubl. data), which was presumably a consequence of the high temperatures in combination with other factors that have been shown to cause mass mortalities among cockles (Callaway *et al.* 2013, Burdon *et al.* 2014). Indeed, exposure to temperatures of 32 °C or more resulted in 100% mortality of cockles and peppery furrow shells *Scrobicularia plana* (Verdelhos *et al.* 2015). The projected increase in frequency, intensity and duration of heat waves (IPCC 2014) may thus pose a serious threat to invertebrate food sources for Wadden Sea birds, especially if the change in temperature is abrupt, which will not allow benthic organisms to acclimate (Gosling 2004).

Changes in riverine run-off, due to projected changes in precipitation, may locally affect benthic invertebrates who are adapted to saltwater. Effects on the distribution of bivalve larvae (Folmer *et al.* 2014) and mortality of bivalves (Kristensen 1958) have been reported.
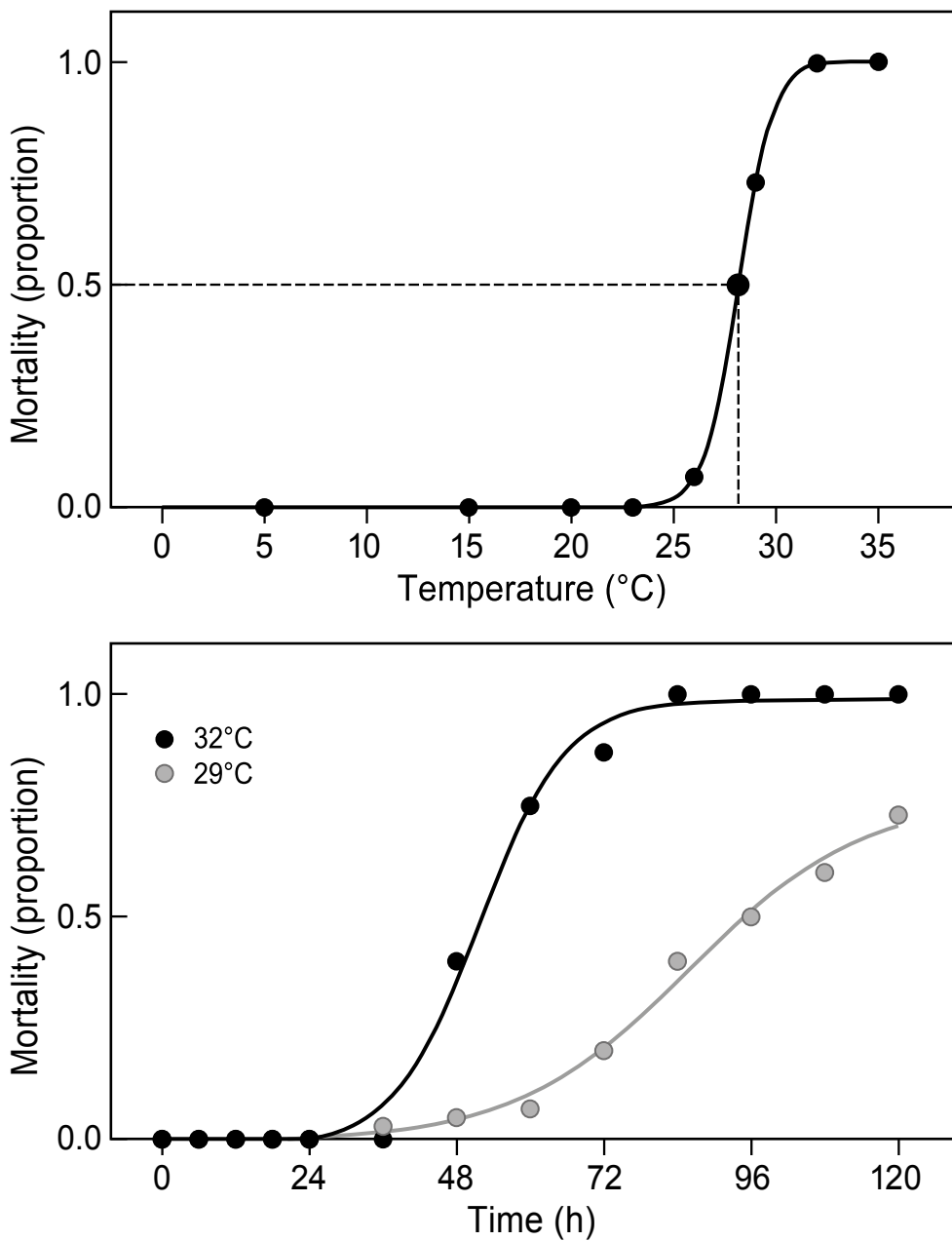
Fig. 4. *Cockles Cerestoderma edule have a higher risk of mortality in higher temperatures (upper panel, with 50% mortality at 28.5 °C) and when exposed to high temperatures for a prolonged period (lower panel). An increased frequency and intensity of heat waves in the Wadden Sea region could have seriously negative consequences for this shellfish which forms an important food base for Wadden Sea birds. Based on Verdelhos et al. 2015.*

4.2 Energy expenditure in a warmer environment

Birds are homeothermic, meaning that they maintain their own body temperatures at constant high levels with minimal metabolic regulation within a range of ambient temperatures, called the thermal neutral zone (Scholander *et al.* 1950). Costs of thermoregulation in the Wadden Sea or in the Arctic breeding grounds can be considerable (Wiersma and Piersma 1994, Piersma *et al.* 2003). When the climate becomes warmer and birds will be more often in their thermal neutral zone, this could be a benefit of climate change. On the other hand, extreme heat especially in the tropical wintering habitat could result in increased energy expenditure and time loss due to behavioural adjustments necessary to prevent overheating. In tropical environments it has been shown that behavioural adjustments to reduce heat load is more important especially when shorebirds are close to depart on migration and contain a lot of subcutaneous fat (Battley *et al.* 2003).

Low temperatures negatively influence the growth of Artic-breeding Wadden Sea birds by an increase in energy expenditure (Piersma *et al.* 2003a) and because (young) chicks need to be brooded by the parents for longer periods in cold weather, reducing the time available for foraging (Krijgsveld *et al.* 2003). At the same time, the arthropod prey for shorebirds is likely less active in colder temperatures, which has been suggested to negatively affect prey detectability (Tulp and Schekkerman 2008).

Thus, higher ambient temperatures may partly mitigate the effects of climate-induced phenological mismatches (McKinnon *et al.* 2013) (see "Phenological mismatches" below). However, to maintain chick growth food abundance is considered more important than weather variation (Machín *et al.* 2018, Saalfeld *et al.* 2019). In conclusion, the benefits of reduced energetic expenses in a warmer climate seem limited. Experiments in which food availability and air temperature are manipulated, and the effects on daily energy expenditure and chick growth will be measured could determine the relative role of (increased) temperatures and (decreased) food availability in a warming Arctic.

5. SEA LEVEL RISE

5.1 Africa

During a period of 7000 years before present, the sea level in the Mauritanian region oscillated within the usual range of natural variations, whereas oscillations of larger magnitude prevailed elsewhere (Certain *et al.* 2018). To the best of our knowledge, no study has modelled projections of the potential for drowning of intertidal tropical mudflats along the East Atlantic flyway.

5.2 Wadden Sea – Disappearing foraging habitat

The predicted strong sea-level rise is expected to accelerate in the future and will result in disappearing intertidal mudflats when sediment import and salt marsh accretion do not keep pace with it. The geological history of the Dutch coast has shown that the Wadden Sea could keep up with the relative level of sea level rise, which caused expansion of the basin. Consequently, the volume of sediment accommodation space increased, causing a net landward sediment transport. Erosion of the adjacent shorelines was an important contributor to the sediment supply, which lead to landward retreat of the entire barrier–inlet basin system while maintaining its basic characteristics (Goussard and Ducrocq 2014, Madeira 2016).

The question is whether the Wadden Sea can still keep pace with the current level of sea level rise including the predicted changes in (extreme) weather. The coasts adjacent to the Wadden Sea nowadays are heavily influenced by human constructions, such as man-made coastal protection works and land reclamation. The combination of human-made coast lines and the expected change in weather patterns will heavily impact the morphology of the Wadden Sea tidal basins and lead to –perhaps irreversible– loss of its natural characteristics (Flemming and Davis Jr. 1994). Field studies suggest that sediment import, tidal-flat and salt marsh accretion can keep pace with sea-level rise when it does not exceed 3-6 mm per year (Wang *et al.* 2015). In such scenarios, systems remain stable, but other systems might degrade and finally drown (Van der Spek and Beets 1992, Madsen *et al.* 2007,

Bartholdy *et al.* 2010, Suchrow *et al.* 2012, Elias *et al.* 2012, van der Spek 2018). Within the Wadden Sea, the drowning of intertidal flats caused by an increase in high-tide levels, is expected to start earlier and proceed faster in tidal basins with lower mean tidal range compared with central basins with a higher mean tidal range (Van Wijnen and Bakker 2001). This would imply that birds might relocate from more affected to less affected tidal basins within the Wadden Sea, but there will be ecological limitations to this possibility through density-dependency (Hofstede 2015).

Van der Spek (2018), based on Wang *et al.* (2018), indicates the critical sea level rises for 2030, 2050 and 2100 under the different scenarios of greenhouse gas emissions as used by the IPCC per tidal basin for the Dutch Wadden Sea. Up to 2030, the effect of accelerated sea level rise will be hardly noticeable, but by the year 2100, the effect depends on the scenario of climate change. In the most modest scenario (RCP2.6), where greenhouse gases will peak between 2010-2020 after which they will decline (Meinshausen *et al.* 2011), there will be hardly any effect of sea level rise until 2100. In the second scenario (RCP4.5 assuming that greenhouse gas emissions will peak in 2040 and then decline), the Vlie basin will drown already in 2030. In the most extreme scenario (RCP 8.5 in which emissions continue to rise throughout the 21st century) the Texel basin will also drown in 2050 followed by the Ameland basin around 2100. Given that we have almost certainly passed the stage of RCP2.6 (United Nations Environment Programme 2019, World Meteorological Organization 2019) , we will have to prepare for at least losing the intertidal mudflats in the Vlie basin.

It will be relevant to combine the models that project the extent and spatial variation in loss of intertidal habitat in the Wadden Sea with the ongoing extensive monitoring programme of intertidal fauna in the Wadden Sea (SIBES) (Bijleveld *et al.* 2012, Compton *et al.* 2013), to forecast how the food base for Wadden Sea birds may change with different projections of sea level rise.

The loss of intertidal foraging areas will result in fewer habitat for Wadden Sea birds to forage and to roost during high tide (Moser 1988, Gill

et al. 2001, Ntiamoa-Baidu et al. 2014) and given the relative importance of these mudflats for the majority of Wadden Sea birds, very likely in smaller population sizes. It is of high priority to investigate the forecasted rate at which foraging habitat for Wadden Sea birds will disappear, which areas are expected to drown first and what the relative importance of these mudflats are in terms of food abundance and distance to available high tide roosts. The effectiveness of different scenarios to restore the natural coast line of the Wadden Sea to keep its natural characteristics and allow it to keep up with the current relative level of sea level rise – at minimum costs and while maintaining a (flexible) protection against flooding are urgently needed.

5.3 Wadden Sea – Disappearing breeding habitat

Six Wadden Sea birds breeding in salt marshes suffered from flooding of their nests during extreme high waters which have increased considerably during the last four decades In Oystercatchers, this even reduced the reproductive output to below stable population levels if they would not adapt (van de Pol et al. 2010), indicating the severity of increased frequency of rare climatic events. Oystercatcher populations have, however, reduced the risks of extreme flooding by nesting at higher elevations. Individuals did not change nest site much throughout their lifetime, but presumably because new birds that enter the population (i.e relatively young birds) selected sites at higher elevations to breed, the population became better protected against flooding of their nests (Munaretto and Klostermann 2011).

6. EFFECTS OF CHANGED WIND REGIMES ON THE MIGRATORY PERFORMANCE OF WADDEN SEA BIRDS

Shorebirds departing from West Africa rely on favourable tailwind, which largely affects their timing of spring migration (van de Pol *et al.* 2010, Bailey *et al.* 2019). Adverse wind conditions during northward Sahara crossings increase the in-flight mortality of shorebirds (Lok *et al.* 2015) consistent with an increased mortality during northward but not southward migratory flights by Spoonbills between West Africa and the Wadden Sea (Loonstra *et al.* 2019). Thus, changes in wind regimes with climate change may influence the success of migratory flights of Wadden Sea birds. Climate models and observations indicate that global atmospheric circulation is being affected by

climate change (IPCC 2013). Relevant for African-wintering Wadden Sea birds specifically, it has been shown that wind force and the frequency of storms in the West-African Sahara region has tripled since the 1980's (Taylor *et al.* 2017). However, changes in wind conditions due to climate change are among the most difficult physical aspects of climate change to forecast. Consequently, changes in wind regimes due to climate change are considered to be of "low confidence" or at best to be "likely" (Collins *et al.* 2013). Thus, whether and to what extent changing wind conditions will affect migratory Wadden Sea birds remains largely unknown.

7. CHANGES IN GEOGRAPHICAL DISTRIBUTION

Because of climate change, the ranges of many birds are shifting to higher latitudes and altitudes, allowing species to survive in new locations (Sekercioglu *et al.* 2008b). Range shifts describe situations when both the southern (or lowest) and northern (or highest) borders of distribution ranges are constrained by climate and can hence move because of climate change. There are situations, however, when only one of these borders is constrained by climate – the other being constrained by geographical barriers, competitors, etc. In such situations, climate warming can either induce a decrease in distribution range – if the southern border is constrained by climate – or an increase. Several predictive models based on habitat utilization by feeding or nesting Arctic geese, for example, follow the latter rationale (Root *et al.* 2003). Species for which habitat is limiting, or which already occur at the extremes of their physiological tolerance, climate change will likely lead to range contractions (Wisz *et al.* 2008, Speed *et al.* 2009). There is ample evidence that species are rapidly changing their distribution due to rapid climate change (Chen *et al.* 2011).

7.1 Distributional changes in Africa

I have not found scientific literature about distributional changes of Wadden Sea birds in West Africa in relation to changed climatic conditions, although Common Greenshank *Tringa nebularia* has been suggested to potentially have shifted its non-breeding distribution northwards from Africa to Europe based on contrasting trends in abundance in Africa and Europe. Similar results were also found for e.g. Grey Plover *Pluvialis squatarola* (van Roomen *et al.* 2015). These suggestions can however not be taken as evidence for distributional changes caused by or correlated with changed climatic conditions. The poor, but improving, spatiotemporal coverage of sites where birds are being counted currently limits such analyses (van Roomen *et al.* 2015).

7.2 Distributional changes in Europe

Wader distribution and abundance within Europe has changed alongside with changes in temperature; several wader species have moved towards the colder extremes of their range, which suggests that they expanded their range due to warmer weather (Maclean *et al.* 2008). It has been suggested that by changing their range, birds diminish cold weather-induced mortality (Austin and Rehfisch 2005). Changes in bird abundance as a result of temperature have often been explained to be the result of changes in survival. For example, Oystercatchers *Haemotopus ostralegus* have an increased risk of mortality in cold winters (Maclean *et al.* 2008) but also leave to warmer areas in severe winters explaining local changes in abundance as well.

In the Wadden Sea, distribution shifts have been reported for species of many taxonomic groups (Philippart *et al.* 2017). Shellfish species that formerly were absent in the Wadden Sea now occur there now (Mieszkowska *et al.* 2006). The milder seawater temperatures may facilitate the establishment of newly introduced warm water species (Philippart *et al.* 2017, Klunder *et al.* 2019), but it is currently unclear how such changes in species composition may impact the functioning of the ecosystem including the birds.

As the Mediterranean climate is projected to become unfavourably hot and dry (Zampieri *et al.* 2009), it is possible that Wadden Sea birds breeding in southern Europe, such as Spoonbills, may move their range northwards with a relatively larger proportion breeding in the Wadden Sea, but previous studies on Spoonbills have shown that the population slowly changes its distribution and may keep on using suboptimal habitat for a long time (Lok *et al.* 2011).

7.3 Arctic breeding distribution: changes in habitat and climate are predicted to result in loss of breeding habitat

The remote (High) Arctic is large and there is relatively little human activity. Hence, Arctic habitat

loss due to human interference has hitherto not been a large threat to Wadden Sea birds. Forecasting the future ranges of birds is complicated because it does not only require predictions of future climatic conditions, but also those of future biotic interactions (e.g. Beale *et al.* 2008, Miller-Rushing *et al.* 2010). Despite these challenges, there is a growing consensus that climate change will result in range shifts towards the poles and higher altitudes, often resulting in range contractions (Preston *et al.* 2008, Pimm 2009). Many Wadden Sea birds breed in the northernmost land on Earth and are thus range-restricted and show severe range contractions. As a result, northern breeding species and species breeding on mountain tops are among the first species groups in which species went extinct due to recent climate change (Parmesan 2006).

Indeed, based on climatic considerations, Wauchope *et al.* (2017) show that climatically suitable breeding conditions of 24 Arctic shorebirds could shift, contract and decline over the next 70 years. An estimated 66–83% of species would lose most currently suitable area. This exceeds, in rate and magnitude, the impact of the mid-Holocene

climatic optimum; the world's last major warming event. Thus, climate change will urgently lead to habitat loss with predicted range contractions and even species extinctions as a result (Wauchope *et al.* 2017).

Besides climatic considerations, the Arctic tundra will experience large climate-change induced changes in biotic interactions (Sekercioglu *et al.* 2008a). For example, Arctic tundra ecosystems are subject of expansion of shrubs (Post *et al.* 2009, Gilg *et al.* 2012, Schmidt *et al.* 2017b and see "Food web changes" below). Shrub expansion of the Arctic tundra increases the risk of shorebird clutch predation (Post *et al.* 2009, Myers-Smith *et al.* 2011, Elmendorf *et al.* 2012, Vowles and Björk 2019) making the smaller suitable area even less profitable.

For Wadden Sea birds specifically, we lack reliable forecasts of future climatic conditions, future biotic interactions and how these might translate into range shifts. Nevertheless, there are few reasons to believe that Wadden Sea birds will not show range shifts, or – in the case of Arctic-breeding species with breeding ranges at the edge of the continent – range contractions.
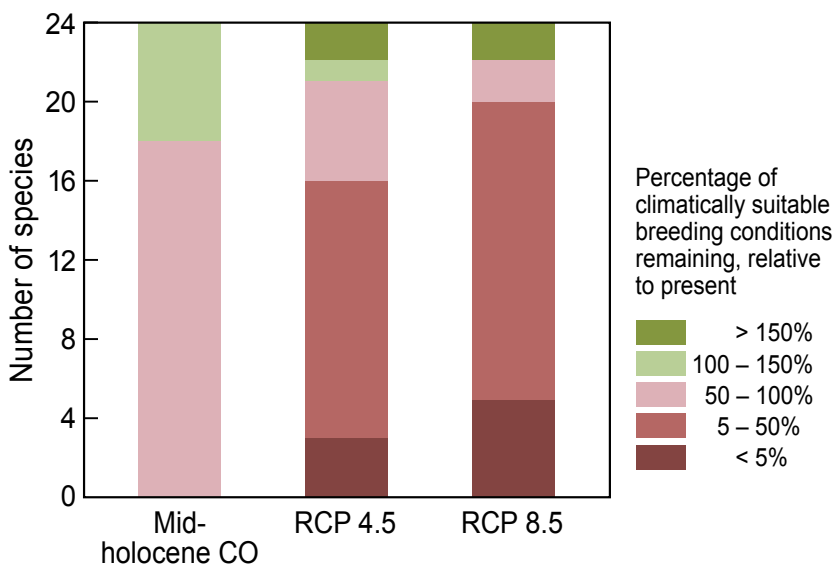
Fig. 5 *The number of 24 Arctic breeding shorebird species gaining (green) or losing (red) climatically suitable breeding conditions relative to the present day. Based on Wauchope et al. (2017).*

8. FOOD WEB CHANGES

In ecosystems, each individual and each species relates to other individuals or species through competition, mutualism, parasitism which impact behaviour, individual fitness, geographic range, and ultimately the structure and dynamics of the community (Hooper *et al.* 2005, Ims *et al.* 2019). Trophic interactions (or: predator–prey interactions) are perhaps the most pronounced. Food webs, in which the predator-prey interactions are depicted, may be considered simplified representations of an ecosystem. Because different (individuals within) species respond differently to changes in the environment, climate change may impact the functioning and stability of ecosystems (Hooper *et al.* 2005, Schmidt *et al.* 2017a). Climate change may strongly disrupt food web dynamics as well as resilience of food webs (Tylianakis *et al.* 2008) and it is thus considered essential to study all (trophic) species interactions to fully understand the impact of climate warming on individual species (van der Putten *et al.* 2010).
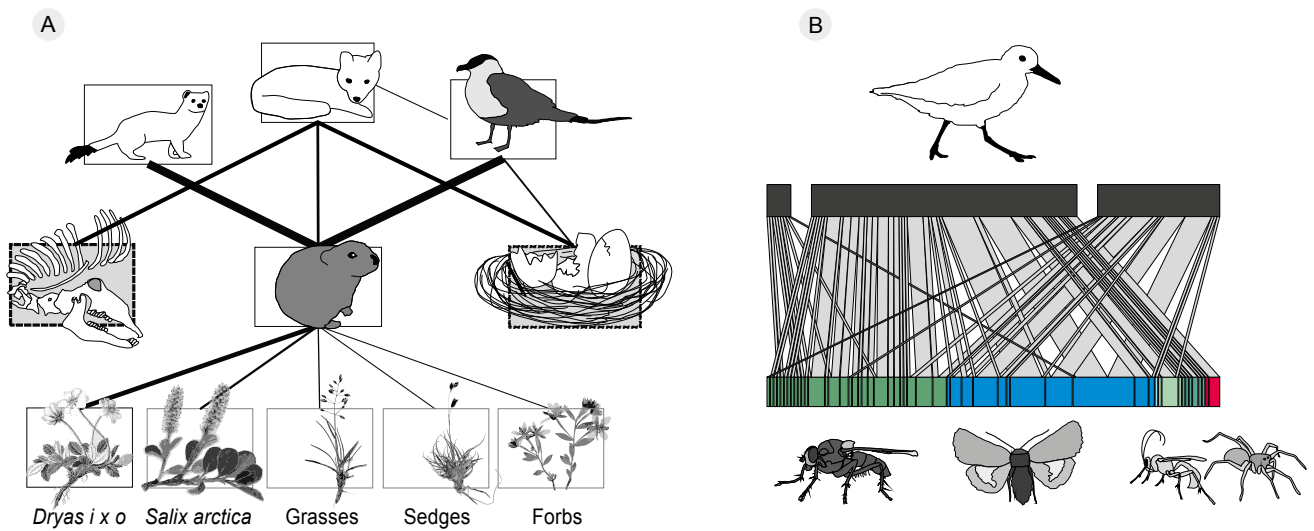
Fig. 6. *Interaction network in an Arctic ecosystem, with antagonistic interactions between species. Each empirically proven interaction is indicated with a line. (A): Within the entire ecosystem lemmings indirectly play a central role in determining the risk of clutch and chick predation. (B): In the upper panel, the species richness of each taxon is represented by the size of each box. Clearly, Diptera (true flies) form the most species-rich taxon, but Arctic-breeding Wadden Sea birds predate on the full spectrum of available artrhopods. Based on Schmidt et al. 2017.*

8.1 Arctic nest and chick predation: indirect effects of faltering lemming cycles

In the tundra ecosystem, lemmings and voles are the primary prey for a number of vertebrate predators (Gilman *et al.* 2010, Schmidt *et al.* 2017a) which also prey upon eggs and chicks of shorebirds and geese (Gilg *et al.* 2006, Schmidt *et al.* 2008, 2012, Ehrich *et al.* 2019). Lemmings and voles are well known for their drastic population cycles, with a more than 200-fold difference between maximum and minimum densities (Summers *et al.* 1998, Blomqvist *et al.* 2002, Mckinnon *et al.* 2013, McKinnon *et al.* 2014), and with cycles typically lasting 3-5 years. In the High Arctic, where most Wadden Sea shorebirds and geese breed, it is especially lemmings (the lemming genera collared lemmings (*Dicrostonyx* ssp.) and brown lemmings (*Lemmus* ssp.)), hereafter "lemmings", that play a central role in the tundra ecosystem (Gilg *et al.* 2003, 2006) and whose abundance can affect the reproductive output of tundra-breeding birds (Ehrich *et al.* 2019).

The reproductive success of most terrestrial Arctic vertebrate predators, such as snowy owls *Bubo scandiacus*, long-tailed skuas *Stercorarius longicaudus* and arctic foxes *Vulpes lagopus,* relies on years with sufficiently high lemming abundances (Blomqvist *et al.* 2002). In the typical lemming cycle this entailed that Arctic vertebrate predators reproduced during lemming peak years and had no or little reproductive output in years with low lemming abundance. In such years with low lemming abundance, predators typically rely to a larger extent on alternative prey, such as eggs and chicks of shorebirds and geese.

Because lemmings fulfil such a central role in the High Arctic predator-prey community (Schmidt *et al.* 2012, Barraquand *et al.* 2014, Pokrovsky *et al.* 2015), their cyclical abundance not only strongly influences the reproductive success of their predators but also that of potential prey other than lemmings. The functional and numerical responses of predators to fluctuating lemming densities result in inter-annual variation in predation pressure on alternative prey (Gilg *et al.* 2003, Krebs 2011). In other words, in years with few lemmings, predators rely on prey alternative to the preferred lemmings, which usually are bird eggs and chicks, whereas during lemming peak years the alternative prey is relatively safe and reproduces well (Angelstam *et al.* 1984). Indeed, in such lemming peak years the reproductive success of Arctic breeding shorebirds and geese in the Wadden Sea is typically higher (Bêty *et al.* 2001, 2002).

Lemming cycles are highly sensitive to climate change (Summers *et al.* 1998, Blomqvist *et al.* 2002, Fraser *et al.* 2012). The duration and type (e.g. rain-on-snow events) of winter weather and snow conditions (e.g. snow hardness and cover) have changed with a warming climate and had negative impacts on the cyclicity of lemming abundance (Kausrud *et al.* 2008, Gilg *et al.* 2009a). As a result, lemming cycles have shown strong decreases in amplitude and even ceased to exist in some parts of the lemming range (Kausrud *et al.* 2008).

Interestingly, a recent study which looked at lemming abundance in long-term monitoring programs did not find evidence for decreasing circumpolar lemming populations, although a negative trend was detected for low arctic populations (Ims *et al.* 2008, 2011, Kausrud *et al.* 2008, Gilg *et al.* 2009a). The authors however warn that due to differences in used methods to monitor lemming abundance, low precision of the data need to be kept in mind. Although it seems likely that climate change affected the mechanisms underlying changes in lemming abundance and cyclicity (Ehrich *et al.* 2019), there is thus no scientific consensus about whether lemmings have decreased in general. Also, despite the many indications of of climate change-induced changes in Arctic food webs (Kausrud *et al.* 2008, Gilg *et al.* 2009b, Ims *et al.* 2011, Bêty *et al.* 2014), there is no compelling evidence for an increased risk of nest loss in Arctic shorebirds (Bulla *et al.* 2019). The appearance of novel predators of bird eggs in the Arctic terrestrial ecosystem (e.g. Prop *et al.* 2015a), which are directly linked to climate-related changes in the Arctic environment, may potentially have large consequences for the reproduction of Wadden Sea birds, but this is insufficiently investigated.

Clearly, ecological communities in the Arctic are changing rapidly as a result of fast increases in temperature and snow melt. However, due to the many (indirect) interactions and feedback loops within (Arctic) food webs it is complicated to forecast how these will affect Wadden Sea birds (Schmidt *et al.* 2017a). Long-term ecosystem monitoring in combination with targeted experiments to understand and predict the future of Arctic breeding Wadden Sea birds will improve this situation.

Collared lemmings (Dicrostonyx ssp.) and other lemming species occur in cyclic abundance on the Arctic tundra and importantly affect the vertebrate food web and have indirect effects on the reproductive success of breeding Wadden Sea birds. Climate change has been suggested to disrupt the lemming cycles, but this is not (yet) reflected in results from long-term monitoring projects. Photo by Jeroen Reneerkens.

8.2 Changes in predation risk in the Wadden Sea

Peregrines *Falco peregrinus*, are the main predator of Wadden Sea shorebirds both in the Wadden Sea and in the Banc d'Arguin (Prop *et al.* 2015b) and they have steeply increased in numbers after a ban in pesticides that had diminished population sizes (Bijlsma 1990, van den Hout *et al.* 2008). In North America, the timing of southward migration by sandpipers was less strongly related to timing of snowmelt than that of the Peregrines, such that sandpipers now experience more predators on their stopover sites than before (Piersma *et al.* 2003b). Both in North America (Niehaus and Ydenberg 2006) and in the Wadden Sea region (Ydenberg *et al.* 2004), an increase in predators, notably Peregrines, was correlated with decreases in individual body masses in shorebirds, presumably enabling faster escapes (Piersma *et al.* 2003b). Also, the staging duration has, presumably because of increased predator encounters, shortened (Ydenberg and Nebel 2005). Thus, a different response of shorebird and their predators to changes in the timing of snow melt in the Arctic, as observed in North America, can profoundly affect ecological interactions at staging sites (Lank *et al.* 2003, Ydenberg *et al.* 2004).

9. PHENOLOGICAL MISMATCHES

One of the best documented adaptations of organisms, including birds, to climate change are changes in the timing of biological events within an annual cycle, usually referred to as 'phenology' (Walther *et al.* 2002, Root *et al.* 2003, Renner and Zohner 2018, Visser and Gienapp 2019). In a warmer world, organisms advance the timing of reproduction. As a response, with earlier warm springs, birds advance the timing of prenuptial migration and reproduction to aim to keep track of the earlier appearing resources, such as plants and invertebrate prey (Both *et al.* 2005a, b, Jonzén *et al.* 2006, Knudsen *et al.* 2011, Kullberg *et al.* 2015).

Generally, lower trophic levels have shown faster phenological advances in response to increasingly early spring temperatures than the higher trophic levels (Voigt *et al.* 2003, e.g. Høye *et al.* 2007, Both *et al.* 2009, Burgess *et al.* 2018) resulting in 'phenological mismatches', i.e. a difference in the timing of interacting species. The mechanisms of variation in phenological changes are often not clear (Chmura *et al.* 2019), but one of the explanations for migratory birds is that consumers have difficulties to advance their timing of reproduction equally fast as the advanced phenology of their prey [21], either because of time constraints when preparing for reproduction or the inability to optimally time migration when reliable cues in the non-breeding range that predict the phenology of prey in the distant breeding area are lacking (Winkler *et al.* 2014). A much-observed consequence is that due to ongoing climate change, the time at which a consumer species' demands for a resource are high does not match with the period when this resource is abundant. When the resource is food, such phenological mismatches are sometimes also referred to as 'trophic mismatches'.

There is a wealth of scientific publications on this topic in relation to climate change (e.g. Thackeray *et al.* 2010, Renner and Zohner 2018, Visser and Gienapp 2019, Zhemchuzhnikov *et al.* 2020) but a word of caution that observed mismatches should not necessarily be interpreted as a negative influence of climate change might be necessary. Most studies on phenological mismatches in birds relate the time of peak demand of offspring in relation to the peak abundance of the (main) prey (Visser and Both 2005). It has generally been observed that

early breeding individual birds within a population have a higher fitness than later breeding individuals (Verhulst and Nilsson 2008, Bulla *et al.* 2019), but there may be costs to breeding early (Drent *et al.* 2003). Observed phenological mismatches may thus be the result of a strategy in which the costs for parents and the benefits for offspring of reproductive timing are optimised (Visser *et al.* 2012). Also, a way for prey to avoid predation could be to avoid temporal synchrony with its predators, but predators should likewise re-establish the synchrony, if there are no constraints in doing so.

Phenological mismatches between avian consumers and their food during reproduction are considered among the most threatening impacts of climate warming on populations (Ockendon *et al.* 2014). Indeed, there is ample evidence that phenological mismatches impact birds' reproductive output (Lameris *et al.* 2018, Zhemchuzhnikov *et al.* 2020) which may affect demography and eventually changes in population size (e.g. Both *et al.* 2006, Saino *et al.* 2011b) but see 'From effects on individuals to populations; what is the evidence that climate change affects populations?', below. Here, I review the evidence and impact of climate change-enhanced phenological mismatches on Wadden Sea birds and their food along the East Atlantic flyway and in Arctic-breeding geese and shorebirds in general.

9.1 Phenological mismatches in Africa

I am not aware of published evidence or indications for Wadden Sea birds being subject to phenological mismatches with interacting prey or predators in African non-breeding locations.

9.2 Phenological changes in the Wadden Sea food web

Differential changes in phenology may have resulted in changes within the food web of the Wadden Sea, creating phenological mismatches between interacting species. Species-specific changes in phenology underline that different species (and even

different life phases within one species) might be subject to differing environmental constraints and subsequently respond differently to environmental changes during their life (Niehaus and Ydenberg 2006). Fish communities in the Wadden Sea did not change their phenology in response to increased Wadden Sea water temperature (van Walraven *et al.* 2017). It has been suggested that due to increasing sea water temperatures, the settlement of juvenile shrimps *Crangon crangon* on the intertidal mudflats has advanced with an increased temporal synchrony with spat of the bivalve Baltic Tellin *Limecola balthica* as a result. This was suggested to lead to an increased predation of shellfish spat and a lower shellfish recruitment (Philippart *et al.* 2003). More recent research, however, showed that bivalves now have advanced their timing of spawning and as such may escape the predation pressure from shrimps (Philippart *et al.* 2014). Recent large recruitment of Baltic Tellins in the Dutch Wadden Sea (Compton *et al.* 2016) suggest that phenological mismatches are not an important factor determining recruitment (anymore). Indeed, trophic mismatches are expected to last for relatively short periods, because only one of the interacting species (the predator) is negatively impacted by it (Renner and Zohner 2018). Alternatively, other factors, such as the now banned mechanical cockle dredging alternatively or additionally explained the poor recruitment of Baltic Tellins in the past (Piersma *et al.* 2001).

It is, to our knowledge, unknown whether any migratory Wadden Sea bird species experiences and suffers from phenological mismatches with their predators or prey in the Wadden Sea or other European staging sites. There is however recent American evidence on two migratory shorebird species that also occur in the Wadden Sea, Red Knot and Ruddy Turnstone *Arenaria interpres* (Tucker *et al.* 2019). The temporal abundance of the main food source used to refuel during migration – eggs of the Horshoe crab *Limulus polyphemus* at Delaware Bay – is highly dependent on water temperature which inter-annually varied during a 22-year study period. In years with cooler water temperature, crabs spawned later, which was associated with later and faster mass gain for the Red Knots. As the inter-annual variation in water temperature is expected to increase with climate

change, the occurrence of this food source may become less predictable, importantly affecting the success of long-distance migrations. In contrast to the Red Knots, Ruddy Turnstones were unaffected by annual variation in horseshoe crab egg availability. It was discussed that, in contrast to the Red Knots, Rudddy Turnstones are generalists foraging on a variety of prey, making them less susceptible for climate change effects on a single food source (Tucker *et al.* 2019).

9.3 Arctic food availability for chicks, chick growth and survival

Many Wadden Sea birds breed on the Arctic tundra (van de Kam *et al.* 2004), where temperature has increased fastest (McBean *et al.* 2005, Post *et al.* 2019). Arctic-breeding bird species have thus often been assumed to suffer most from increased shifts in phenology of the prey (e.g. van Gils *et al.* 2016, Reneerkens *et al.* 2016, Lameris *et al.* 2018). Indeed, phenology has changed fastest at higher latitudes (Post *et al.* 2018) there is evidence that food sources advanced fastest at the highest latitudes, with indications that phenological mismatches increase the fastest in strength in the north (McBean *et al.* 2005). Due to limited and unbalanced long-term datasets, it is currently unknown whether faster increases in phenological mismatches also more likely come with (stronger) negative fitness consequences for birds (Zhemchuzhnikov *et al.* 2019).

Interestingly, there was little evidence for changes in the phenology, of several vertebrate species, including snow goose on the Canadian Arctic tundra despite a 24-year long dataset (Gauthier *et al.* 2013). A study on Arctic invertebrates in Siberian Russia reconstructed the abundance of food availability of Arctic Wadden Sea shorebirds based on correlations with weather variables and found that the peak arthropod abundance had advanced with seven days between 1973-2003 (Tulp and Schekkerman 2008), thus likely creating a phenological mismatch for breeding birds if they had not advanced their laying date in accordance. However, egg laying dates could not similarly be reconstructed, so it remained

speculation whether the degree of phenological mismatch has increased during this period. In fact, there are very few long-term datasets of the phenology of both Arctic geese or shorebirds and their food, while this is a requirement to attribute phenological mismatches to climate change (Renner and Zohner 2018).

An exception is a 17-year long study on Sanderlings *Calidris alba* breeding in Greenland (Reneerkens *et al.* 2016), of which a large part of the population importantly relies on the Wadden Sea during migration (Loonstra *et al.* 2016, Reneerkens *et al.* 2020). During a 17-year period the median date of emergence of food (insects and spiders) had advanced in response to an earlier snow melt, but the birds had not advanced their breeding phenology, resulting in phenological mismatch between the time of maximal food requirement of Sanderling chicks and the abundance of the food (Reneerkens *et al.* 2016). Similarly, Barnacle geese *Branta leucopsis* experienced an increasingly early period of high food quality in the Siberian Arctic, but although they speeded up their northward migration by skipping previously used staging grounds, their faster migration resulted in lower fuel stores at arrival in Siberia necessitating a longer pre-laying refuelling and still a phenological mismatch with lower chick survival as a result (Lameris *et al.* 2018). Almost all shorter studies on Arctic-breeding geese and shorebirds report trophic mismatches, but not always convincingly. Only one of three studied sandpiper species breeding on the Arctic tundra showed a change in median laying date between 1954 and 2005-2008, but the sample sizes for the historic data were so small (range of n = 2-9) that this result should be taken with care (McKinnon *et al.* 2012). While in only one year in the three study years (2005–2008) sandpiper hatch dates and peak abundance of their food were matched, it remains uncertain whether this is a negative effect resulting from climate change or adaptive (Visser *et al.* 2012). Indeed, only one of the three studied species appeared to show reduced chick growth due to a mismatch with Tipulidae, which were presumed to be the main food source of Arctic sandpiper chicks, even though it is now well-described that Arctic sandpipers eat the wide variety of available arthropods (Wirta *et al.* 2015).

There is extensive geographical variation in the extent of phenological mismatches between shorebirds and their prey in the Arctic region and this variation was well correlated with changes in the time of snow melt (Kwon *et al.* 2019). Such geographic variation in the extent of phenological mismatches was also found in Hudsonian Godwits *Limosa haemastica* (Senner *et al.* 2016) where only one of two studied populations experienced a phenological mismatch. Interestingly also, not all chicks were equally affected by the mismatch; only older chicks showed reduced growth at days with low food availability. Similarly, deviation of average growth in Greenlandic Sanderling chicks did not depend on their hatch date relative to the median date of the food peak (Reneerkens *et al.* 2016). However, chick growth was overall poorer in years with narrow food peaks and it was suggested that the shape of the food peaks need to be taken into account when assessing the extent of phenological mismatch (Durant *et al.* 2005, Vatka *et al.* 2016, Reneerkens *et al.* 2016). Especially for Arctic shorebirds, arthropod food abundance critically depends on the large daily variation in weather (Tulp and Schekkerman 2008, Reneerkens *et al.* 2016, Machín *et al.* 2018, Saalfeld *et al.* 2019, Zhemchuzhnikov *et al.* 2020), complicating (comparisons between) studies of phenological mismatches (Zhemchuzhnikov *et al.* 2020). Nevertheless, all available studies indicate that long-term climatic changes could potentially have large effects on shorebird populations via reduced reproductive output caused by phenological mismatches if the birds do not adapt to their changed environment (see 'Can Wadden Sea birds adapt to climate change? Plasticity and evolution').
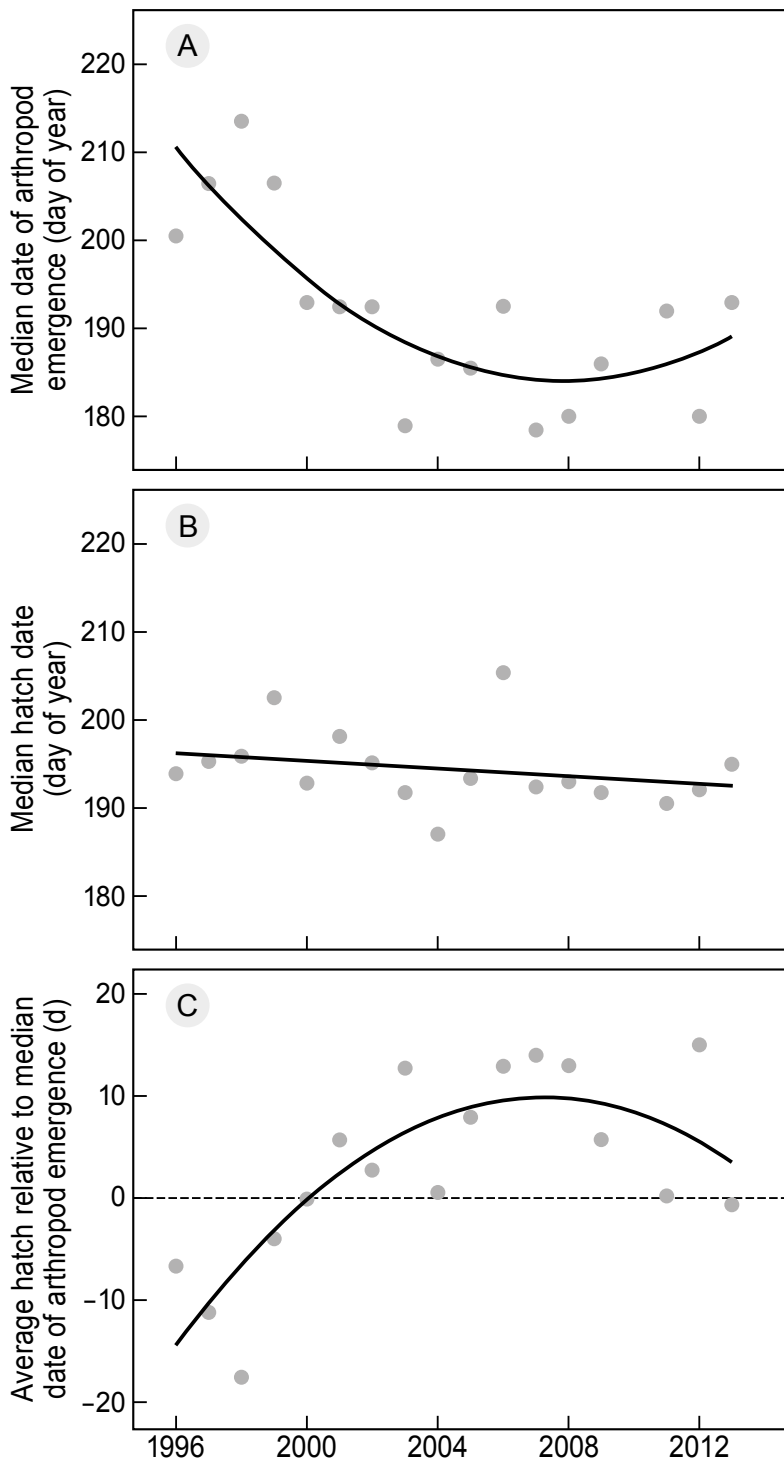
Fig. 7. *The dates of peak arthropod abundance (a), hatch dates of Sanderling Calidris alba and the resulting mismatch between both (c) in Zackenberg, Northeast Greenland, between 1996-2013. Positive values in (c) indicate average hatch dates after the peak in prey availability. Based on Reneerkens et al. 2016.*

A Sanderling Calidris alba with a complete clutch of four chicks (Zackenberg, Greenland). Photo by Jeroen Reneerkens. Late hatching chicks only suffer from an increasingly earlier appearance of insect and spiders, as a result of increasingly warmer summers, if this appearance is very peaked.

10. CAN WADDEN SEA BIRDS ADAPT TO CLIMATE CHANGE? PLASTICITY AND EVOLUTION

Given the numerous expected and shown environmental changes due to climate change, the essential question arises whether Wadden Sea birds can adapt to such changes and whether such adaptations will be sufficiently fast. Of course, this will to a large extent depend on the rate of change of temperature and accompanying climate change effects, which in turn depends on global socio-economic developments. The IPCC uses six different climate change scenarios on shorter and longer terms (IPCC 2014). Ultimately, the ability of species and ecosystems to deal with the consequences of climate change will depend on species-specific characteristics (e.g., potential for rapid adaptation, phenotypic plasticity, or dispersal capability (Parmesan 2006) in relation to the strength and speed of experienced climate change effects. This will set an upper limit to the rate of climate change that may happen without resulting in population declines or loss of biodiversity.

As explained by Visser (2008), in a changing environment, populations need to shift their distribution of phenotypes such that the average fitness for the shifted phenotypic distribution is higher than that of the original distribution when compared within the current environment. This can be achieved through micro-evolution in which the relative frequency of individuals with the best adapted genotypes in a population increases or via phenotypic plasticity, in which the genotype distribution does not change but animals exhibit non-genetic plastic responses to a changed environment. Which of these two mechanisms play the largest role in adjusting to climate change, especially in the context of changes in phenology, is subject of scientific debate, but at present it is unclear which processes explain the observed patterns of advanced phenology in birds (Charmantier and Gienapp 2014). However, clear evidence for (micro-)evolutionary adaptation to climate change is rare (Gienapp et al. 2008). Observed genetic adaptations to a warmer climate have been shown to modulate local effects of climate change, but there is little evidence that they will be sufficient to buffer negative effects at the species level (Parmesan 2006).

A current experimental study convincingly showed that a migratory passerine in a period of 21 years has shifted its endogenous circannual clock 9 days forward (Helm et al. 2019). The circannual clock, together with environmental cues, aids the timing of annual life history events, such as the onset of migration (Gwinner 1996, Åkesson et al. 2017) and has been argued to put a major constraint to phenotypical plastic responses to phenological advancements of the environment due to climate change (Åkesson et al. 2017). Thus, this study suggests that micro-evolutionary responses to climate change may help bird populations to adapt to climate change. It should be noted though that this study should not be regarded evidence for such evolutionary response because it is still unknown whether there is a genetic basis for the advancement.

In general, long-distance migratory birds, such as Wadden Sea birds, have very consistent annual patterns and do not seem to plastically respond to changes in their environment (Conklin et al. 2013). Some long-lived Wadden Sea birds, such as Spoonbills, adapt slowly to changing habitats along their flyway and take suboptimal decisions (Lok et al. 2011) . Also, many Sanderlings annually migrate to areas along the East Atlantic flyway where their fitness prospects are low (Reneerkens et al. 2020). Imperfect knowledge about alternative habitat and/or disadvantages of switching to other sites are possible explanations for such sub-optimal strategies. It has been shown that changes in strategies in next generations of individuals may explain how populations can adapt to change event though individuals within populations are conservative (Gill et al. 2014, Verhoeven et al. 2018, Tombre et al. 2019).

Whether individual plasticity, micro-evolution and/or inter-generational changes are enough to deal with the fast-changing climate change at various stages within their life cycle is hard to predict. A current meta-analysis suggests that global warming has not resulted in morphological

adjustments in animals, but that have resulted in phenological responses. Such advances have shown to be adaptive for some bird species, but imperfect as evidenced by the observed consistent selection for earlier timing (Radchuk *et al.* 2019), clearly indicating the strength of selection which climate change is forcing upon animal populations worldwide. A clear case study of how a healthy ecological state of the Wadden Sea may help Wadden Sea birds to compensate for climate change effects is provided in Box 1.

11. FROM EFFECTS ON INDIVIDUALS TO POPULATIONS. WHAT IS THE EVIDENCE THAT CLIMATE CHANGE AFFECTS POPULATIONS?

There is ample evidence that climate change importantly affects several demographic aspects in birds (Forchhammer *et al.* 1998, e.g. Visser and Both 2005) and there is a consensus that such effects of climate change will also impact reproduction and/or survival and likely will lead to changes in population size of birds (Both *et al.* 2006, Jiguet *et al.* 2010, Saino *et al.* 2011a, Knudsen *et al.* 2011). However, predicting how much and which populations will change in size because of climate change is one of the largest current challenges of ecologists (Thuiller 2007). Especially, in migratory birds, such as most Wadden Sea birds, understanding population regulation is complicated by the numerous factors involved at various stages in the annual cycle in geographically distinct areas (Newton 2004, van Oudenhove *et al.* 2014). Yet, very few studies on avian migrants have addressed how multiple factors affect population declines (Knudsen *et al.* 2011). Furthermore, the consequences of demographic aspects on changes in population sizes also depend on other processes such as density dependence and emi- and immigration (Sæther *et al.* 2000, SÆther *et al.* 2004, Sæther and Engen 2010). When birds' fitness depends on the density of the population, e.g. via competition for food, the direct effect of climate change effects, such as the consequences of a phenological mismatch, can be counteracted or enhanced by subsequent changes in the population density (Johansson *et al.* 2015). In a passerine hole-nesting bird, the Great Tit *Parus major*, for example, it has been described that during a 40-year period the increasingly warm springs created a phenological mismatch between the birds and the occurrence of their food, which lead to reduced fitness of the most mismatched individuals. However, the inter-annual variation in population mismatch did not influence population growth because the consequent smaller population resulted in a reduced competition for food (Reed *et al.* 2013a, b). Thus, it is important to consider whether effects of climate change are density-dependent or independent, if we want to understand whether climate change effects may result in changes in population size (Turchin 1995, Sæther *et al.* 2004). For Wadden Sea birds, we have no such information, but we do know that density-dependency regulates populations of geese and shorebirds (Moser 1988, Gill *et al.* 2001, Ntiamoa-Baidu *et al.* 2014) Following Sæther *et al.* (2004), another important aspect to consider when trying to understand the effects climate change may have on changes in population size is figuring out whether climate change mainly affects the reproductive success or the survival of bird species. For obvious logistical reasons, unfortunately only few studies have studied the relative contributions of different climate variables at different times of the year to temporal variation in the fluctuations in population size. Importantly, none of the studies reviewed by Sæther *et al.* (2004), included shorebirds or geese, let alone Wadden Sea birds specifically. This makes it impossible to quantify whether climate change effects have the largest influence on changes in population size via reproduction or survival, in general and on Wadden Sea birds specifically, although in general it seemed that precocial birds – such as shorebirds and geese – weather conditions during the breeding season influences annual variation in change in population size.

A relevant study on Red Knots *Calidris canutus* in the Dutch Wadden Sea, shows that low "apparent" survival (i.e. a combination of survival and site fidelity) during periods of food shortage was compensated for by higher survival during the summer period, by sequential density dependence (Rakhimberdiev *et al.* 2015). The existence of such seasonal compensation indicates that lower local survival effects in the Wadden Sea, e.g. through loss of intertidal feeding habitat, can – within certain limits – be compensated for by a relaxed competition during the summer, but only if there are density-dependent effects acting during those periods. For Red Knots these are assumed to be

more likely to take place during preparation for migration in the Wadden Sea rather than at the Arctic tundra where the birds breed in very low densities (Rakhimberdiev *et al.* 2015). It is essential to notice that (1) such compensatory effects in apparent survival can be brought about by the buffering effect of alternative nearby locations, (2) there are limits to such seasonal compensation and (3) seasonal compensation in apparent adult survival does not necessarily prevent population declines, because reproductive might still be hampered and/ or juvenile birds might have had low survival probabilities (Rakhimberdiev *et al.* 2015). Climate change will very likely negatively affect all aspects in a Wadden Sea bird's life history along its flyway (this report) and due to the global scale of it, likely equally much for connected wetlands, at least within similar regions.

For most Wadden Sea bird species our knowledge about their ecology in the (African) winter areas are insufficient to reliably predict how changing wintering conditions will affect population dynamics.

Studies on Arctic-breeding shorebirds suggested that phenological mismatches may result in population declines, but without directly linking the extent of the mismatches to the population declines (van Gils *et al.* 2016, Kwon *et al.* 2019). Within the North American Arctic, phenological mismatches between shorebirds and their prey varied geographically and two species show regional population declines in the part of their range where the mismatches were largest (Kwon *et al.* 2019). A study on *canutus* Red Knots, breeding in Siberia and wintering in West Africa, showed that in years with early snowmelt in Siberia, juvenile Red Knots at a stopover site during southward migration in Poland has shorter bills, which was suggested to be caused by food shortage due to phenological mismatches (van Gils *et al.* 2016). In their West African wintering area shorter-billed juveniles suffered from larger mortality because they could not sufficiently reach their deeply buried shellfish prey but had to rely more on the unfavourable, but shallowly buried, rhizomes of seagrass. Thus, possible climate change effects in the Arctic (van Gils *et al.* 2016) may carry-over to the non-breeding area, which complicates demographic effects at the population level in migratory Wadden Sea birds. Indeed, assessing the relative contribution of climate variables at different seasons is often impossible because effects of climate variation in a given season can affect demographic variables in later seasons (Sæther and Engen 2010). It must be clear that (the continuation of ongoing) long-term demographic studies of Wadden Sea birds that monitor all demographic aspects in relation to all relevant ecological (including climatological) variables are vital to detect which climate variables influence Wadden Sea birds and how.

One of the population-level variables that would be useful to systematically measure on an annual basis would be the number of juvenile birds appearing in a population. In geese, in which families migrate and stay together in the non-breeding ground, and in which juveniles can also in mid-winter be easily distinguished from adults, this is already systematically done and has been used to look at (indirect) climate change effects on population-level reproductive output (e.g. Nolet *et al.* 2013). For shorebirds this is more complicated for various reasons (Robinson *et al.* 2005), but a systematic field approach during a short period of the year, by many (volunteer) observers at many sites along the flyway and perhaps focused at a few key species seems a useful approach to include in ongoing monitoring schemes of demographic variables in Wadden Sea birds (Lemke *et al.* 2012).

A Red Knot Calidris canutus brooding its offspring, Zackenberg, Greenland (Photo by Jeroen Reneerkens). Climate change effects on Wadden Sea birds at the level of the individual, e.g. due to phenological mismatches occur, but it is still greatly unknown to what extent this affects their populations.

12. THE GRAND CHALLENGE – CAN WE PROTECT THE WADDEN SEA AGAINST CLIMATE CHANGE EFFECTS?
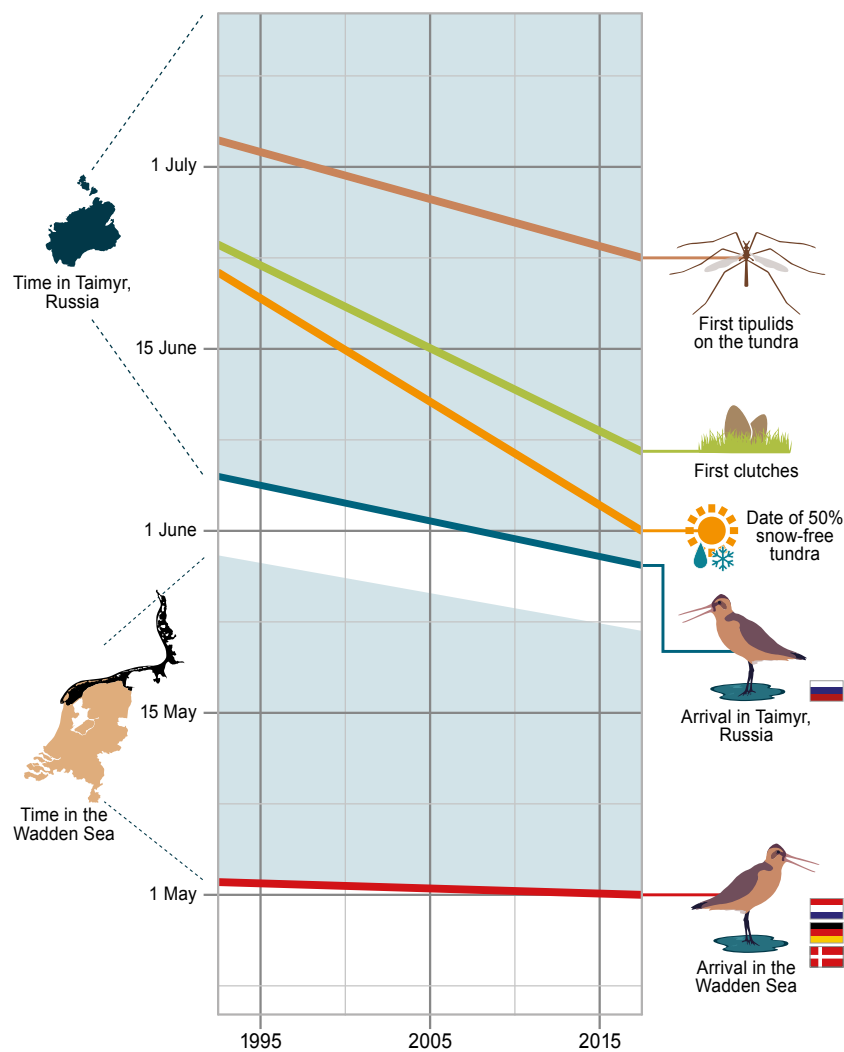
Predicted climate change scenarios may substantially threaten the integrity and future existence of some of the most biologically important ecological regions worldwide (Beaumont *et al.* 2011). Assessing the consequences of climate change for biodiversity, and how they might be mitigated, has been referred to as the "Grand Challenge in ecology" (Thuiller 2007). The aspect that is complicating as well as worrying, is that ecosystems worldwide are already exposed to substantial threats from other anthropogenic pressures, such as habitat destruction, habitat fragmentation, habitat degradation, pollution and over-harvesting. All of these threats are affecting Wadden Sea birds too (Piersma *et al.* 2001, 2016, Baker *et al.* 2004, van Gils *et al.* 2006, Laursen and Frikke 2008, Studds *et al.* 2017) in addition to the effects of climate change summarised in this report. All of these factors, including climate change, are symptoms of the excessive consumption of the wealthy human lifestyle (Ripple *et al.* 2019), which will be near-impossible to change fast enough for natural values worldwide to not increasingly suffer from.

It is of vital importance to decrease the emissions of greenhouse gases as fast as possible to zero (Ripple *et al.* 2019) However, we can not instantly stop climate change, even if we were to stop the global emissions of greenhouse gases today (Wetherald *et al.* 2001). Thus, mitigation is the most effective approach for policymakers, landowners and conservationists is mitigation to allow the Wadden Sea ecosystem to adjust to all the (expected) effects of climate change (see Box 1). A healthy state of the Wadden Sea ecosystem will make it easier for Wadden Sea birds to adapt to ongoing changes. That implies no more (over-)exploitation of shellfish, shrimp, lugworm and fish, no hunting, no extraction of gas and salt and maximally limit human disturbance of birds especially at high tide roosts, especially if this has scientifically been proven to negatively Wadden Sea bird populations. While all of these measures –from a conservationists point of view- will already be obvious and considered urgent, ongoing climate change makes such protection measures even more urgent if we are to conserve the natural values of the Wadden Sea and its international key function for the well-being of global flyway populations.

If there is a large probability of losing intertidal mudflats due to sea level rise, we will need to assess whether giving the Wadden Sea space inland, while keeping the human population safe against floods (e.g. by using flood barriers as in the Oosterschelde) will be an effective measure.

A warmer climate will impact human behaviour too. When the Mediterrenean area becomes uncomfortably hot in early spring and summer, with an increased probability of long-lasting and more severe heatwaves (Zampieri *et al.* 2009), the Wadden Sea area, especially now that it has received the UNESCO status of World Heritage, may become even more attractive for visiting tourists, putting an even larger pressure on the possibilities for birds to rest their high tide roosts.

Figure showing phenological trends for Bar-tailed Godwits. Y-axis dates from 1 May to 1 July; X-axis years 1995, 2005, 2015. Labels: First tipulids on the tundra; First clutches; Date of 50% snow-free tundra; Arrival in Taimyr, Russia; Arrival in the Wadden Sea. Side labels: Time in Taimyr, Russia; Time in the Wadden Sea.

Box 1. Fuelling conditions in the Wadden Sea can mitigate Arctic warming effects in Bar-tailed godwits *Limosa lapponica*

Bar-tailed Godwits are faced with advancement of their arthropod prey (in this case tipulidae) due to earlier snow melt. For the chicks to profit from maximal prey abundance during their growth (i.e. to avoid phenological mismatches) they thus need to similarly advance the laying of their eggs. This can only be achieved by earlier arrival from their tropical wintering grounds in tropical West Africa (the Banc d'Arguin or the Bijagós archipellago). They can do so by a faster migration, possibly at the cost of reduced survival. The birds hardly advanced departure from West Africa but reduced their time in the Wadden Sea to refuel. They compensated for the reduced refuelling time by increasing refuelling rates, but these rates were insufficient in years when lugworm abundance was low. In such years, godwits left the Wadden Sea with lower body stores that compromised their subsequent survival probability. Or, in other words, shortening their refuelling period in the Wadden Sea (and consequent timely arrival on their breeding grounds) came at the cost of lower survival, especially in years when lugworm densities in the Wadden Sea were low.

Thus, conditions such as food availability and human disturbance in the Wadden Sea determine the ability of Bar-tailed godwits to cope with climate-related changes in the Arctic (Rakhimberdiev *et al.* 2018) .

Copied from Piersma (2019).

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Table 1 *List of publications that show fitness effects of Arctic breeding geese, ducks and shorebirds. For each record, the reference to the publication is given, whether it concerned an observational study or a model (Obs/Mod), the species, region, flyway, during which years the study was conducted, whether the effect was positive or negative, via which factor the effect was expected or shown to cause the effect, what was measured/determined for the bird and when and where and which climate variable was measured/determined and when and where.*

1st_author	year	Obs/Mod	species	region	fly-way	years	effect	via	bird_what	bird_when	bird_where	factor	climate_what	climate_when	climate_where
Anderson *et al.* 2015	2015	Obs	Pink-footed goose	Svalbard	EAF	2003 - 2007; 2010 - 2014	positive	nesting propensity				less snow-cover			
Anderson *et al.* 2015	2015	Obs	Pink-footed goose	Svalbard	EAF	2003 - 2007; 2010 - 2014	positive	Nest success				less snow-cover			
Aubry *et al.* 2013	2013	Obs	Lesser snow goose	Southern Hudson Bay, Canada	AF	1978 - 2005	negative	*juvenile body mass*	body mass	pre-fledge	breeding grounds	winter and summer temperatures breeding grounds	tempera-ture	year	breeding grounds
Aubry *et al.* 2013	2013	Obs	Lesser snow goose	Southern Hudson Bay, Canada	AF	1978 - 2005	positive	*juvenile body mass*	body mass	pre-fledge	breeding grounds	positive growing degree days in spring	tempera-ture	spring	breeding grounds
Barshep *et al.* 2012	2012	Obs	Curlew Sandpiper	Poland	EAF	1984 - 2000	negative	*number of juveniles on stopover*	propor-tion	juvenile	stopover	June temperature breeding grounds	tempera-ture	June	breeding grounds
Brook *et al.* 2015	2015	Obs	Canada goose	Southern Hudson Bay, Canada	AF	1993 - 2010	negative	chick growth rate				mismatch with food peak grass or NDVI)			
Clausen and Clausen 2013	2013	Obs	Brent Goose	Denmark	EAF	1989 - 2012	negative	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	delay in migration timing (based on spring departure)	delay migration	spring	breeding grounds

Clausen and Clausen 2013	2013	Obs	Brent Goose	Denmark	EAF	1989 - 2012	positive	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	date of snow melt breeding grounds	snow melt	summer	breeding grounds
Cleasby *et al.* 2017	2017	Obs	Brent Goose	Ireland	EAF	2003 - 2014	negative	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	June Northern Atlantic Oscilation Index	NAO	June	breeding grounds
Cleasby *et al.* 2017	2017	Obs	Brent Goose	Ireland	EAF	2003 - 2014	positive	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	June Northern Atlantic Oscilation Index	NAO	June	breeding grounds
Cleasby *et al.* 2017	2017	Obs	Brent goose	Ireland	EAF	2003 - 2014	positive	Female surival				June NAO			
Cleasby *et al.* 2017	2017	Obs	Brent goose	Ireland	EAF	2003 - 2014	negative	number of juveniles in wintering grounds				June NAO			
Dickey *et al.* 2008	2008	Obs	Greater snow goose	Bylot Isl., Canada	AF	1989 - 2004	positive	*breeding propensity*	breeding propen-sity	nest	breeding grounds	Higher spring temperatures (and lower snow cover)	tempera-ture	spring	breeding grounds
Dickey *et al.* 2008	2008	Obs	Greater snow goose	Bylot Isl., Canada	AF	1989 - 2004	negative	*ratio young:adult*	propor-tion	pre-fledge	breeding grounds	Extreme high or low NAO	NAO	spring	wintering grounds
Dickey *et al.* 2008	2008	Obs	Greater snow goose	Bylot Isl., Canada	AF	1989 - 2004	negative	*juvenile body mass*	body mass	pre-fledge	breeding grounds	Higher spring temperatures	tempera-ture	spring	breeding grounds
Doiron *et al.* 2015	2015	Obs	Greater snow goose	Bylot Isl., Canada	AF	1991 - 2010	negative	*juvenile body mass and size*	body mass	pre-fledge	breeding grounds	Earlier date of peak nitrogen / mismatch	food peak mismatch	summer	breeding grounds
Drever and Clark 2007	2007	Obs	Northern Pintail	Saskatche-wan, Canada	AF	1980 - 2000	negative	nest success				higher spring temperatures			
Drever *et al.* 2012	2012	Obs	Melanitta species	Canada	AF	1972 - 2008	negative	population trend				duration of snow cover in spring			
Hartman *et al.* 2013	2013	Obs	Velvet Sco-ter	Baltic Sea	EAF	1977 - 2007	positive	population trend				winter NAO			

Iles *et al.* 2018	2018	Obs	Lesser snow goose	Southern Hudson Bay, Canada	AF	1990 - 2015	positive	*juvenile percentage moulting flocks*	proportion	pre-fledge	breeding grounds	summer temperature	temperature	summer	breeding grounds
Jensen *et al.* 2014	2014	Obs	Pink-footed goose	Denmark	EAF	1981 - 2011	positive	*juvenile percentage wintering grounds*	proportion	juvenile	wintering grounds	earlier snowmelt	snowmelt	spring	breeding grounds
Jensen *et al.* 2014	2014	Obs	Pink-footed goose	Denmark	EAF	1981 - 2011	positive	*juvenile percentage wintering grounds*	proportion	juvenile	wintering grounds	more thaw days	temperature	summer	breeding grounds
Jensen *et al.* 2014	2008	Mod	Pink-footed goose	Svalbard	EAF		positive	*nesting habitat*	change in cover	habitat	breeding grounds	Increased temperature	temperature	summer	breeding grounds
Kéry *et al.* 2006	2006	Obs	Pink-footed goose	Denmark	EAF	1989 - 2003	positive	adult survival				warm, wet winters and early springs staging sites			
Lameris *et al.* 2018	2018	Obs	Barnacle goose	NW-Russia	EAF	2003 - 2009; 2014 - 2015	negative	*juvenile survival*	survival	pre-fledge	breeding grounds	earlier snowmelt (incurring earlier peak nitrogen)	snowmelt	spring	breeding grounds
Lameris *et al.* 2017	2017	Mod	Barnacle goose	NW-Russia	EAF		negative	*reproductive success*	proportion	juveniles	breeding grounds	warmer spring temperatures	temperature	spring	breeding grounds
Lecomte *et al.* 2009	2009	Obs	Snow goose	Bylot Island, Canada	AF	1995 - 2005	positive	Nest success				more rainfall			
Lehikoinen *et al.* 2013	2013	Obs	Long-tailed Duck	Finnish Lapland	EAF	2005 - 2015	negative	*population trend*	trend	population	breeding grounds	more rainfall previous season	rainfall	summer	breeding grounds
Nolet *et al.* 2013	2013	Obs	Brent Goose	Netherlands	EAF	1955 - 2010	positive	*number of juveniles at wintering site*	proportion	juvenile	wintering grounds	onset of spring in breeding grounds	temperature	spring	breeding grounds
Nolet *et al.* 2013	2013	Obs	Brent Goose	Netherlands	EAF	1955 - 2010	negative	*number of juveniles at wintering site*	proportion	juvenile	wintering grounds	higher number of lemmings	rodents	summer	breeding grounds
van Ouden-hove *et al.* 2014	2014	Obs	Greater snow goose	Bylot Isl., Canada	AF	1989 - 2011	positive	*clutch size*	clutch size	nest	breeding grounds	spring temperature	temperature	spring	breeding grounds

van Ouden-hove *et al.* 2014	2014	Obs	Greater snow goose	Bylot Isl., Canada	AF	1989 - 2011	positive	*hatching probablility*	hatching proba-blility	nest	breeding grounds	spring temperature	tempera-ture	spring	breeding grounds
van Ouden-hove *et al.* 2014	2014	Obs	Greater snow goose	Bylot Isl., Canada	AF	1989 - 2011	negative	*breeding propensity*	breeding propen-sity	nest	breeding grounds	spring temperature	tempera-ture	spring	breeding grounds
van Ouden-hove *et al.* 2014	2014	Obs	Greater snow goose	Bylot Isl., Canada	AF	1989 - 2011	negative	*recruitment probability*	recruit-ment	juvenile	breeding grounds	temperatures during winter and migration period	tempera-ture	winter	wintering grounds
Pöysä and Väänänen 2018	2018	Obs	Eurasian Wigeon	Finland	EAF	1978 - 2015	no	number of juveniles shot in winter				Summer temperature breeding grounds			
Ross *et al.* 2017	2017	Obs	Lesser snow goose	Canada central Arctic	AF	1997 - 2014	negative	*juvenile percentage moulting flocks*	propor-tion	pre-fledge	breeding grounds	mismatch with food peak	food peak	mismatch	breeding grounds
Ross *et al.* 2017	2017	Obs	Ross goose	Canada central Arctic	AF	1997 - 2014	negative	*juvenile percentage moulting flocks*	propor-tion	pre-fledge	breeding grounds	mismatch with food peak	food peak	mismatch	breeding grounds
Ross *et al.* 2015	2015	Obs	Greater Scaup	Canada	AF	1968 - 2010	negative	population trend				lower snow cover in winter and spring			
Schmidt *et al.* 2011	2011	Obs	Trumpeter Swan	Alaska	AF	1968 - 2005	positive	number of occupied grid cells				more days with tempera-tures above freezing			
Sedinger *et al.* 2006	2006	Obs	Brent goose	Alaska	AF	1985 - 2000	negative	breeding propensity				higher Sea Surface Temperature wintering grounds			
Trinder *et al.* 2009	2009	Obs	Barnacle goose	Scotland	EAF	1960 - 2000	positive	*proportion juveniles wintering*	propor-tion	juvenile	wintering grounds	temperature breeding grounds (Svalbard) in summer	tempera-ture	summer	breeding grounds
Trinder *et al.* 2009	2009	Obs	Barnacle Geese	Scotland, UK	EAF	1960 - 2001	positive	number of juveniles in wintering grounds				temperature breeding grounds (Svalbard)			

Trinder *et al.* 2009	2009	Obs	Barnacle Geese	Scotland, UK	EAF	1960 - 2001	positive	number of juveniles in wintering grounds				temperature wintering grounds			
[281]	2000	Obs	Greater white-front-ed goose	Germany, Netherlands	EAF	1947 - 1995	positive	*juvenile percentage*	propor-tion	juvenile	wintering grounds	June tem-perature breeding grounds	tempera-ture	summer	breeding grounds
Zöckler and Lysenko 2000	2000	Obs	Greater white-front-ed goose	UK	EAF	1962 - 1995	positive	*juvenile percentage*	propor-tion	juvenile	wintering grounds	June tem-perature breeding grounds	tempera-ture	summer	breeding grounds
Aharon-Rot-man *et al.* 2015	2015	Obs	Curlew Sandpiper	Australia	EAAF	1980 - 2012	positive	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	June tem-perature breeding grounds	tempera-ture	June	breeding grounds
Aharon-Rot-man *et al.* 2015	2015	Obs	Ruddy Turn-stone	Australia	EAAF	1980 - 2012	positive	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	July tempera-ture breeding grounds	tempera-ture	July	breeding grounds
Aharon-Rot-man *et al.* 2015	2015	Obs	Red-necked Stint	Australia	EAAF	1980 - 2012	positive	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	May tem-perature breeding grounds	tempera-ture	May	breeding grounds
Aharon-Rot-man *et al.* 2015	2015	Obs	Sharp-tailed Sandpiper	Australia	EAAF	1980 - 2012	no	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds		tempera-ture		
Aharon-Rot-man *et al.* 2015	2015	Obs	Red Knot	Australia	EAAF	1980 - 2012	no	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds		tempera-ture		
Aharon-Rot-man *et al.* 2015	2015	Obs	Bar-tailed Godwit	Australia	EAAF	1980 - 2012	positive	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	July tempera-ture breeding grounds	tempera-ture	July	breeding grounds
Aharon-Rot-man *et al.* 2015	2015	Obs	Curlew Sandpiper	Sweden	EAF	1945 - 2008	negative	*juvenile percentage wintering grounds*	propor-tion	juvenile	wintering grounds	predation index (Tom-kovich *et al.*)	predation index	summer	breeding grounds

Ballantyne and Nol 2015	2015	Obs	Whimbrel	Southern Hudson Bay, Canada	AF	1973 - 2006	negative	*breeding pairs*	breeding propensity	nest	breeding grounds	vegetation change (increase shrubs and trees)	vegetation change	year	breeding grounds
Beale *et al.* 2006	2006	Obs	Dunlin	North Wales, UK	EAF	1970 - 2004	positive	number of juveniles in wintering grounds				temperature at breeding grounds (hightes recruitment under intermediate temp)			
Beale *et al.* 2006	2006	Obs	Dunlin	North Wales, UK	EAF	1970 - 2004	no	number of juveniles in wintering grounds				rainfall breeding grounds			
Carroll *et al.* 2015	2015	Mod	Eurasian Golden plover	UK	EAF		negative	*population trend*	trend	population	breeding grounds	food abundance via water level (drought)	temperature	summer	breeding grounds
Forchhammer *et al.* 2008	2008	Obs	Common Ringed Plover	East Greenland	EAF	1996 - 2005	no	*territories*		population	breeding grounds	snow melt	snowmelt	summer	breeding grounds
Forchhammer *et al.* 2008	2008	Obs	Sanderling	East Greenland	EAF	1996 - 2005	no	*territories*		population	breeding grounds	snow melt	snowmelt	summer	breeding grounds
Forchhammer *et al.* 2008	2008	Obs	Red Knot	East Greenland	EAF	1996 - 2005	no	*territories*		population	breeding grounds	snow melt	snowmelt	summer	breeding grounds
Forchhammer *et al.* 2008	2008	Obs	Dunlin	East Greenland	EAF	1996 - 2005	no	*territories*		population	breeding grounds	snow melt	snowmelt	summer	breeding grounds
Forchhammer *et al.* 2008	2008	Obs	Ruddy Turnstone	East Greenland	EAF	1996 - 2005	no	*territories*		population	breeding grounds	snow melt	snowmelt	summer	breeding grounds
Forchhammer *et al.* 2008	2008	Obs	Long-tailed Skua	East Greenland	EAF	1996 - 2005	no	*territories*		population	breeding grounds	snow melt	snowmelt	summer	breeding grounds
Fuller *et al.* 2008	2008	Mod	Sanderling	Great Arctic Reserve, USA	AF	2004	negative	*breeding habitat*	change in cover	habitat	breeding grounds	climate warming (A2 scenario, IPCC 2007)	temperature	year	breeding grounds

Fuller *et al.* 2008	2008	Mod	Dunlin	Great Arctic Reserve, USA	AF	2004	negative	*breeding habitat*	change in cover	habitat	breeding grounds	climate warming (A2 scenario, IPCC 2007)	tempera-ture	year	breeding grounds
Fuller *et al.* 2008	2008	Mod	Whimbrel	Great Arctic Reserve, USA	AF	2004	negative	*breeding habitat*	change in cover	habitat	breeding grounds	climate warming (A2 scenario, IPCC 2007)	tempera-ture	year	breeding grounds
Fuller *et al.* 2008	2008	Mod	American Golden Plover	Great Arctic Reserve, USA	AF	2004	negative	*breeding habitat*	change in cover	habitat	breeding grounds	climate warming (A2 scenario, IPCC 2007)	tempera-ture	year	breeding grounds
Fuller *et al.* 2008	2008	Mod	Red-necked Phalarope	Great Arctic Reserve, USA	AF	2004	negative	*breeding habitat*	change in cover	habitat	breeding grounds	climate warming (A2 scenario, IPCC 2007)	tempera-ture	year	breeding grounds
Jehl 2007	2007	Obs	Semipal-mated Sandpiper	Southern Hudson Bay, Can-ada	AF	1940 - 2001	no	population trend				climate change			
Kwon *et al.* 2018	2018	Obs	Western Sandpiper	Alaska	AF	1993 - 1996; 2010 - 2014	no	*clutch size*	clutch size	nest	breeding grounds	colder pre-laying period	tempera-ture	spring	breeding grounds
Kwon *et al.* 2018	2018	Obs	Semipal-mated Sandpiper	Alaska	AF	1993 - 1996; 2010 - 2014	no	*clutch size*	clutch size	nest	breeding grounds	colder pre-laying period	tempera-ture	spring	breeding grounds
Kwon *et al.* 2018	2018	Obs	Red-necked Phalarope	Alaska	AF	1993 - 1996; 2010 - 2014	no	*clutch size*	clutch size	nest	breeding grounds	colder pre-laying period	tempera-ture	spring	breeding grounds
Kwon *et al.* 2018	2018	Obs	Western Sandpiper	Alaska	AF	1993 - 1996; 2010 - 2014	no	*nest survival*	survival	nest	breeding grounds	colder pre-laying period	tempera-ture	spring	breeding grounds
Kwon *et al.* 2018	2018	Obs	Semipal-mated Sandpiper	Alaska	AF	1993 - 1996; 2010 - 2014	no	*nest survival*	survival	nest	breeding grounds	colder pre-laying period	tempera-ture	spring	breeding grounds
Kwon *et al.* 2018	2018	Obs	Red-necked Phalarope	Alaska	AF	1993 - 1996; 2010 - 2014	no	*nest survival*	survival	nest	breeding grounds	colder pre-laying period	tempera-ture	spring	breeding grounds
Lehikoinen *et al.* 2016	2016	Obs	Ringed plover	Finnish Lapland	EAF	2005 - 2015	negative	*population trend*	trend	popula-tion	breeding grounds	less rodents present	rodents	summer	breeding grounds
Lehikoinen *et al.* 2016	2016	Obs	Temminck's Stint	Finnish Lapland	EAF	2005 - 2015	negative	*population trend*	trend	popula-tion	breeding grounds	less rodents present	rodents	summer	breeding grounds

Reference	Year	Type	Species	Location	Flyway	Period	Direction	Response	Category	Stage	Grounds	Driver	Driver short	Season	Driver location
Lehikoinen *et al.* 2016	2016	Obs	Dunlin	Finnish Lapland	EAF	2005 - 2015	negative	*population trend*	trend	population	breeding grounds	less rodents present	rodents	summer	breeding grounds
Lehikoinen *et al.* 2016	2016	Obs	Red-necked phalarope	Finnish Lapland	EAF	2005 - 2015	negative	*population trend*	trend	population	breeding grounds	less rodents present	rodents	summer	breeding grounds
Machín *et al.* 2018	2018	Obs	Eurasian Golden plover	Sweden	EAF	2011 & 2013	no	*chick growth rate*	growth rate	juvenile	breeding grounds	mismatch with food peak	food peak	summer	breeding grounds
McKinnon *et al.* 2012	2012	Obs	Bairds Sandpiper	Bylot Isl., Canada	AF	2005 - 2008	negative	*chick growth rate*	growth rate	juvenile	breeding grounds	mismatch with food peak Tipulids	food peak	summer	breeding grounds
McKinnon *et al.* 2012	2013	Obs	Dunlin	Southern Hudson Bay, Canada	AF	2010-2011	positive	*chick growth rate*	growth rate	pre-fledge	breeding grounds	summer temperature	temperature	summer	breeding grounds
McKinnon *et al.* 2012	2012	Obs	Bairds Sandpiper	Bylot Island, Canada	AF	2006 - 2008	negative	chick growth rate				mismatch with food peak (insects)			
Murray *et al.* 2018	2018	Obs	Bar-tailed Godwit	North-Western Australia	EAAF	1995 - 2012	positive	*population trend*	trend	population	wintering grounds	temperature	temperature	summer	breeding grounds
Murray *et al.* 2018	2018	Obs	Bar-tailed Godwit	East Australia - New Zealand	EAAF	1995 - 2012	no	*population trend*	trend	population	wintering grounds	temperature	temperature	summer	breeding grounds
Pearce-Higgins *et al.* 2010	2010	Obs	Eurasian Golden plover	UK	EAF	1972 - 2005	negative	*population trend*	trend	population	breeding grounds	abundance of food Tipulids	food peak	summer	breeding grounds
Pearce-Higgins *et al.* 2010	2010	Obs	Eurasian Golden plover	UK	EAF	1988, 1996–98	negative	*reproductive success*	proportion	juveniles	breeding grounds	abundance of food Tipulids	food peak	summer	breeding grounds
Rakhimberdiev *et al.* 2018	2018	Obs	Bar-tailed Godwit	Mauritania	EAF	2003 - 2016	negative	*population trend*	trend	population	wintering grounds	snowmelt via shorter refuelling time!!!	snowmelt	summer	breeding grounds
Reneerkens *et al.* 2016	2016	Obs	Sanderling	East Greenland	EAF	2007 - 2013	no	*chick growth rate*	growth rate	pre-fledge	breeding grounds	mismatch with food peak	food peak	mismatch	breeding grounds
Reneerkens *et al.* 2016	2016	Obs	Sanderling	East Greenland	EAF	2007 - 2013	negative	*chick growth rate*	growth rate	pre-fledge	breeding grounds	width of food peak	food peak	width	breeding grounds
Ryan *et al.* 2016	2016	Obs	Dunlin	North Wales	EAF	1990 - 2011	positive	juvenile survival				more rainfall			
Ryan *et al.* 2016	2016	Obs	Dunlin	North Wales	EAF	1990 - 2011	no	Adult survival				more rainfall			

Ryan *et al.* 2016	2016	Obs	Dunlin	North Wales	EAF	1990 - 2011	positive	juvenile survival				less frost days			
Senner *et al.* 2016	2016	Obs	Hudsonian Godwit	Southern Hudson Bay, Canada	AF	2009 - 2011	negative	*growth rate*	growth rate	juvenile	breeding grounds	mismatch with food peak	food peak	summer	breeding grounds
Senner *et al.* 2016	2016	Obs	Red Knot	Poland	EAF	1984 - 2015	negative	juvenile body size				earlier snowmelt			
Senner *et al.* 2016	2016	Obs	Red Knot	Mauritania	EAF	1984 - 2015	negative	juvenile survival				earlier snowmelt			
Weiser *et al.* 2018b	2018	Obs	Western Sandpiper	Arctic		2010 - 2014	positive	*probabillity of laying full clutch*	clutch size	nest	breeding grounds	earlier snowmelt	snowmelt	spring	breeding grounds
Weiser *et al.* 2018b	2018	Obs	Western Sandpiper	Arctic		2010 - 2014	positive	*probabillity of laying full clutch*	clutch size	nest	breeding grounds	higher temperatures	temperature	summer	breeding grounds
Weiser *et al.* 2018b	2018	Obs	Red-necked Phalarope	Arctic		2010 - 2014	positive	*probabillity of laying full clutch*	clutch size	nest	breeding grounds	higher temperatures	temperature	summer	breeding grounds
Weiser *et al.* 2018b	2018	Obs	Western Sandpiper	Arctic		2010 - 2014	positive	*daily nest survival*	survival	nest	breeding grounds	higher temperatures	temperature	summer	breeding grounds
Weiser *et al.* 2018b	2018	Obs	Semipalmated Sandpiper	Arctic		2010 - 2014	positive	*daily nest survival*	survival	nest	breeding grounds	higher temperatures	temperature	summer	breeding grounds
Weiser *et al.* 2018b	2018	Obs	other shorebirds in ASDN	Arctic		2010 - 2014	no	*reproductive success*	proportion	prefledge	breeding grounds	higher temperatures	temperature	summer	breeding grounds
Weiser *et al.* 2018a	2018	Obs	American Golden Plover	Nome, Alaska	AF	2010 - 2014	no	adult survival				earlier springs			
Weiser *et al.* 2018a	2018	Obs	Dunlin	Nome, Alaska	AF	2010 - 2014	no	adult survival				earlier springs			
Weiser *et al.* 2018a	2018	Obs	Semipalmated Sandpiper	Nome, Alaska	AF	2010 - 2014	no	adult survival				earlier springs			
Weiser *et al.* 2018a	2018	Obs	Western Sandpiper	Nome, Alaska	AF	2010 - 2014	no	adult survival				earlier springs			
Weiser *et al.* 2018a	2018	Obs	Red-necked Phalarope	Nome, Alaska	AF	2010 - 2014	no	adult survival				earlier springs			

Weiser *et al.* 2018a	2018	Obs	Red Phala-rope	Nome, Alaska	AF	2010 - 2014	no	adult sur-vival				earlier springs			
Weiser *et al.* 2018a	2000	Obs	Red Knot	England	EAF	1971 - 1986	positive	*juvenile percentage*	propor-tion	juvenile	wintering grounds	may tem-perature breeding grounds	tempera-ture	summer	breeding grounds
Weiser *et al.* 2018a	2000	Obs	Red Knot	South Africa	EAF	1971 - 1986	negative	*juvenile percentage*	propor-tion	juvenile	wintering grounds	may tem-perature breeding grounds	tempera-ture	summer	breeding grounds
Weiser *et al.* 2018a	2000	Obs	Curlew Sandpiper	England	EAF	1969 - 1994	negative	*juvenile percentage*	propor-tion	juvenile	wintering grounds	may tem-perature breeding grounds	tempera-ture	summer	breeding grounds
Weiser *et al.* 2018a	2000	Obs	Red Knot	South Africa	EAF	1969 - 1994	positive	*juvenile percentage*	propor-tion	juvenile	wintering grounds	June tem-perature breeding grounds	tempera-ture	summer	breeding grounds