

Drivers of productivity in a subarctic seabird: Arctic Terns in Iceland



Freydís Vigfúsdóttir

**A thesis submitted for the degree of Doctor of Philosophy.
School of Biological Sciences
University of East Anglia, UK**

December 2012

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*To Rósa Sigurjónsdóttir,
my Mum,*

*...for never ending encouragement,
enthusiasm and
love*

Thesis abstract

Marine ecosystems are changing rapidly in response to anthropogenic and environmental stresses, and seabird populations that depend on marine resources are in decline in many areas of the world. Iceland supports internationally important populations of many seabird species and, although fishing pressures in Icelandic waters are relatively low, the impacts of current climatic and oceanic changes are predicted to be particularly severe at high latitudes, including Iceland. However, little is known about the current status and demography of Icelandic seabird populations. In this thesis, I explore the breeding demography of Arctic Terns, *Sterna paradisaea*, at colonies throughout the W and NE of Iceland, between 2008 and 2011. Although Arctic Tern productivity varied among colonies, it was generally low in both regions, primarily because of very low chick survival rates. Low chick survival was primarily a consequence of low growth rates throughout the pre-fledging period, and the application of forensic ecology techniques showed that chick mortality occurred throughout each breeding season and at all ages. Prey composition and prey delivery rates varied regionally and among colonies. The main high quality marine prey are sandeels, *Ammodytes* spp., in W-Iceland and capelin, *Mallotus villosus*, in NE-Iceland, but non-marine prey of low nutritive value comprised a large proportion of chick diet in both regions. While productivity in W-Iceland increased with prey delivery rates, in NE-Iceland prey delivery was either inconsistent or low in quality, and productivity was always low. A suite of changes in marine prey communities appears to be impacting Icelandic Arctic Terns. These may include fishing impacts on capelin abundance and/or oceanic and climatic influences on the abundance and availability of sandeels, which are not fished in Iceland. These changes may also be impacting other seabird species in Iceland, for which there is also some evidence of recent low productivity.

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Acknowledgements

It has been almost four years since my days in Norwich began and the Arctic Tern project was initiated and many people I would like to thank.

Firstly, I'm proud and honoured to be able to thank my supervisor and good friend Jenny Gill. It has truly been an educational journey, both academically as well as in school of life and I cannot think of anyone who would have guided me better through these now almost four years of educational fun. Among many things, one thing I will always remember you taught me Jenny – is that science is fun and it's totally possible to talk science in a meeting communicated entirely through laughter. My co-supervisors Tomas G. Gunnarsson, Director of South Iceland Research Centre and Gudmundur A. Gudmundsson, at the Icelandic Institute of Natural History, have both stood by me and guided me through bitter and worse and without their guidance I would not be the same person today. In particular, towards the end of my writing up their scientific input and supervision was invaluable. It is truly a privilege for a student like me to get supervision like this team has proven to provide.

Additionally, back in land of fire and ice, where to I migrated every summer to chase fluffy things and collect death, many colleagues provided insight and help that were essential for this project to happen. Firstly, Jon Einar Jonsson, Director of University of Iceland's Snæfellsnes Research Centre, was extremely resourceful and helpful at many of the practical issues a field study like this one faces. Without your help this study would not have been the same. My colleagues at the Icelandic Institute of Natural History have nurtured me from the very start of my ornithological upbringing. In particular I would like to thank Kristinn Haukur Skarphedinsson for his insightful comments and incredibly helpful honesty when ever constructive criticism was needed. Olafur Karl Nielsen is one of the finest scientists I have worked with and always had good words of wisdom to share. Additionally, Erling Olafsson, entomologist at the Icelandic Institute of Natural History gets special thanks for assistance on insect information and species identification on non-feathered flying things. Kristjan Lilliendahl at the Icelandic Marine Research Institute gets many thanks for seabird research guidance through the years. Last but not least Professor Emeritus Arnthor Gardarsson, who has been an inspiration and a mentor through all my years of higher education.

Many friends and colleagues at the University of Iceland have followed me through this journey. I want to thank in particular for friendship and academic companionship: Gunnar Hallgrímsson, Yann Kolbeinsson and Halfdan H. Helgason.

I want specially thank the numerous field workers that helped out in the field. In particular these people who gave a considerable amount of their time for this study: For helping out in 2008: Livia Bentson, in 2009: Karen Jordan, Cat Morrison, Jonas P.

Jonasson, in 2010: Jon Einar Jonsson (also assisted in 2009), Hen Bellman, Steinunn Guðmundsdóttir, Karl Phillips (also joined in 2011), David Showler, Rosa Sigurjonsdottir (also helped in 2009), Birgitta Stefánsdóttir, and in 2011: Rebecca Laidlaw, Harry Charnock, Richard Hillard that all joined for a journey to the worlds' end (really!), while Ellen Magnúsdóttir guarded the snow mountain peninsula. Without your help this would never have reached this stage – and definitely not been as much fun!

Local farmers and landowners get special thanks for local information and logistic support in the field. In particular on Snaefellsnes peninsula: Sæmundur Kristjánsson, Sævar Friðbjófsen and Smári Lúðvíksson at Rif, Svava Svandís Guðmundsdóttir at Langaholt and Hafdís and Geir at Bjarg at Arnarstapi. On Melrakkasletta, Haraldur Sigurdsson and his family at Núpsskatla get many thanks for local support and for housing us at their farm just below the Arctic Circle. Additionally, Gudmundur Orm at Kopasker, who provided local information and helped us collecting the final data (dead stuff) towards the end in the NE field site.

The Icelandic Institute of Natural History and the University of Iceland's Snaefellsnes Research Centre were my case partners through this study. Their support, logistically and academically was invaluable and a great experience. Many people at these institutes were greatly helpful in various aspects of this study. Heida gets special thanks for data input. We thank the Icelandic Meteorology Office for kindly providing data on weather.

Many thanks to Norman Ratcliffe, Francis Daunt, Carsten Egevang, Ævar Petersen and Martin Perrow for various pointers on fieldwork practicalities and general tern-advice.

My dear friends and colleagues at UEA. So many great people have been there for me as friends and colleagues. I want to thank my office mates, Aly, Matt, Elli, Lewis, Anna, and James, for great fun and specially their support and tea-chocolate-biscuit-bringing manor during my writing up. My housemate and friend Eveliina I want to thank for being super great friend. The girls in stitch n' bitch – thanks for great fun and friendships through the years. Becky and Leila thanks and woop woop. Danielle Peruffo and Amanda Bretman get special thanks for being great friends – friends indeed!

Finally, friends and family back home. My parents who have always stood by me, my sister Sóley and her wonderful family, my brothers and all extended ends of my family have all been helpful through every stage of this journey.

This study was supported by Icelandic Research Fund of Graduate Students, the British Chevening Scholarship, University of East Anglia, BOU: British Ornithologists' Union, the Richard Warn Memorial Fund, John and Pamela Salter Charitable Trust, the Icelandic Innovation Fund and Palmi Jonssons' Fund of Nature Conservation

Takk fyrir!

Team tern...

Supervisors



Field assistants and volunteers



Chapter 1

Chapter 1

General Introduction

Drivers of productivity in avian populations

Understanding the mechanisms driving the responses of species to environmental change can greatly enhance our ability to predict the consequences of future changes and develop appropriate policy responses. Identification of the impacts of environmental change on species and populations is needed in order to design appropriate strategies and actions for their conservation, and to use species responses to indicate potential wider community and ecosystem responses. Large-scale biological responses to climatic variability and global climate change have been observed to be particularly pronounced in marine ecosystems (Harley *et al.* 2006). As a result of past changes in air temperatures, ocean temperatures have risen in recent decades (Belkin 2009; Burrows *et al.* 2011), and this warming trend is amplified toward polar regions (Serreze *et al.* 2007; Graversen *et al.* 2008). Further ocean warming, along with other predicted physical changes such as sea level rise and declines in the extent of sea ice, are expected to have persistent and intensified effects on marine ecosystems in the future (Stenseth *et al.* 2002). For seabird populations that depend upon marine ecosystems, changes in the distribution of prey can have direct effects through changes in bottom-up food web dynamics (Ware and Thomson 2005), as seabird population trends are strongly influenced by variation in prey abundance (Veit *et al.* 1996; Montevercchi and Myers 1997; Thompson and Ollason 2001; Frederiksen *et al.* 2006; ICES 2009; Jennings *et al.* 2012), which can in turn be strongly influenced by fishing pressure (Frederiksen *et al.* 2004), and environmental conditions such as changes in sea temperature (Dulvy *et al.* 2008). Ongoing depletion of fishing stocks and observed, and future predicted, shifts in fish distributions in response to rising sea temperatures (Perry *et al.* 2005), may therefore have considerable and persistent negative effects on seabird populations (Burthe *et al.* 2012; Frederiksen *et al.* 2012), which are likely to be manifest in low chick survival, reduced productivity, decreased adult survival and possibly population declines (Szostek and Becker 2011; Sandvik *et al.* 2012).

Recent changes in seabird populations

Almost 25% of all seabird species are currently listed as threatened or considered of special conservation concern, making seabirds one of the most threatened groups of birds in the world (IUCN 2012; Croxall *et al.* 2012). Globally, there has been strong evidence of steady and, for some species, dramatic changes in seabird populations in many areas in recent decades (Schreiber and Burger 2002; Butchart *et al.* 2004; Boyd *et al.* 2006). Threats to seabird populations include loss and degradation of breeding habitats due to invasive species, coastal development, physiological constraints due to lack of food and pollution, mortality induced by-catch and climate change (Lewison *et al.* 2012; Sydeman *et al.* 2012). Climatic induced influences on seabird populations can operate indirectly via changes in local or regional food webs and pelagic habitats (Sydeman *et al.* 2012; Frederiksen *et al.* 2012). In recent decades, breeding densities of several seabird species have decreased across the North Atlantic (Frederiksen 2010; Sydeman *et al.* 2012; ICES 2012). Although population growth rates in long-lived species, such as seabirds, are most sensitive to changes in adult survival (e.g. Ezard 2006, Stahl and Oli 2006), repeated low breeding success in some species has been sufficient to result in population declines (e.g. Jenouvrier *et al.* 2005a, 2005b, 2009; Rolland *et al.* 2009). Reports of repeated annual breeding failures from most major North Atlantic seabird areas (Frederiksen 2010) coincide with measures of population declines for numerous species across the North Atlantic (Mavor *et al.* 2008; Barrett *et al.* 2012). Some studies have shown that environmental conditions were poor enough to negatively affect adult survival during a period of population decline (e.g. Sandvik *et al.* 2005; Frederiksen *et al.* 2008), but most studies have linked declines in productivity to declines in food availability (Frederiksen *et al.* 2006; Heath *et al.* 2009), in particular during chick-rearing (Anker-Nilssen *et al.* 1997; Davis *et al.* 2005; Barrett 2007).

Measuring demographic change in marine organisms

Environmental and climatic changes can influence demographic processes both directly (e.g. through survival or reproductive capacity) and indirectly (e.g. through changes in food availability, predation or competition) (Stenseth *et al.* 2002; Frederiksen *et al.* 2004; Gordo 2007). Measuring these responses in most marine organisms is complex, time-consuming and usually relies on remote measures of the consequences of demographic changes, such as large-scale surveys of changes in population sizes or distribution (Dulvy *et al.* 2008). By contrast, seabirds are generally conspicuous and relatively easily studied, and thus provide an opportunity to explore the consequences of changes in the marine environment through direct measures of different components of reproductive success at a wide range of

spatial scales. Seabirds depend upon marine resources to survive and reproduce, and are thus vulnerable to changing marine conditions (Furness and Tasker 2000; Carscadden 2002; Boyd *et al.* 2006; Piatt and Sydeman 2007). In addition, many species nest in large but discrete colonies and thus provide opportunities to explore spatial and temporal variation in demographic processes in large numbers of individuals. Previous studies of seabirds have shown that changes in population sizes and/or breeding success can provide rapid indications of environmental changes, particularly changes in the abundance or availability of their marine prey species (Boyd *et al.* 2006; Piatt and Sydeman 2007; Parsons *et al.* 2008). Seabirds are of particular value because of their status as higher predators in the marine environment (Furness and Camphuysen 1997; Boyd *et al.* 2006; Piatt and Sydeman 2007); changes to seabird demography are thus likely to indicate impacts at lower trophic levels that are less readily observed (Parmesan and Yohe 2003; Parsons *et al.* 2008).

Drivers of seabird productivity and populations

Although introductions of non-native predators have had severe impacts on seabird productivity in many cases (e.g. Jones *et al.* 2008), changes in food abundance can also strongly impact seabird productivity. Food resources in the marine environment can be highly variable and unpredictable, which may explain some aspects of seabird life histories like longevity, delayed maturation and slow reproduction (Furness and Monaghan 1987; Gaston 2004). The long lifespan of seabirds allows bet-hedging life history strategies in which annual reproductive effort can be varied to reduce risks to their own survival (Catry *et al.* 1998). Limited resources can lead to trade-offs between resource allocations for possible future reproduction versus current breeding output (e.g. Williams 1966), and the degree to which such trade-offs are expressed may be indicative of the level of constraints to which the individuals are subjected. Therefore, survival rates of adult seabirds are relatively insensitive to annual changes in food availability compared to their breeding success, and population sizes are unlikely to change greatly unless adult survival is affected (Hamer *et al.* 2001; Ezard *et al.* 2006). Seabirds exposed to declines in food resources are expected to respond by reducing their reproductive output. By exploring this aspect through an integrated modelling approach, (Cairns 1987) found that adult survival, breeding success, chick growth, colony attendance and activity budgets could all vary with changes in food availability in a non-linear fashion, in relation to different parameters. For example, in response to slight declines in food supplies, changes in activity budgets were predicted while, with more severe degradation of feeding conditions, changes in breeding success, chick growth and colony attendance were evident. Only when food was extremely scarce was adult survival negatively affected (Cairns 1987). However, different seabird

species may respond in different ways to resource constraints, particularly in relation to adjustments in different breeding parameters, which has to be accounted for when using seabirds as indicators of marine food supply (Furness and Camphuysen 1997). While many studies have described how seabirds respond to changes in food availability, and have consequently proposed using seabird abundance and demography as indicative signals of marine food supplies (e.g. Cairns 1987; Furness and Camphuysen 1997; Durant *et al.* 2009), little is known about current changes in, and interactions between, prey populations and seabird demography in Iceland.

Icelandic seabirds in a changing environment

The waters surrounding Iceland support one of the richest marine ecosystems in the North Atlantic region (Astthorsson and Vilhjalmsson 2002; Astthorsson *et al.* 2007). Iceland is situated in the middle of the North Atlantic, and is surrounded by cool currents from the Arctic Ocean at the North coast which meet warmer boreal waters from the Gulf Stream off the West and the East coast (Fig. 1.1).

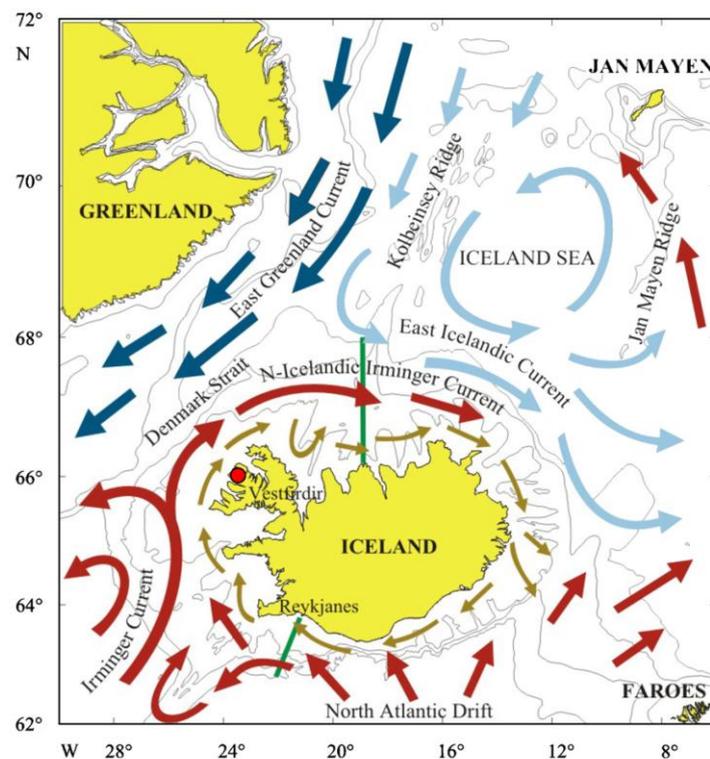


Fig. 1.1: Ocean currents around Iceland. Red arrows indicate warmer boreal waters and blue arrows colder arctic waters. (Reproduced from Astthorsson *et al.* 2007).

These oceanic conditions support a wide range of sea life, including large commercial fish stocks as well as huge populations of seabirds, and are consequently of huge biological and economical importance (Astthorsson *et al.* 2007). Over the last 15 years, the waters in the South and West of Iceland have warmed by 1-2°C and many southern commercially fished species have extended their ranges further north, and northern species ranges have retreated further north (Valdimarsson *et al.* 2012). Further hydrographic changes with warming sea temperatures are predicted for the future at high latitudes, including Icelandic waters (IPCC 2007). Understanding the dynamic and complex marine environment of Iceland is therefore of great value, given the importance of marine resources to the Icelandic economy and the importance of Iceland for marine biodiversity.

A large proportion of many of the largest breeding seabird populations in the North Atlantic can be found in Iceland (Gardarsson 1995), highlighting the international importance of Icelandic waters as seabird habitat. Dietary studies indicate that these populations of seabirds rely mainly on sandeel (*Ammodytes* spp.) to the South and the West of Iceland, and capelin (*Mallotus villosus*) as well as krill (Euphausiacea) in the waters of the North and East (Thompson *et al.* 1999; Lilliendahl 2009). In contrast to the North Sea, sandeel populations are not harvested in Icelandic waters, but capelin populations, the largest pelagic fish stock in Icelandic waters (Astthorsson *et al.* 2007) are heavily exploited (Anon. 2012).

In 2005-2008, a country-wide population census of cliff-breeding seabird species (Fulmar *Fulmarus glacialis*, Kittiwake *Rissa tridactyla*, Razorbill *Alca torda*, Common *Uria aalge* and Brünnich's Guillemots *Uria lomvia*) in Iceland showed that these populations had declined by 16-43% since 1983-1986 (Gardarsson *et al.* 2011; A. Gardarsson pers. comm.). Additionally, studies at 5 to 10 year intervals between the mid-eighties and 2005 in colonies in Southwest and Northeast Iceland showed that numbers of apparently occupied nests (AON) of Fulmars and Brünnich's Guillemots had declined by 2-3% and 7% per annum respectively, and 9% annual declines were evident for Razorbills and Common Guillemots between 1999 and 2005. Kittiwake populations showed evidence of regional declines, with AON in the largest colonies in the north-east declining by 75% (Gardarsson 2006). Low levels of annual productivity since 2005 have also been reported for Lesser Black-backed Gulls *Larus fuscus* in Southwest Iceland (Hallgrimsson 2011) and for Atlantic Puffins *Fratercula arctica* in South Iceland (E. S. Hansen, pers. comm.). Despite the indication from these studies that many Icelandic seabird populations are in decline and have been subjected to repeated low breeding success in recent years, there have been no studies explicitly aimed at quantifying changes in seabird breeding success or identifying the environmental and demographic drivers of these changes.

The Arctic Tern – living on the edge

The Arctic Tern *Sterna paradisaea* has a circumpolar distribution between the Boreal and High Arctic zones, with current estimates of the global population ranging from ~0.8-2.7 million breeding pairs (Hatch 2002; Ratcliffe 2004). The largest estimated breeding populations are in Alaska, Eastern Arctic Canada and Iceland, but more than half of the world population breeds in the North Atlantic (Ratcliffe 2004). Under favourable conditions, Arctic Terns can lay up to three eggs, but may be expected to lay around two eggs and produce one to two fledged chicks. However, in poor years, the frequency of one egg clutches increases and pairs often fail to produce any chicks (e.g. Monaghan *et al.* 1989; Suddaby & Ratcliffe 1997; Robinson *et al.* 2001; Hatch 2002). For example, following a severe decline in abundance of sandeels (*Ammodytes marinus*) after mid 1980s in Shetland waters (Wright & Bailey 1993) Arctic Terns were subjected to six consecutive years of breeding failure on Shetland (Walsh *et al.* 1990) due to abandonment of clutches and chicks starving soon after hatching (Monaghan *et al.* 1989, 1992). The Arctic Tern performs the longest annual migration recorded in the animal kingdom, from breeding colonies in the Arctic to the winter quarters in the Antarctic, travelling total annual average distances of more than 60 thousand kilometres (Egevang *et al.* 2010). The Arctic Tern has been listed among species of special concern in a synthesis report on Nordic seabirds, as it is currently showing signs of declining populations and increased breeding failure across the North Atlantic breeding range (Frederiksen 2010). The life-history and migration of the Arctic Tern is likely to make the species particularly vulnerable to environmental changes (Monaghan *et al.* 1989; Parsons *et al.* 2008). In migratory species, the timing of peak food abundance can greatly influence breeding success (Both *et al.* 2006). The extraordinary pole-to-pole migration of the Arctic Tern means that individuals typically only have sufficient time at the breeding grounds for one successful nesting attempt, making them particularly sensitive to the timing of prey availability. In addition, Arctic Terns are surface-feeders, limiting the range of prey available to them and their capacity to cope with changes in prey depth. The consequences of altered prey availability for seabirds can be dramatic (Furness and Tasker 2000); declines in sandeel availability in Shetland in the 1980s resulted in rapid declines in Arctic Tern numbers and breeding success (Monaghan *et al.* 1989; Furness 2007). As terns within a colony tend to forage in similar locations, understanding the influence of prey distribution and abundance requires studies to operate at a range of spatial scales. Iceland supports numerous and widely distributed Arctic Tern colonies which are exposed to a broad range of local environmental conditions, e.g. different water masses driven by mixing of temperate and Arctic sea currents around Iceland (Astthorsson and Vilhjalmsón 2002; Valdimarsson *et al.* 2012). Thus, this system provides an ideal opportunity to explore within- and between-colony environmental drivers of demography.

Arctic Terns in Iceland

Arctic Tern colonies are distributed all around the Icelandic coastline and inland (Fig. 1.2). Colonies vary considerably in size, from scattered colonies of just a few tens to hundreds pairs to 'super-colonies' of thousands of pairs. Super-colonies with estimated numbers of breeding pairs exceeding 5000 pairs are only found in coastal areas. Colonies located inland, well away from accessible marine foraging area, are typically small, with estimated numbers of breeding pairs usually in dozens. Estimates of the total population size of Arctic Terns in Iceland are in the range of 250,000 - 500,000 breeding pairs (Asbirk *et al.* 1997), which equates to c. 20-30% of the world population (Mitchell *et al.* 2000). Population trends have not been systematically recorded but anecdotal evidence from scientists, birdwatchers and landowners suggests population declines, along with poor breeding success, in recent years.

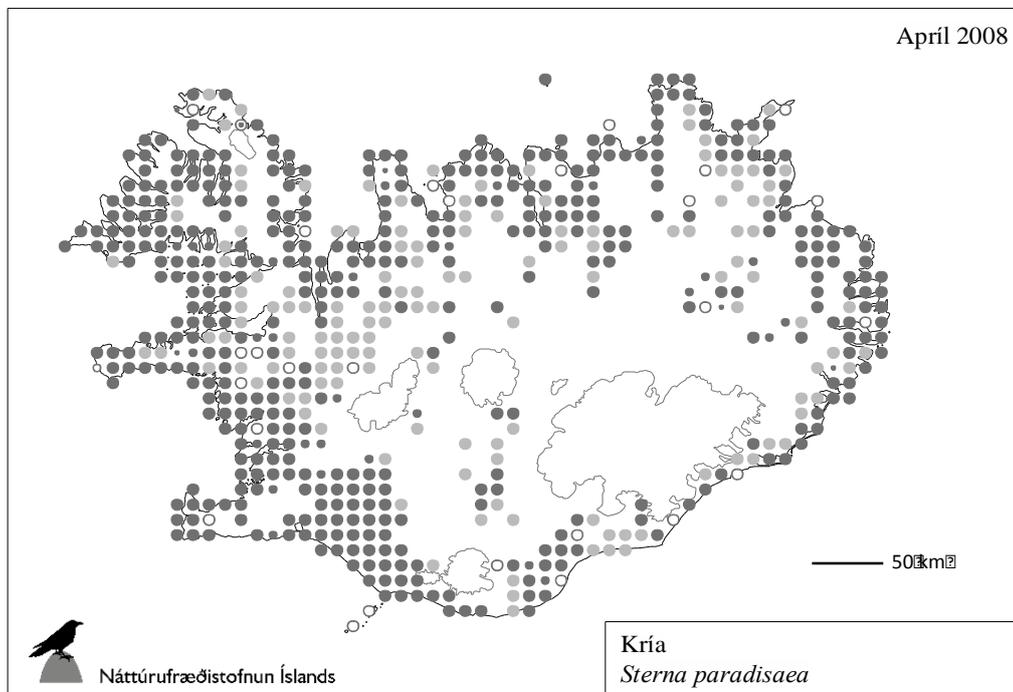


Fig. 1.2: Distribution of Arctic Tern colonies in Iceland on a 10x10 km square grid. Open circles: deserted squares; Filled black: current breeding; Filled grey: potential but unconfirmed breeding. Reproduced with permission from the Icelandic Institute of Natural History.

Thesis structure and aims of this study

Understanding the drivers of demography in Icelandic-breeding seabirds is important not only because Iceland supports internationally important populations of many species, but also because seabird provisioning of chicks with fish and invertebrate prey may provides a means of quantifying variability in marine resources over large spatial and temporal scales. Breeding seabirds can thus potentially be used as terrestrial sentinels for changes within the marine

environment (Furness and Camphuysen 1997; Boyd *et al.* 2006; Piatt and Sydeman 2007; Parsons *et al.* 2008). The main focus of this study was therefore to quantify Arctic Tern productivity at a wide range of colonies with access to differing resources, in order to identify potential factors driving Arctic Tern productivity and the scales over which they may operate.

In this study, the Arctic Tern is used as a study system in which to explore variation in breeding success over 15 colonies in two regions of Iceland. Between 2008 and 2011, Arctic Tern clutch sizes, hatching success, chick growth rates and fledging success were quantified in colonies throughout the Snaefellsnes peninsula in West Iceland and, in 2011, the same data were collected from colonies on the Melrakkasletta peninsula in North-East Iceland. In addition, the composition of prey delivered to Arctic Tern chicks and the rates of prey delivery were quantified on colonies in both regions in 2010 (Snaefellsnes) and 2011 (Melrakkasletta). In **chapter two**, current levels of productivity in 10 Arctic Tern colonies throughout the Snaefellsnes peninsula are quantified, and the extent of between-year and between-colony variations in different components of productivity are assessed. Between 2008 and 2011, a total of 698 nests were monitored and there was very little annual or between-colony variation in clutch size among these nests. Hatching success of these nests was consistently high (between 80-100%), but fledging success was low in all years, although with some variation between colonies. The observed breeding failure was characterized by mass mortality of chicks so, in order to explore potential causes of these demographic patterns, the chick mortality was explored in further detail in **chapter three**. In this chapter, the variation in timing of chick mortality between colonies and years is quantified. The large number and wide geographic spread of colonies precluded sufficiently frequent surveys of colonies to assess timing of mortality, and so forensic ecology techniques were employed to estimate timing of mortality of individual chicks. Chick carcasses were collected from 10 colonies in West Iceland throughout each breeding season in 2008 to 2010, and the lengths of blowfly larvae on these carcasses were used, along with local weather data and models of temperature-dependent larval growth rates, to estimate dates of chick mortality. These estimates indicated that mortality occurred throughout the season in all colonies, and there was no evidence of synchronised concentrations of mortality within or between colonies. Some evidence of annual variation in the timing of mortality was detected, with chicks in 2008 dying earlier, and at a significantly younger age, than in 2009 and 2010. The scale and timings of chick mortality across these colonies suggested a persistent and chronic cause of mortality.

Consequently, in order to explore potential causes of this high chick mortality, in **chapter four** the evidence for impacts of predation pressure, weather conditions and constraints on food supplies on chick mortality are assessed. The proportion of

chicks known to have died or fledged, the timing of mortality in relation to weather conditions and the relationships between chick growth rates and chick survival in different colonies and at different stages of the pre-fledging period are all quantified. These analyses suggest no strong evidence of weather-induced mortality or high levels of predator pressure, but daily changes in body mass strongly and significantly influenced survival probabilities of Arctic Tern chicks across all colonies. The low Arctic Tern productivity in W-Iceland in 2008-2011 therefore appears to have primarily been caused by extensive chick mortality driven by starvation. However, the reasons for such high levels of chick starvation are not known. Consequently, in **chapter five** the variation in dietary composition and prey delivery rates among colonies with differing levels of productivity and with differing access to prey resources are assessed. This study took place on colonies in both the West and Northeast of Iceland, in order to compare conditions in parts of Iceland with very different oceanic conditions. Prey composition and size varied greatly between regions and colonies. In West Iceland, higher delivery rates were associated with greater fledging success, but sandeels were delivered at low rates at all colonies. In Northeast Iceland, capelin replaced sandeels as the main marine prey, but delivery rates of capelin were either very low or very inconsistent, and fledging success in Northeast Iceland was similarly low. A synthesis of these findings is provided in **chapter six**, together with consideration of the wider implications for Arctic Terns and other seabirds in Iceland.

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Chapter 2

Chapter 2

Annual and between-colony variation in productivity of Arctic Terns in W Iceland

Abstract

Among many seabird species at temperate and Arctic latitudes, there has been an increasing frequency of reports of widespread breeding failure and population declines. As seabirds are among the higher predators in marine ecosystems, demographic changes within their populations can reflect impacts elsewhere in the ecosystems, making them valuable indicators of changes to marine resources. The Arctic Tern *Sterna paradisaea* may be especially vulnerable to environmental changes, because of their pole-to-pole migrations. Individuals typically only have sufficient time at the breeding grounds for one successful nesting attempt, making them very sensitive to timing of prey availability. Population declines are evident among numerous Arctic Tern populations and many other seabird species around the North Atlantic, but little is known about the status of the huge seabird populations breeding in Iceland. Arctic Terns are numerous in Iceland, and large numbers of colonies throughout the country are exposed to a range of local and regional environmental conditions. The goal of this study was to quantify current levels of productivity in Arctic Terns in Iceland, and to explore the extent to which this varies among 10 colonies across the Snaefellsnes peninsula in W-Iceland. Between 2008 and 2011, the clutch size of 698 nests did not vary significantly between colonies or years, and hatching success was consistently high (between 80-100 %). However, fledging success was low in all years, although with some variation between colonies. We discuss the potential causes of these demographic patterns and the implications for the conservation of this species in Iceland.

Keywords: Animal ecology, Demography, Breeding success, Sub-Arctic, Seabirds, Arctic Tern

Introduction

During the past decade, breeding densities of several seabird species have decreased across the North Atlantic (Frederiksen 2010; Sydeman *et al.* 2012; ICES 2012). Although population growth rates in long-lived species, such as seabirds, are most sensitive to changes in adult survival (e.g. Ezard 2006, Stahl and Oli 2006), repeated low breeding success in some species has been sufficient to result in population declines (e.g. Jenouvrier *et al.* 2005a, 2005b, 2009; Rolland *et al.* 2009). Reports of repeated annual breeding failures from most major North Atlantic seabird areas (Frederiksen 2010) coincide with measures of population declines for numerous species across the North Atlantic (Mavor *et al.* 2008; Barrett *et al.* 2012). Some studies have shown that environmental conditions were poor enough to negatively affect adult survival during a period of population decline (e.g. Sandvik *et al.* 2005; Frederiksen *et al.* 2008), but most studies have linked declines in productivity to declines in food availability (Frederiksen *et al.* 2006; Heath *et al.* 2009), in particular during chick-rearing (Anker-Nilssen *et al.* 1997; Davis *et al.* 2005; Barrett 2007). Predation (e.g. Becker 1995) and extreme weather (Thompson and Furness 1991; Aebischer 1993; Robinson *et al.* 2002), are also known to affect productivity in colonial seabirds.

To date the most detailed information on the past and current status of seabird populations comes from colonies around the North Sea and along the Norwegian coast (see overview in Frederiksen 2010). In this region, both large-scale, long term population monitoring and detailed within-colony studies have provided evidence that seabird population trends are strongly influenced by variation in prey abundance (Veit *et al.* 1996; Montevecchi and Myers 1997; Thompson and Ollason 2001; Frederiksen *et al.* 2006; ICES 2009; Jennings *et al.* 2012), which can in turn be influenced by fishing pressure and environmental conditions such as changes in sea temperature (Dulvy *et al.* 2008). Ongoing depletion of fishing stocks and observed and future predicted shifts in fish distributions in response to rising sea temperatures (Perry *et al.* 2005), are therefore of growing concern for the fate of seabird populations. At high latitudes, human impacts on marine ecosystems such as fishing (Halpern *et al.* 2008) may be lower but climate-driven environmental changes are predicted to be particularly severe (IPCC 2007). Very large seabird populations are found in the sub-Arctic and Arctic areas (Mitchell *et al.* 2000; Frederiksen 2010) but, with the exception of Norwegian coastal populations (Barrett *et al.* 2012), very few high latitude seabird populations have been studied in detail, and information on these populations are rarely available (Frederiksen 2010). The implications of current and future environmental changes for demography of seabirds breeding at higher latitudes are therefore largely unknown.

A large proportion of many of the largest seabird populations in the North Atlantic can be found in Iceland (Gardarsson 1995), highlighting the international importance of Icelandic waters as seabird habitat. Iceland is in the middle of the North Atlantic, and is surrounded by cool currents from the Arctic Ocean at the North coast which meet warmer boreal waters from the Gulf Stream off the West and the East coast. These oceanic conditions support a wide range of sea life, including large commercial fish stocks as well as huge populations of seabirds (Astthorsson *et al.* 2007). Dietary studies indicate that these populations of seabirds rely mainly on sandeel (*Ammodytes* spp.) to the South and the West of Iceland, and capelin (*Mallotus villosus*) as well as krill (Euphausiacea) in the waters of the North and East (Thompson *et al.* 1999; Lilliendahl 2009). In contrast to the North Sea, sandeel populations are not harvested in Icelandic waters, but capelin populations, the largest pelagic fish stock in Icelandic waters (Astthorsson *et al.* 2007) are heavily exploited, with average annual total landings of 824 thousand tons since 1984 (Anon. 2012).

In 2005-2008, a country-wide population census of cliff-breeding seabird species (Fulmars *Fulmarus glacialis*, Kittiwakes *Rissa tridactyla*, Razorbills *Alca torda*, Common *Uria aalge* and Brünnich's Guillemots *Uria lomvia*) in Iceland showed that these populations had declined by 16-43% since 1983-1986 (Gardarsson *et al.* 2011; A. Gardarsson pers. comm.). Additionally, studies at 5 to 10 year intervals between the mid-eighties and 2005 in colonies in Southwest and Northeast Iceland showed that numbers of apparently occupied nests (AON) of Fulmars and Brünnich's Guillemots had declined by 2-3% and 7% per annum respectively, and 9% annual declines were evident for Razorbills and Common Guillemots between 1999 and 2005. Kittiwake populations showed evidence of regional declines, with AON in the largest colonies in the north-east declining by 75% (Gardarsson 2006a). All of the above populations have been shown to use the same food resources; the sandeel (*Ammodytes marinus*) in the South and West of Iceland, while on the North coast the capelin was the most important food item for 5 out of 6 species (Lilliendahl and Sólmundsson 1998; Thompson *et al.* 1999). Despite the indication from these studies that most Icelandic seabird populations are in decline and have been subjected to repeated annual breeding failures during the last decade, there have been no studies explicitly aimed at identifying the environmental and demographic drivers of these changes.

Arctic Terns *Sterna paradisaea* provide an opportunity to explore the problem these seabird populations are encountering. They are ground-nesters which often breed in dense colonies, allowing easy access to both eggs and chicks for productivity measures. Iceland supports numerous Arctic Tern colonies which are

widely distributed and are exposed to a broad range of local environmental conditions, including weather, access to feeding grounds and oceanic conditions. And their pole-to-pole migration (Egevang *et al.* 2010) and late arrival on the Icelandic breeding grounds (e.g. Gunnarsson and Tómasson 2012) means that individuals are on a tight schedule for breeding, which may make them particularly sensitive to environmental changes. Their body condition could reflect environmental conditions experienced during migration but are also likely to be influenced by local conditions in Iceland, as nesting typically occurs 3-4 weeks after arrival. The relative ease with which Arctic Terns can be studied in the breeding season, in comparison to many other seabirds, makes them potentially good indicators of the impact of environmental changes on seabird populations. Both the large population and numerous accessible colonies in Iceland facilitate the study of where and to what degree Arctic Tern productivity is declining.

Around 20-30% of the world's Arctic Terns breed in Iceland (Asbirk *et al.* 1997), in colonies ranging from tens to tens of thousands of pairs, and their breeding status in Iceland is therefore a key issue for the global conservation of the species. The Snaefellsnes peninsula in W-Iceland supports numerous Arctic Tern colonies of varying sizes, and provides a wide range of oceanic, estuarine and freshwater foraging opportunities. In this study, we quantify current levels of productivity in Arctic Tern colonies throughout the Snaefellsnes peninsula, and assess the extent of between-year and between-colony variations in different components of productivity.

Methods

Study area and colonies

The study was conducted on Snæfellsnes peninsula from 2008 to 2011. Snæfellsnes is situated in W-Iceland, and comprises a mountainous terrain surrounded by coastal lowlands. The peninsula stretches 100 km into the Atlantic Ocean, between the bays of Faxafloi and Breidafjordur (Fig. 2.1). The peninsula supports numerous seabird colonies, both of cliff breeders and ground nesters. Arctic Tern colonies are found along the whole coastline of the peninsula.

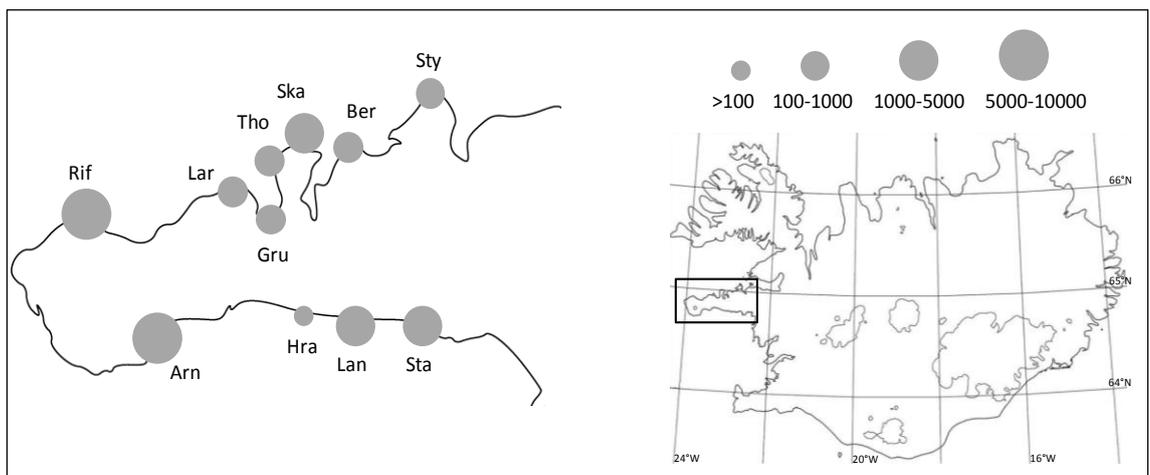


Fig. 2.1. Location and size (pairs) of Arctic Tern study colonies on Snæfellsnes peninsula and the location of the peninsula in western Iceland (inset). Sty: Stykkisholmur, Ber: Berserkseyri, Ska: Skallabudir, Tho: Thordisarstadir, Gru: Grundafjordur, Lar: Larvadall, Rif: Rif, Arn: Arnarstapi, Hra: Hraunsmuli, Lan: Langaholt, Sta: Stakkhamarsnes.

During the study period, between 66 and 272 Arctic Tern nests located in between 4 and 10 colonies were monitored through to fledging or failure each year (Table 2.1). Study nests were located close to the middle of colonies to avoid sampling of nests at colony edges, which may disproportionately comprise inexperienced breeders. The distances between the colonies ranged from 10-90 km; as Arctic Tern foraging ranges are typically less than 10 km from the colony (Rock *et al.* 2007), the foraging ranges of individuals from these colonies are not likely to overlap much. Colonies also varied in size, ranging from 50-10,000 pairs. Colony size was estimated in orders of magnitude as the approximate maximum number of birds in the air when the birds were flushed from the ground while researchers were in the colony (Fig 2.1). The nesting habitat within the colonies typically comprised dry sand and gravel, sometimes with thick grass up to 10-30 cm height.

Table 2.1. Numbers of Arctic Tern nests monitored in each colony each year of the study. Colony order is presented according to colony size (from smallest (top) to largest (bottom)). See Figure 2.1 for colony locations and details.

Colony	2008	2009	2010	2011
Hra		14	9	
Ber		18	11	17
Sty	12	21	28	14
Sta	11			
Gru		23	25	19
Tho		20		
Lar		24	16	
Ska		34		
Lan		33	48	15
Arn	25	34	28	
Rif	18	51	36	31
Total	66	272	201	96

Data collection

Measuring Arctic Tern productivity

Arctic Tern clutch size, hatching success and productivity were measured for ca. 25 nests per colony in each year (Table 2.1). To aid nest and chick relocation, these nests were enclosed within low (30 cm high) chicken-mesh wire fences. In 2008 and 2009, between 2 and 4 large (10 – 20 m²) fences were erected around groups of 5-12 nests in each colony, and in 2010 and 2011 most nests were fenced individually in fences of ca. 1-2 m². To minimize disturbance and the risks of nest desertion, enclosures were erected after the terns had completed, on average, more than half of the incubation in each colony.

In 2008, clutch size, hatching success and the number of fledglings per pair were measured in four colonies, and for between 11 and 25 nests per colony (Table 2.1). Clutch size was measured for each nest but colony visits in this year were too infrequent to allow hatching and fledging success of individual nests to be measured, thus only overall colony averages could be estimated for these metrics in this year.

In 2009-2011, 5-10 colonies were studied and an average of 25 nests (SD: 11.03, range: 9 - 51) were monitored within each colony. Individual fencing of nests and more regular visits allowed the calculation of the following metrics: clutch size (eggs per nest), hatching success (% hatched eggs per nest), number of fledged chicks per egg laid, number of fledged chicks per egg hatched and number of fledged chicks per nest.

Colonies were first visited after the first few days of egg-laying, and egg floatation (Rahn and Paganelli 1989) was used to estimate egg incubation stages and predicted hatching dates. Clutch size was determined after mid-incubation (ca. 10 days post-egg laying) and nests were revisited at least once before hatching so that any additions to clutches could be detected. Nests were visited every 1-3 days around the predicted hatching date to measure the hatching success of each nest. Arctic Terns are semi-precocial and chicks typically remain in the nest for the first 3 days after hatching. Eggs that were not hatched and cold by at least 10 days after the predicted hatching date were declared unsuccessful. Chicks were ringed and measured just after hatching and the colonies were re-visited every 3-5 days in order to relocate chicks. At each recapture, measurements of mass (measured to the nearest 0.1 g with an electronic scale), wing length (measured to the nearest 1 mm with a wing ruler), and the combined head plus bill length (or skull) (measured to the nearest 0.01 mm with digital callipers) were recorded for each chick. Chicks were considered to have fledged successfully if they reached at least 80 g in mass and/or 100 mm wing length and were not relocated on subsequent visits.

Data analysis

Annual and between-colony variation in clutch size, hatching success, number of fledglings per egg laid, fledglings per chicks hatched and fledglings per nest were explored with generalized linear models. Year and colony were defined as fixed factors. The dependent variable was either the number of eggs (clutch size), number of eggs hatched (hatching success) or number of chicks fledged (fledging success) per nest and was modelled with a Poisson distribution and a logit-link function. For hatching success, the number of eggs in each clutch was included as an offset, and fledging success was modelled with offsets of (a) number of eggs (chicks fledged/egg), (b) number of hatched eggs (chicks fledged/egg hatched) or (c) no offset (chicks fledged per pair). Statistical analyses were conducted in SPSS 16.0 and full models are presented for completeness, as exclusion of non-significant factors or interactions did not alter the model findings.

Results

General variation in productivity

Between 2008 and 2011, Arctic Tern productivity in colonies across the Snaefellsnes peninsula varied little between years (Table 2.2). Overall, the modal clutch size was two and ranged from 1-3, with 15% of nests having one egg, 83% having two and 2% having three. Hatching success (chicks hatched per egg laid) was consistently high, with around 80-100% of all eggs hatching in all years (Table 2.2), and 96.6% of two and three-egg clutches hatched all eggs. However, fledging success was low in all years, ranging from 0.05 to 0.5 chicks per pair, and was lowest in 2008 and highest in 2010 (Table 2.2).

Table 2.2. Annual productivity of Arctic Tern nests on colonies across the Snaefellsnes, West Iceland between 2008 and 2011. See Table 2.1 for details of sample sizes.

	2008			2009			2010			2011		
	Mean	S.D.	<i>n</i>									
Clutch size	2.03	0.39	66	1.74	0.53	272	1.82	0.44	201	1.40	0.57	96
Chicks hatched per egg laid	0.93		134	0.93	0.24	474	0.89	0.25	366	0.83	0.35	134
Chicks fledged per egg laid	0.02		134	0.06	0.22	474	0.28	0.36	366	0.09	0.28	134
Chicks fledged per chick hatched	0.02		124	0.07	0.24	427	0.34	0.40	297	0.13	0.33	85
Chicks fledged per pair	0.05		66	0.11	0.35	272	0.51	0.51	201	0.11	0.35	96

Between colony-variation in productivity

Arctic Tern clutch sizes did not vary significantly between colonies (Table 2.3), and were typically around 1.5-2 eggs per nest on average (Fig. 2.2a). However, there was weak significant annual variation, with clutch sizes being smaller in 2011 than in previous years. There was no significant interaction between colony and year, indicating that clutch sizes in 2011 were generally lower in all colonies.

Hatching success was consistently high, with at least 70% of eggs hatching in all colonies and years except for Rif in 2011, (Fig. 2.2b), and there was no significant variation among years or colonies (Table 2.3).

The number of fledglings per egg laid, per hatchling and per nest all varied significantly both between colonies and between years, and the annual variation did not differ significantly between colonies (Table 2.3). Most colonies produced less than half a chick per egg laid (Fig. 2.2c) and per egg hatched (Fig. 2.2d), and only one colony in one year reached on average of one fledgling per nest (Fig. 2.2e). Fledging success in most colonies was higher in 2010 than in other years; in 2009,

none of the measured hatchlings fledged in six out of ten colonies and in 2011 only two out of five colonies fledged any of the measured hatchlings (Fig. 2.2d).

Overall, two colonies, Berserkseyri (Ber) and Stykkisholmur (Sty) had higher fledging success across all years (Fig. 2.2 c-e). Both of these colonies are located on the eastern part of the north coast of the peninsula (Fig. 2.1). Rif, which is located at the western end of the peninsula, and the largest colony, had the poorest success overall, with no monitored nests producing fledglings in any of the four years (Fig. 2.2 c-e).

Table 2.3. Results of generalized linear models of annual and between-colony variation in five breeding success parameters of Arctic Terns on Snaefellsness peninsula, W Iceland, between 2009 and 2011. See Table 2.1 for details on sample sizes.

	Clutch size			Hatching success			Fledged per egg laid			Fledged per egg hatched			Fledged per pair		
	W	df	p	W	df	p	W	df	p	W	df	p	W	df	p
Colony	3.39	9	0.95	4.16	9	0.90	13364.92	6	<0.001	10023.53	6	<0.001	10073.53	6	<0.001
Year	6.15	2	0.05	1.35	2	0.51	12.10	2	<0.001	12.53	2	<0.001	13.83	2	<0.001
Colony*Year	3.66	11	0.98	2.71	11	0.99	2.59	4	0.63	4.14	4	0.39	3.77	4	0.44

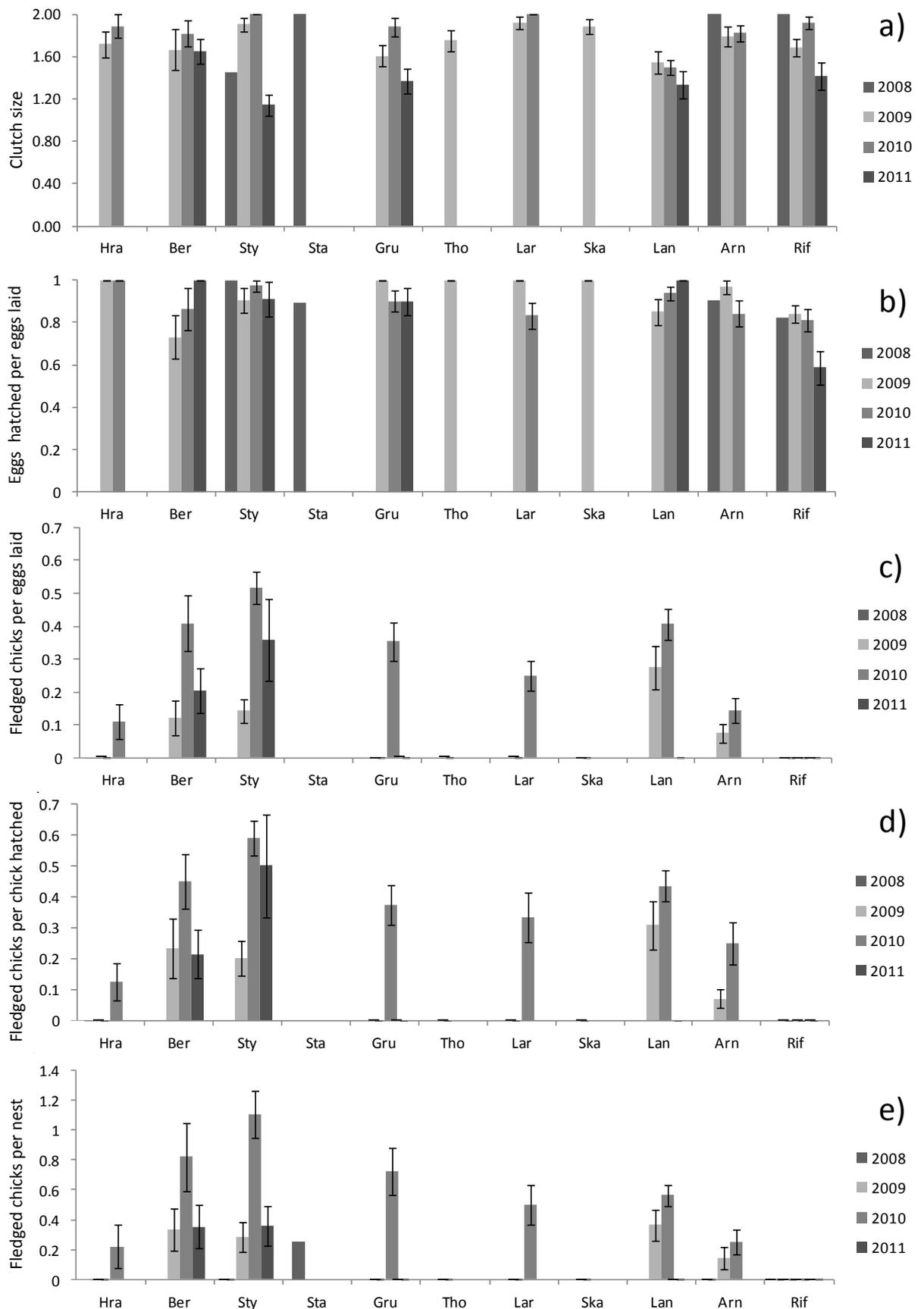


Fig. 2.2. Annual and between-colony variation in mean (\pm SE) Arctic Tern (a) clutch size, (b) hatching success, (c) fledged chicks per eggs laid, (d) fledged chicks per chick hatched and (e) fledged chicks per nest. Colony order is presented according to colony size (from smallest (left) to largest (right)). Black dashed lines indicate zero values. See Figure 1 for colony locations and details.

Discussion

The Snaefellsnes area in W-Iceland supports tens of thousands of breeding Arctic Terns, in colonies spread all along the coastal fringe of the peninsula. Between 2008 and 2011, productivity of colonies all around the peninsula was very low, with several colonies fledging no chicks from the nests that were monitored, and no colonies exceeding 0.5 chicks/egg laid. Fledging success was slightly higher in 2010 than in the other years, but even in that year only one colony (Stykkisholmur) had an average productivity exceeding one fledgling per nest. The lowest fledging success was recorded on Rif, in the far west of the peninsula, where no fledgling success was measured in any of the four years. Anecdotal information from local landowners suggested that poor productivity in these Arctic Tern colonies had been evident since 2005, and similar low levels of productivity have been reported for Lesser Black-backed Gulls *Larus fuscus* in Southwest Iceland since 2005 (Hallgrímsson 2011). Historically, Rif has been a large colony counting pairs in thousands, suggesting that conditions at this location must have been sufficiently favourable in the past to attract large numbers of breeding birds and/or to facilitate high levels of productivity and natal recruitment. The very low current level of productivity at Rif suggests that those conditions may no longer be present.

Across all tern colonies in all years, clutch sizes were close to the modal clutch of two and hatching success was usually around 90%. This suggests that conditions for adults were sufficiently good for egg production and incubation to hatch the eggs. The low productivity is primarily a consequence of the post-hatching phase of the breeding season when conditions for chick-rearing appear to be constraining fledging success.

Possible reason for why so few hatchlings fledge could include mortality of chicks caused by predation, unfavourable weather condition or starvation. A wide range of predators occur on the Snaefellsnes peninsula, including mammalian (Arctic Fox *Vulpes lagopus* and American Mink *Neovison vison*) and avian (Herring Gulls *Larus argentatus*, Lesser Black-backed Gulls and Black-headed Gulls *Chroicocephalus ridibundus*, Arctic Skua *Stercorarius parasiticus*, Short-eared Owl *Asio flammeus*, Gyr Falcon *Falco rusticolus*, White-tailed Eagle *Haliaeetus albicilla*, Raven *Corvus corax*) predators. However, there is no evidence to suggest any significant recent increases in predator numbers or activity and the high hatching success (and the fact that very few unhatched eggs went missing) on all colonies would suggest a limited impact of predator activity at least at the egg stage. Predation of chicks could be implicated in the low productivity, but only one event of predation of a chick (by a black-headed gull) was observed during the four seasons of fieldwork in all colonies.

Extreme and prolonged unfavourable weather conditions are known to impact ground-nesting, colonial birds with semi-precocial chicks (Robinson *et al.* 2002) and the Snaefellsnes peninsula can experience periods of low temperatures and high winds. Given the consistency of the low productivity on colonies right across the peninsula, weather-induced mortality would likely have to involve large-scale weather events, rather than local variations in temperature and rainfall. While few extreme weather events were apparent during these years, the potential role of weather conditions could be explored in more detail by exploring the timing of severe weather and its association with chick mortality events.

Starvation is also a known cause of death of chicks and driver of productivity. Starvation can result from low prey abundance, insufficient size (Harris *et al.* 2006) and/or low nutritious value of the available resources (Wanless *et al.* 2005). Changes in the spatial or temporal distributions of prey can also influence their availability, resulting in insufficient food during chick rearing (Burthe *et al.* 2012).

Over the last decade, numerous seabird species in Iceland have demonstrated population declines and some species have been measured having poor productivity (Gardarsson 2006a, 2006b; Gardarsson *et al.* 2011). Observations of the declines and breeding failures are across both cliff breeding auks, fulmars and kittiwakes as well as ground-nesting gulls and burrowing puffins. What all of these species have in common is summer diet (Lilliendahl and Sólmundsson 1998; Thompson *et al.* 1999). At the South and West coast of Iceland all of these seabirds depend primarily on sandeel during the summer time when they produce chicks. Sandeel abundance has been monitored in selected locations in South and West Iceland annually since 2006 by the Icelandic Marine Research Institute. These surveys show that sandeel densities were much lower than elsewhere in the North Atlantic (e.g. Greenstreet *et al.* 2006) and that densities declined between years during the survey period (Bogason and Lilliendahl 2008). Additionally, some year classes were totally absent from the population. Declines in sandeel abundance in response to overfishing have been reported in the North Sea, together with implications for the species preying on sandeel (Frederiksen *et al.* 2004), but sandeels are not fished in Icelandic waters.

During the last 15 years the waters in the South and West of Iceland have warmed by 1-2°C and many southern commercially fished species have extended their ranges further north, and northern species ranges have retreated further north (Valdimarsson *et al.* 2012). Warming sea temperatures in the North Sea have been linked to e.g. decline in sandeel recruitment (Arnott and Ruxton 2002) and long term changes in sandeel sizes (Frederiksen *et al.* 2011). Further hydrographic changes with warming sea temperatures have been predicted in the future at high

latitudes, including Icelandic waters (IPCC 2007). The implications of such events in Iceland would be of international importance for numerous seabird species as Iceland supports such large population sizes of many species. In order to evaluate the possible impacts of the predicted environmental changes on seabird populations, further research is needed to identify the drivers of demographic changes and to quantify the spatial and temporal patterns and magnitude of breeding success and mortality events.

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Chapter 3

Chapter 3

Using forensic ecology to explore synchrony of mortality in colonial seabird

Abstract

Understanding the demographic patterns influencing changes in population abundance often requires information on the scale and extent of mortality at different life stages. However, quantifying spatial and temporal variability in patterns of mortality can be difficult, especially in remote and sparsely populated areas. Here we use forensic techniques, in which time of death is estimated from growth rates of blowfly larvae on carcasses, to explore the spatial and temporal synchrony of chick mortality in Arctic Tern colonies in Iceland. Arctic Tern populations in West Iceland have experienced high levels of chick mortality in recent years, and identifying the level of spatial and temporal synchrony in mortality may help to identify potential causes. Chick carcasses were collected from 10 colonies in West Iceland throughout each breeding season in 2008 to 2010, and the lengths of blowfly larvae on these carcasses were used, along with local weather data and models of temperature-dependent larval growth rates, to estimate dates of chick mortality. These estimates indicated that mortality occurred throughout the season in all colonies, and there was no evidence of synchronised concentrations of mortality within or between colonies. Some evidence of annual variation in the timing of mortality was detected, with chicks in 2008 dying earlier, and at a significantly younger age, than in 2009 and 2010. The scale and timings of chick mortality across these colonies suggested a persistent and chronic cause of mortality.

Keywords: Forensic ecology, chick mortality, Sub-Arctic, seabirds, Arctic Tern, Iceland

Introduction

Understanding the causes of population changes is central to designing strategies for species conservation and management. Population changes often result from environmentally-driven changes in demography (Newton 1998), but quantifying these relationships is often challenging. Assessing patterns of changes in demography can help to identify the drivers of those changes when supporting data are scarce. Local environmental conditions can always influence demography, but when population size changes over larger spatial scales, identifying the scales over which similar environmental changes are operating becomes increasingly important. The scale of spatial and temporal synchrony in population change and associated demographic parameters can help to identify the scale over which drivers of those changes may be operating (e.g. Chamberlain and Crick 1999; Morrison *et al.* 2010). However, the abundance and demographic data needed to explore levels of synchrony at different spatial and temporal scales are often not available, especially in sparsely populated and remote areas.

Many colonial seabird populations in the North Atlantic region that have been in decline in recent decades have been subjected to strong declines in productivity (Frederiksen 2010). Some population changes, in particular around the North Sea (Frederiksen *et al.* 2006) and along the Norwegian coast (Anker-Nilssen *et al.* 1997), have been monitored closely and changes in productivity been linked to resource availability (Frederiksen *et al.* 2004; Barrett *et al.* 2006; Furness 2007), as well as predation (Votier *et al.* 2007) and extreme weather conditions (Frederiksen *et al.* 2008). Many other populations which have not been studied as thoroughly have shown signs of population declines and repeated breeding failures (Frederiksen 2010). Several factors could impact these productivity failures, including increased predation causing adult or brood mortality, unfavourable weather conditions causing egg or chick mortality or decreased availability of food resources for adults and/or their young. Exploring the timing of mortality at different spatial scales can be useful in understanding the mechanisms driving such mortality events.

Iceland supports internationally important breeding populations of many seabirds (Gardarsson 1995), but recent declines in many of these seabird populations have been widely reported (Gardarsson 2006; Gardarsson *et al.* 2011). Identifying potential environmental drivers of these declines is complex because population monitoring data are scarce and the marine habitats and resources that they exploit are often very difficult to measure. Arctic Tern *Sterna paradisaea* colonies in Iceland are widely distributed around the country, and are exposed to a broad range of local environmental conditions, including weather, access to feeding grounds and oceanic conditions. Their pole-to-pole migration (Egevang *et al.* 2010) and late

arrivals on the Icelandic breeding grounds (e.g. Gunnarsson and Tómasson 2012) mean that individuals are on a tight schedule for breeding, which may make their breeding particularly sensitive to environmental changes, e.g. weather and resource availability, or predation events. Arctic Tern productivity in colonies in western Iceland has been low in the last few years, largely as a result of high chick mortality (Chapter 2). However, the extent to which chick mortality patterns vary seasonally, between colonies and among years is not known.

Forensic approaches are widely used to determine the time of death of human bodies, and these approaches can allow estimation of time since death for a longer time periods than other medical techniques (Amendt *et al.* 2004). Calliphorid flesh fly species (Blowflies) are the most commonly used indicator species in forensic studies (Greenberg and Kunich 2002; Amendt *et al.* 2004, 2011). The Calliphoridae family comprises roughly 130 genera and about 1000 species worldwide, although only a few species are specifically used for forensic purposes (Greenberg and Kunich 2002). Many calliphorid species are oviparous and can be attracted over great distances by odour (Anderson 2001), and these species are often the primary colonizers of cadavers (Amendt *et al.* 2004). Adults can arrive within minutes of death and lay eggs on cadavers within hours (Greenberg 1991; Sharanowski *et al.* 2008). Accordingly, the presence of calliphorids can be used to estimate the minimum post-mortem interval (PMI) with a good degree of accuracy (Amendt *et al.* 2004, 2011; Davies and Harvey 2012). Calliphorids are therefore among the most important species for forensic studies (Byrd and Castner 2001).

Blowflies typically lay up to 300 eggs per batch, three or four times in the life of a fly and the eggs are normally fertilized at the time of oviposition. The outer shell of the egg is tough and can withstand harsh conditions, but the embryo is sensitive to desiccation. After hatching, the maggot undergoes three instar stages (with two intervening moults), and growth rate varies with the ambient temperature (Donovan *et al.* 2006). When maggots reach their maximum size at the third instar, they stop feeding and leave the carcass for several days as a post-feeding larva. The total length of the life cycle is slightly lengthened in cooler temperatures (Donovan *et al.* 2006). The duration between the three larval stages, the pupa stage and post-feeding larval dispersal can be useful to estimate the minimum time since death of the carcass on which the eggs were laid, by assessing the length of time the larvae have been growing (Greenberg and Kunich 2002). Studies of blowfly arrivals on small mammal carcasses (rats and mice) show that the carcasses can be quickly consumed by the maggots of the first flies (Kneidel 1984), making studies of small mammals not easily transposable to insect succession on larger bodies such as humans. However, this means that calliphorids are ideal for forensic studies on small carcasses.

In Iceland, two calliphorid species are known to lay eggs on dead or dying animals, *Calliphora vicina* and *C. uralensis*. *C. vicina* (the European bluebottle fly) is black and dark metallic blue-green and usually 10-14 mm long. Larvae of this species are commonly found on human corpses in temperate regions throughout the United States and Europe. It is considered a primarily spring and autumn species in the temperate zone, and a summer-flying species in sub-polar regions. *C. uralensis* is less well described but the two species are morphologically and behaviourally similar and in Iceland. Both blowfly species have a similar distribution and are present in summer, during the breeding season of the Arctic Tern (E. Olafsson pers. comm.; Anon 2012). In this paper we aim to describe and apply forensic methods of using blowfly larval growth rates to estimate the timing and variation of mortality using individual Arctic Tern chick carcasses from colonies spanning a 100 km peninsula in West Iceland.

Methods

Study area

The study was conducted on Snaefellsnes peninsula from 2008 to 2010. Snaefellsnes is situated in W-Iceland, and comprises a mountainous terrain surrounded by coastal lowlands. The peninsula stretches 100 km into the Atlantic Ocean, between the large bays of Faxafloi and Breidafjordur (Fig. 1). The peninsula supports numerous seabird colonies, both of cliff breeders and ground nesters. Arctic Tern colonies of varying size are found along the whole coastline of the peninsula.

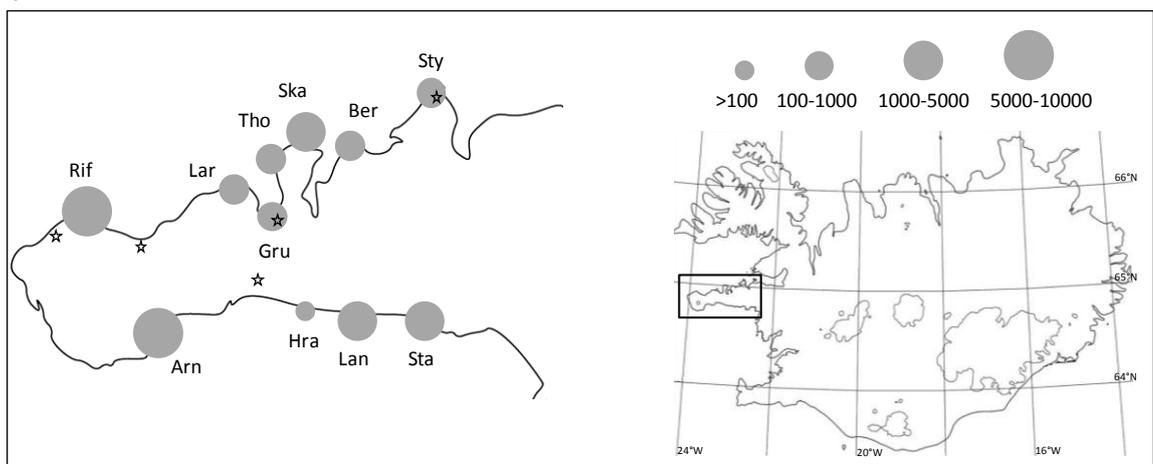


Fig. 3.1. Location and size (pairs) of Arctic Tern study colonies on Snaefellsnes peninsula and the location of the peninsula in western Iceland (inset). Sty: Stykkisholmur, Ber: Berserkseyri, Ska: Skallabudir, Tho: Thordisarstadir, Gru: Grundarfjordur, Lar: Larvadall, Rif: Rif, Arn: Arnarstapi, Hra: Hraunsmuli, Lan: Langaholt, Sta: Stakkhamarsnes. Stars indicate locations of weather stations.

Nest monitoring

During the study period, 8-9 Arctic Tern colonies were monitored each year (Table 3.1) and an average of 39 chicks (range: 5-158, SE: 0.29) in each colony were followed through to hatching or failure. To aid nest and chick relocation, these nests were enclosed within low (30 cm high) chicken-mesh wire fences. In 2008 and 2009, between 2 and 4 large (10 – 20 m²) fences were erected around groups of 5-12 nests in each colony, and in 2010 most nests were fenced individually in fences of ca. 1-2 m². To minimize disturbance and the risks of nest desertion, enclosures were erected after the terns had completed, on average, more than half of the incubation in each colony. Chicks were ringed and measured just after hatching and the colonies were re-visited every 3-5 days in order to relocate chicks for growth rate measurements. On each ringing and recapturing event, measurements of chick mass using a digital scale (to the nearest 0.1 g), wing length using a wing ruler (to the nearest 1 mm) and skull length using digital vernier callipers (head plus bill, to the nearest 0.1 mm) were recorded.

Collection of chick carcasses

Colonies were visited and individual nests were checked every 3-5 days and, during these visits, all carcasses of known (ringed) chicks were collected if found, along with a sample of unknown (un-ringed) chicks around the monitored nests. Arctic Terns are semi-precocial and chicks typically remain in the nest for the first 3 days after hatching. Carcasses of very young chicks were thus usually found in the nest bowl or by the nest. Older chicks often wander away from the nest but these were located during thorough searches within fenced areas. In the field, each chick carcass was placed in individual airtight zip lock sample bags and labelled with chick's ring number (if ringed), time, date and location of collection. Sample bags were then placed immediately in a cooler box (4°C) in the field, to limit decomposition of carcasses and larval growth, and transferred to a freezer within 8 hours of collection.

Collection and measurement of blowfly larvae

Defrosted chicks were examined in the laboratory for blowfly larvae or eggs on their exterior. Hatched blowfly larvae typically crawled out of the corpse and were readily visible in the zip lock sample bag. These larvae were collected and then the carcass was searched thoroughly for any remaining larvae. Unhatched blowfly eggs, typically 1-2 mm long, were less visible but often tucked under feathers in batches of dozens. Each infested carcass contained larvae in the range of tens to hundred

and usually all of very similar sizes. For each carcass, the length of the largest larva was measured, as this is likely to represent the first blowfly eggs laid on the carcass. Larvae were measured to the nearest 1 mm with a ruler. Chick corpses were then examined further for any ectoparasites visible by eye and endoparasites in the gut during dissections. Measurements of mass (measured to the nearest 0.1 g with an electronic scale), wing length (measured to the nearest 1 mm with a wing ruler), and the combined head plus bill length (or skull) (measured to the nearest 0.1 mm with digital callipers) were also recorded.

Estimation of dates of chick mortality

Arctic Tern chick carcasses were found infested with blowfly eggs or larvae of the *Calliphora* genera. Species identification of the larvae indicated either *Calliphora vicina* or *C. uralensis* but those are also the only two known *Calliphora* species common in the Icelandic insect fauna that lay on carcasses (E. Olafsson pers. comm.; Anon 2012). Patterns of temperature dependence growth rates have been well described for *C. vicina*. Here we use these growth rate estimates and assume that these represent both blowfly species. The date of death of each chick was estimated to the nearest day, assuming that blowfly eggs are laid within 24 hours of death, from the length of the longest larva using the temperature-dependent growth rate model of *Calliphora vicina* from Donovan *et al.* (2006):

$$\log_e(\text{length}) = a + bADH (1 - \delta ADH / (1 + 0.25 \beta)) / (1 + \beta \delta ADH), \quad (1)$$

where ADH = accumulated degree hours and values for $a = 0.632$, $b = 0.002042$, $\delta = 0.00016663$ and $\beta = 1.797$.

The model accounts for different larval growth rates at different temperatures, between 4°C and 30°C, where the minimum developmental temperature was estimated to be 1°C and 4700 ADH were required for development from egg hatch to the point of pupation.

Here, the larvae length (mm) was the known unit so the formula was solved for ADH. This model accounts for the different growth rate of the larvae under different temperature conditions. Hence, variable growth rates under fluctuating temperature in the field could be accounted for. Hourly air temperature data, measured at five locations around the Snaefellsnes peninsula (Fig. 3.1), were provided by the Icelandic Meteorology Office (www.vedur.is). Temperature

measures did not vary significantly between the different locations (all between-station correlations of hourly temperature, $r=0.79$, $n=8525$, $p<0.001$) so here the average hourly temperature across the five locations was used. The cumulative hourly temperature was then used to back-calculate the number of hours for which each larvae had been growing since collection in the field, and this was rounded to the nearest day, to give the estimated date of death of each chick.

Estimating chick ages and hatching dates

In order to estimate the date of hatching of each chick, the age of each chick at death was estimated from their skull (head plus bill) length at death, using the relationship between skull length and age for chicks ringed in the nest just after hatching and therefore of known age (Fig. 3.2; skull lengths of chicks that died and survived did not differ significantly through the pre-fledgling period (Chapter 4)). Skull lengths of all chicks collected as carcasses were used to estimate age at death using the equation in Figure 3.2 and age at death was subtracted from date of collection to give the estimated date of hatching of each chick.

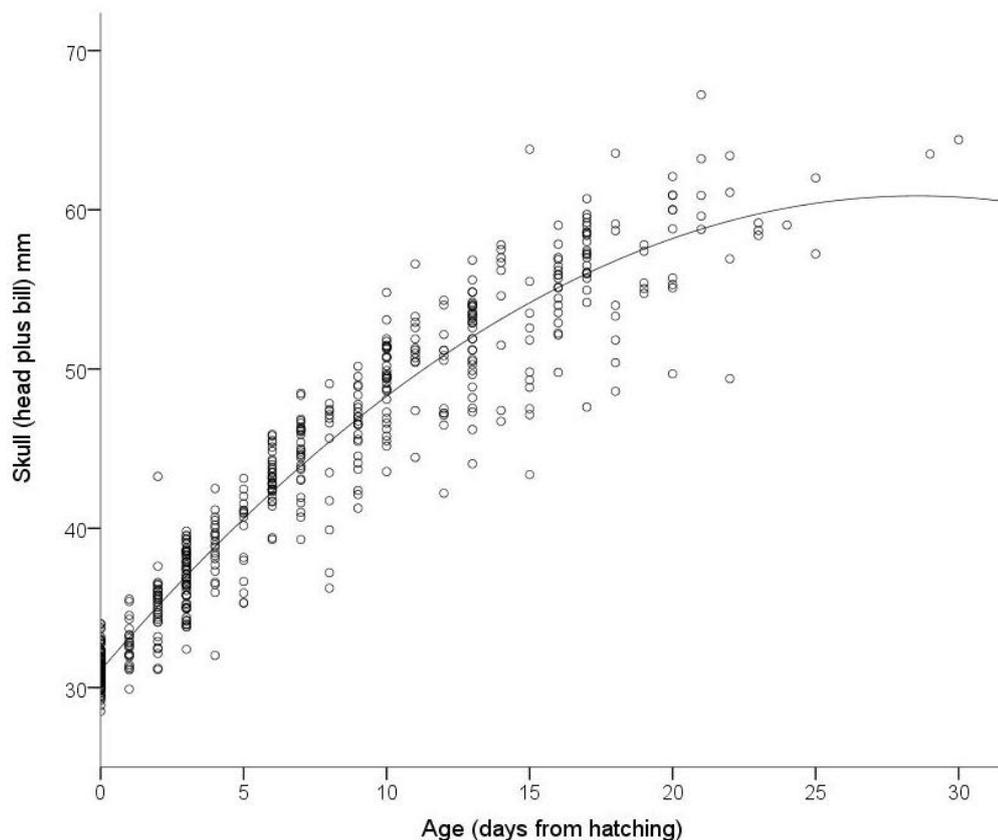


Fig. 3.2. The relationship between age (days from hatching) of chicks and skull (total head) length (mm) for Arctic Tern chicks hatched on colonies around the Snaefellsnes peninsula (Fig. 3.1) between 2009 and 2011. Fitted equation: $y = -0.037x^2 + 2.087x + 31.08$.

Statistical Analyses

In order to account for the timing of chick hatching in analyses of the timing of chick mortality in each colony, the cumulative number of these chicks that hatched each day was subtracted from the number dying each day within each colony, to give the number (of sampled chicks) that were alive on each day in each colony. Annual and between-colony variation in time (ordinal days from 1st June) of mortality of individual chicks was explored with generalized linear models with a normal error distribution. Year and colony were defined as fixed factors. The dependent variable was date of death with number of chicks alive each day in each colony included as an offset. The seasonal pattern of mortality and how this varied between colonies was explored with generalized linear models with a normal error distribution, with date of death of each chick as the dependent variable, colony, week and a colony * week interaction term as predictors, and the number of chicks alive each day in each colony included as an offset. These models were constructed separately for each of the three years of the study. Statistical analyses were conducted in SPSS 16.0 and full models are presented for completeness, as exclusion of non-significant factors or interactions did not alter the model findings.

Results

Annual range and pattern of mortality

Of the 1150 chicks that were collected from across the Snaefellsnes peninsula between 2008 and 2010, 78.4% contained blowfly eggs or larvae and 12.4% had evidence of having been eaten by larvae that had then left the carcass in the post-feeding stage. The remaining 9.1% of carcasses were mainly freshly dead or found just prior to death. A total of 949 of these 1150 Arctic tern carcasses collected were both examined for larval presence and were in a condition suitable for measures of body size and mass (Table 3.1). Carcasses were collected from seven colonies in all three years and additionally from two colonies (Larvadall and Skallabudir) in two years and one colony (Stakkhamarsnes) in one year. In 2008, a larger number of carcasses were collected than in subsequent years as a result of a greater effort in sampling. 40% of the carcasses were of chicks ringed soon after hatching, providing information on their origin, and frequent recaptures allowed estimation of their last known date alive.

Table 3.1. Total number of arctic tern chick carcasses collected in each study colony in each year (see Fig. 3.1 for colony names and locations).

Colony	2008	2009	2010
Arn	99	23	14
Ber	7	11	8
Gru	32	17	27
Hra	43	8	2
Lan	35	45	43
Lar		17	22
Rif	158	85	52
Ska	14	32	
Sta	108		
Sty	14	28	5
	510	266	173

The timing of chick mortality varied significantly between years and between colonies, and the pattern of annual variation differed significantly between colonies (i.e. interaction was highly significant, Table 3.2). Chick mortality occurred earlier in 2008 than in 2009 and 2010 (Fig. 3.3), with estimated chick mortality dates (ordinal days from 1 June) ranging from 16 -54 in 2008, 17 - 63 in 2009 and 29 - 69 in 2010, and thus spanning 38, 46 and 40 days respectively (Fig. 3.3a-c). In 2008, mortality was more concentrated in time and 95% of the mortality had taken place by 11th July, but in 2009 and 2010, this figure was not reached until 26th July in and 1st August, respectively (Fig. 3.3d). The continuous increase in cumulative mortality dates in each of the three years (Fig. 3.3d) suggests no seasonal concentration of mortality around specific dates.

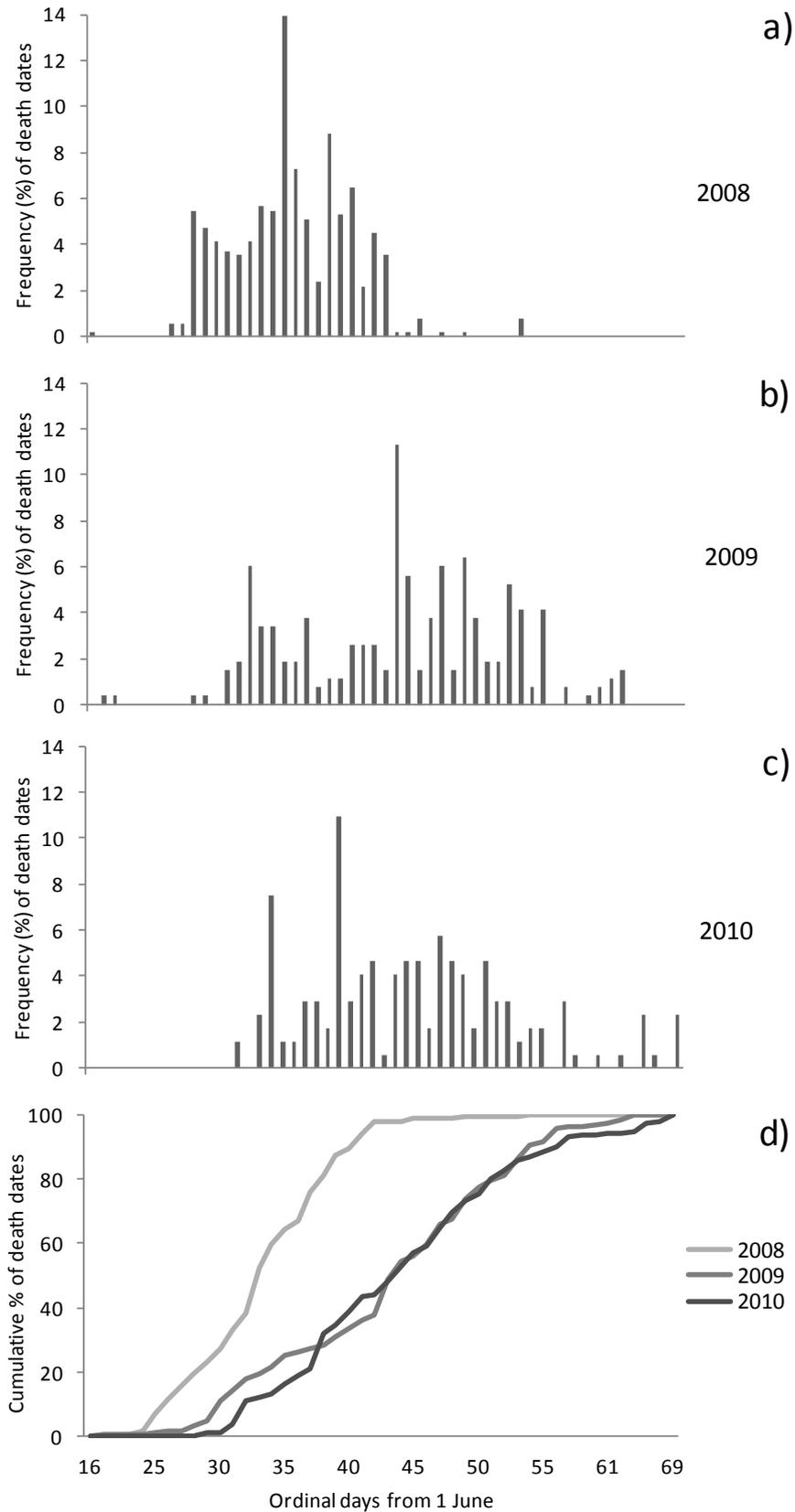


Fig. 3.3. Frequency distributions of estimated mortality dates (% of chicks dying on each date) of Arctic Tern chicks across the Snaefellsnes peninsula in a) 2008, b) 2009, c) 2010, and d) seasonal cumulative mortality of Arctic Tern chicks throughout each breeding season.

Table 3.2. Results of a) generalized linear models of annual and between-colony variation in mortality dates and b) general linear model of annual and between-colony variation in age at death of Arctic Tern chicks on Snaefellesnes peninsula, W Iceland, between 2008 and 2010.

	a) Mortality date			b) Age at death		
	W	df	<i>p</i>	<i>F</i>	df;df	<i>p</i>
Colony	12461.31	9	<0.001	8.807	9;923	<0.001
Year	3464.57	2	<0.001	114.091	2;923	<0.001
Colony*Year	5285.32	14	<0.001	438.61	14;923	<0.001

Table 3.3. Results of generalized linear models of between-colony variation in weekly mortality of Arctic Tern chicks on Snaefellesnes peninsula, W Iceland, between 2008 and 2010.

		W	df	<i>p</i>
2008	Colony	29.00	8	<0.001
	Week	17.25	5	<0.001
	Colony*Week	18.50	18	0.42
2009	Colony	186.72	8	<0.001
	Week	164.62	7	<0.001
	Colony*Week	201.10	22	<0.001
2010	Colony	59.37	7	<0.001
	Week	62.21	5	<0.001
	Colony*Week	74.84	19	<0.001

Variation between colonies in each year

The earlier dates of mortality in 2008 could result from earlier hatching dates in that year, but hatching dates varied little between years (mean hatching date 2008 31.15 ± 0.22 SE (ordinal days from 1 June); 2009 mean 32.81 ± 0.41 ; 2010 mean 34.91 ± 0.46 , Fig. 3.4). The time interval between hatching and mortality was therefore shorter in 2008 than in 2009 and 2010 (Fig. 3.4) and, in 2008, chicks died at significantly younger ages (Table 3.2b; Fig. 3.5). With the exception of Grundarfjordur (Gru), most chicks died within 5 days of hatching in 2008 while, in 2009 and 2010, the average age at death was typically between 10 and 20 days since hatching (Fig. 3.5). However, the annual variation in timing and age of mortality varied significantly among colonies (Table 3.2, Figs 3.4 and 3.5), which may suggesting some between-colony variation alongside the annual variation in chick mortality. The weekly pattern of mortality differed significantly among colonies, except in 2008 (Table 3.3).

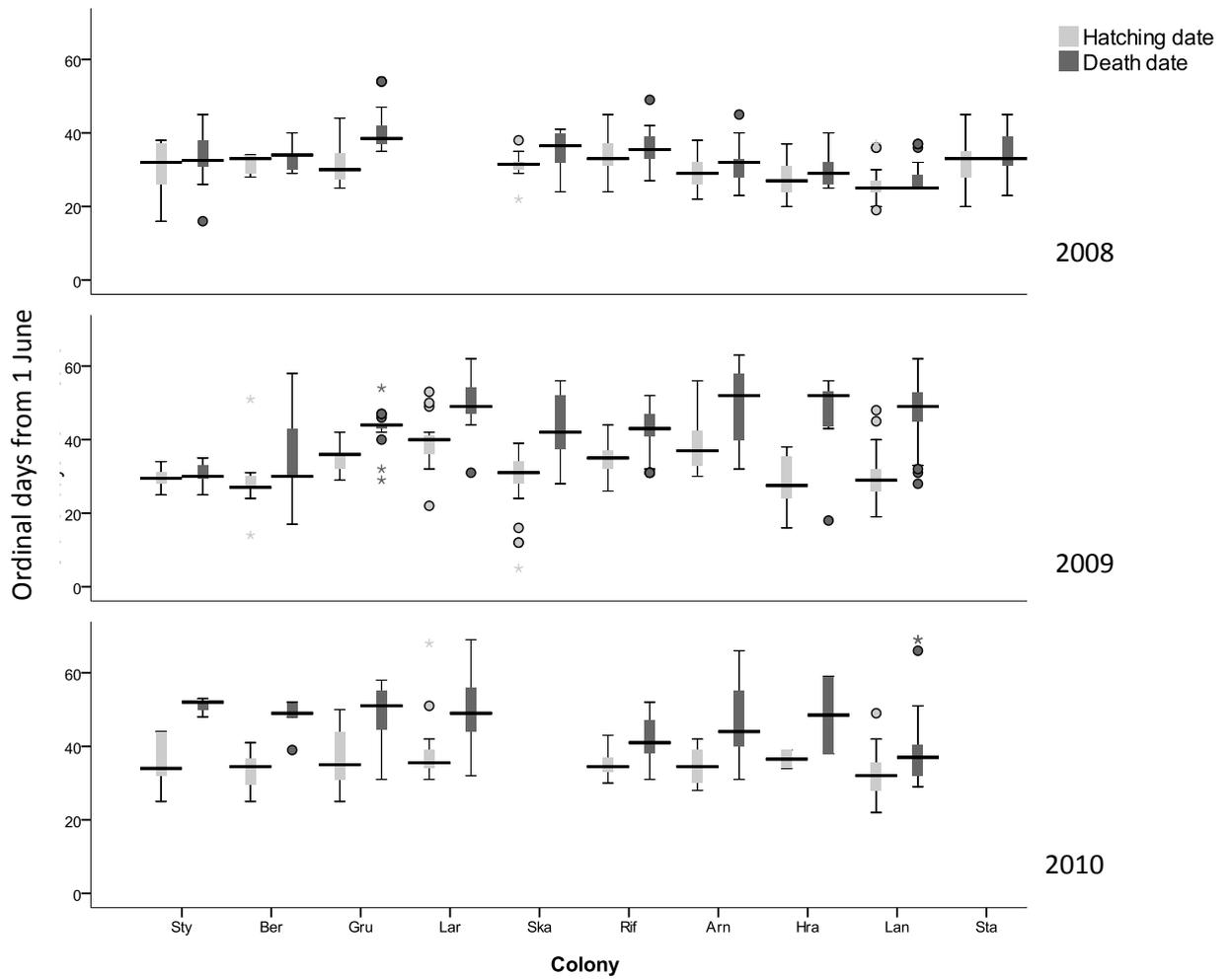


Fig. 3.4. Annual and between-colony variation in estimated hatching dates and dates of mortality (median, inter quartile and outliers) of Arctic Tern chicks on colonies around the Snaefellsnes peninsula. Colony order is presented geographically, from north-east to south-east. See Fig. 1 for colony locations and details.

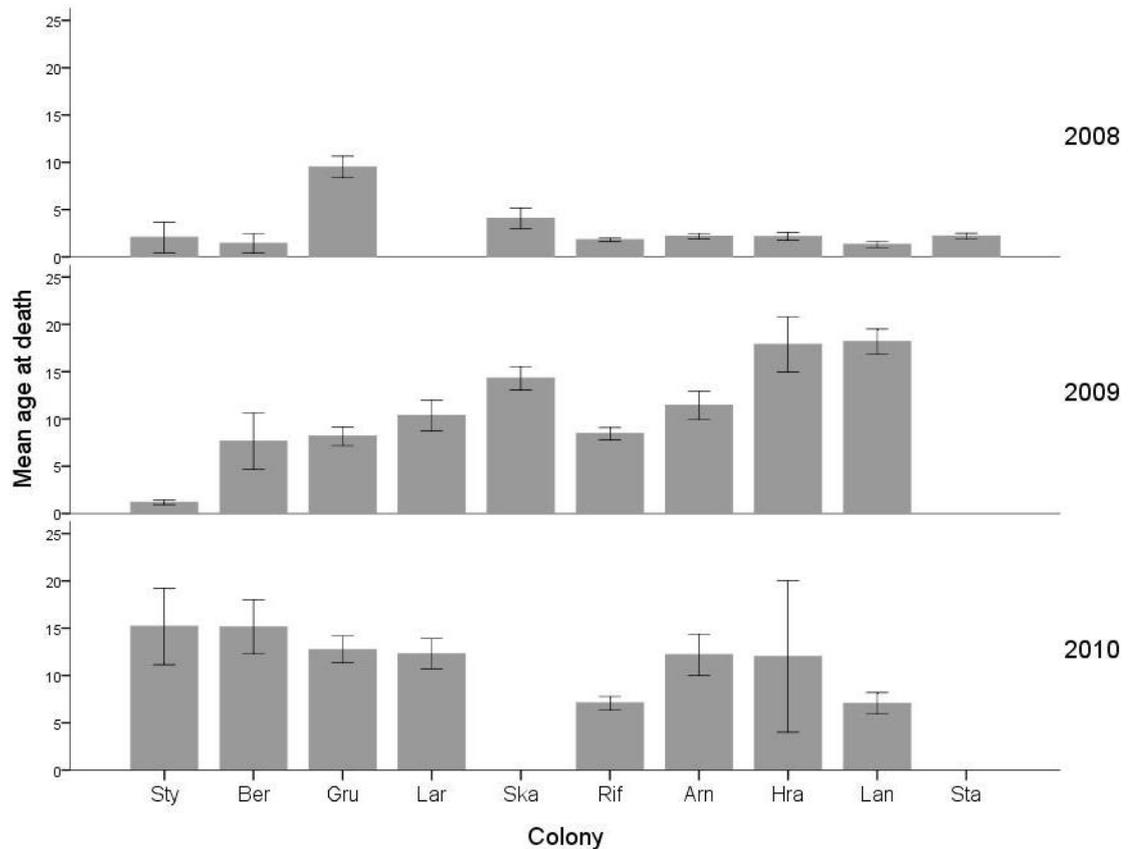


Fig. 3.5. Mean (\pm SE) estimated chick age at death in each colony studied across Snaefellsnes peninsula in 2008-2010. Colony order is presented geographically, from north-east to south-east. See Fig. 3.1 for colony locations and details.

Within colony variation in mortality each year

The cumulative pattern of timing of chick mortality across the colonies suggests continuous mortality throughout the breeding season, and little variation in the onset of mortality among colonies in each year, except for Grundarfjordur in 2008 which was slightly later and Stykkisholmur in 2009 which was slightly earlier than other colonies (Fig. 3.6). Although the levels of chick mortality varied significantly between weeks in all years (Table 3.3), the lack of any clear steps in the cumulative mortality curves suggests that mortality was not concentrated around particular dates in any of the colonies (Fig. 3.6). The weekly pattern of mortality varied significantly between colonies in 2009 and 2010, but not in 2008 (Table 3.3), suggesting that local factors influenced mortality in the latter two years, at least. The more synchronous chick mortality across colonies in 2008 is in part because most chicks died within a few days of hatching in that year, while mortality occurred throughout the pre-fledging period in the other two years (Fig. 3.7).

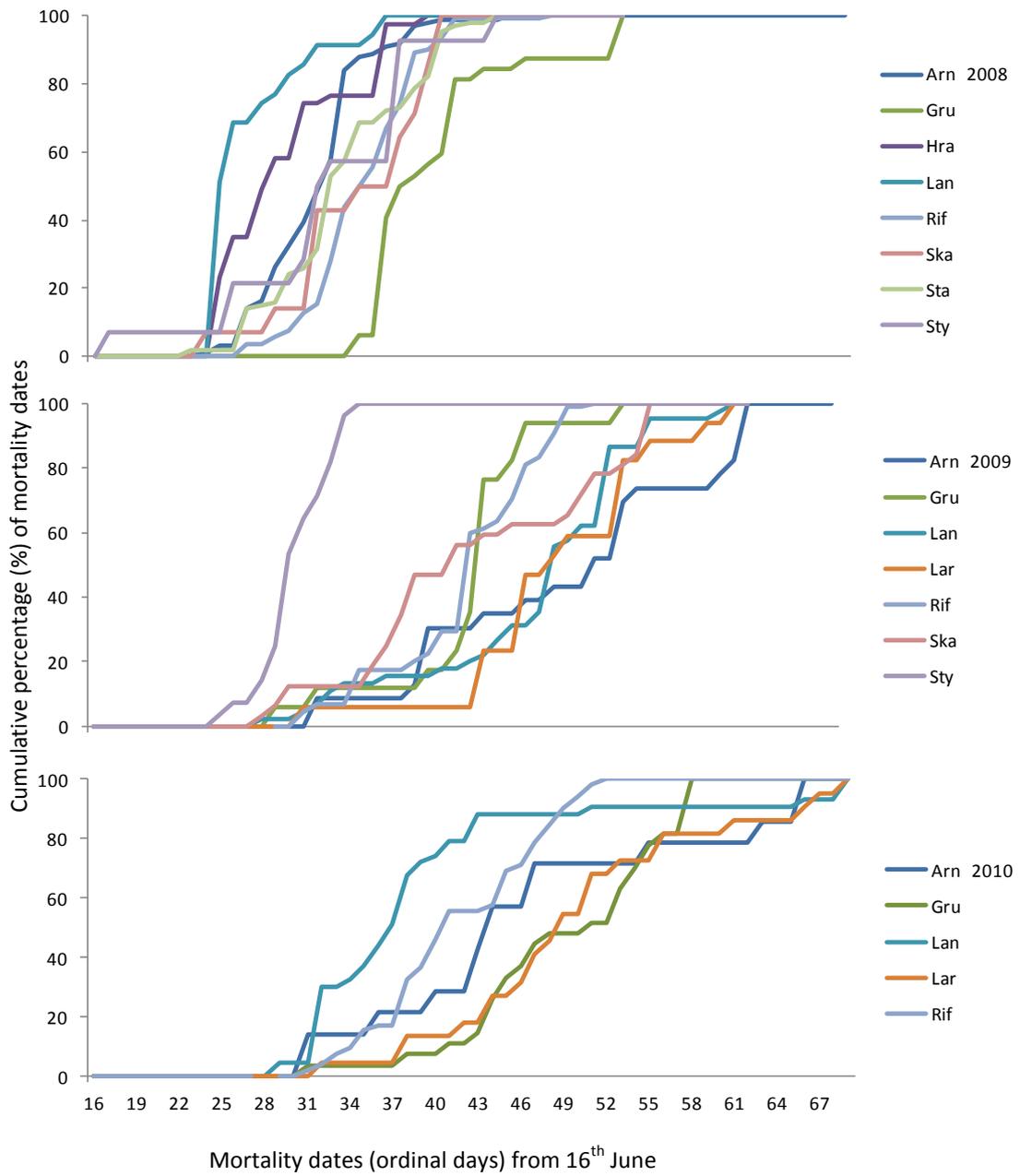


Fig. 3.6. Annual and between-colony variation in the cumulative timings of mortality of Arctic Tern chicks on colonies throughout Snaefellesnes peninsula, between 2008 and 2010.

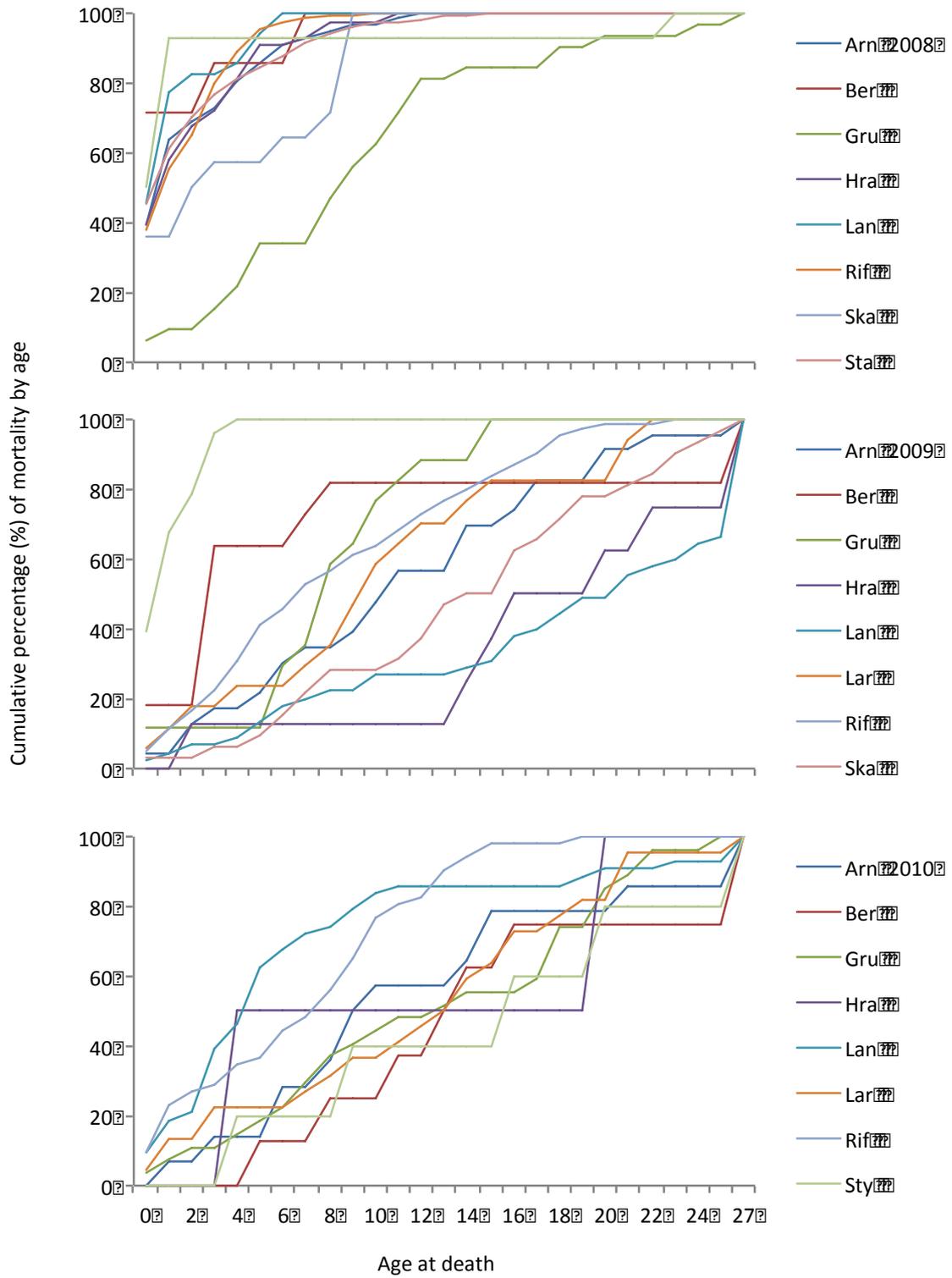


Fig. 3.7. Annual and between-colony variation in the cumulative mortality by age of Arctic Tern chicks on colonies throughout Snaefellesnes peninsula, between 2008 and 2010.

Discussion

Forensic ecology methods can provide a valuable tool to evaluate the timing of mortality events in cases where direct measurement of timing of mortality of individuals is not possible, for example in studies operating over spatial scales that are too large to allow sufficiently frequent visits to study locations. In this study we were able to compare timings of mortality at multiple sites spread over 200 km of coastline, and thus to assess the spatial scale of synchrony of chick mortality across 10 Arctic Tern colonies and over three consecutive breeding seasons. Mortality occurred throughout the season in all colonies, and there was no evidence of any synchronised concentration of mortality within or between colonies. Some evidence of annual variation in the timing of mortality was detected, with chicks in 2008 dying at a significantly younger age than in 2009 and 2010 and, as hatching dates were similar in all three years, mortality dates were earlier in 2008 than in 2009 and 2010. Overall, no periodic events causing the mortality were detected but more continuous driver(s) seemed to be the underlying cause demonstrated by the chronic and persistent chick mortality.

A range of different factors can influence chick mortality and can operate at different spatial and temporal scales. Unfavourable weather conditions can increase mortality (Robinson *et al.* 2002) and could operate over a large (e.g. regional) spatial scales, but severe weather conditions are most likely to also be time-restricted. Predators can also drive low breeding success through chick predation (Becker 1995) but these effects are likely to operate on site-specific scales and may operate in a non-chronic fashion, depending on the range and density of predators in the area and the extent to which their activities are linked to key points in their own breeding seasons. Resource limitations are known to drive breeding success and influence chick survival in many seabird species (Wanless *et al.* 2005; Szostek and Becker 2011), and resource constraints can occur across large areas and can be persistent over time (Heath *et al.* 2009). Information on timing of mortality events thus provides a tool to relate the mortality to timings of possible drivers in order to assess potential causes of mortality and to distinguish among different factors.

The observed mortality of Arctic Tern chicks between 2008 and 2010 operated across colonies on Snaefellsnes peninsula and thus over a large geographical scale. Within each season, chick mortality was persistent throughout the season but seemed to have happened earlier, or to have been more severe, in 2008 than in 2009 and 2010. Conditions that lead to high chick mortality may have occurred earlier in the season in 2008 and/or the cause(s) of the chick mortality may have varied between years.

The short and synchronous breeding season of Arctic Terns makes it a very difficult task to visit large numbers of colonies sufficiently frequently to directly quantify the dates of mortality of individual chicks. The forensic ecology techniques employed here allowed us to estimate dates of mortality for large numbers of chicks across multiple colonies over a large geographical area, and to explore the synchronicity of mortality across a wide range of breeding colonies. In order for this technique to be useful, the main requirements are that carcasses are available at the appropriate time and place relative to the study question, and that identification of the blowfly species and information on its distribution, behaviour and on the temperature-dependent larval growth rates are available. This method may therefore be particularly useful in colonial species where large samples of individuals can be examined and the variation between individuals within breeding area explored. Additionally, the semi-precocial behaviour of chicks like Arctic Terns aids relocation of carcasses, as they tend to stay in or close to the nest during chick rearing. This method can be useful in many different systems where it is necessary to understand patterns of mortality in space and time.

The limitations of the methods mainly concern the specific details of the insect life history traits and larval behaviour. In the post-feeding stage of blowfly larvae, the larvae often leave the carcasses, particularly if it is small in size and may not therefore provide sufficient resources (Greenberg and Kunich 2002; Donovan *et al.* 2006). The time it takes larvae to reach this stage is therefore the time limit between encountering a chick between its last life stage and the date of carcass collection. In the *Calliphora* species that occurred in this study, published studies suggest that this time limit was a maximum of 15 days (Donovan *et al.* 2006). However, in warmer climates the larvae growth rate might be faster and this time limit might be shorter (Greenberg and Kunich 2002). Additionally, in Iceland there are only two insect species that lay eggs in animal carcasses, and are useful in this regard, the blowflies *C. vicina* and *C. uralensis* (E. Olafsson pers. comm.; Anon 2012). This might not be the case in other countries, in particular in warmer climates with higher insect diversity. But as widely described in the forensic literature, insects colonize carcasses in a predictable order (Amendt *et al.* 2004), and information on the life history of the particular species is often available. However, there is some information that suggests that there are geographical differences within the same species in regards to larval development temperature boundaries and diurnal activity differences in the adult behaviour during oviposition (McWatters and Saunders 1996, 1998).

Systems where this technique might be appropriate and of use may be in cases in which mass mortalities can occur, such as in disease outbreaks, mass starvation or weather-related mass-mortality events for migrants (Newton 2007). Additionally, the method can be used where areas of interest are inaccessible, and cannot be

visited as frequently as needed in order to assess patterns of mortality of a given study population. For example, current concerns over bird collisions with structures such as wind turbines during periods with adverse weather conditions (Drewitt and Langston 2006) may find these forensic ecology techniques useful for assessing dates of mortality of individuals from remote areas.

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Chapter 4

Chapter 4

Causes of extensive Arctic Tern chick mortality across colonies in West Iceland

Abstract

Seabird demography is closely linked to marine environmental conditions, especially during the breeding season when their foraging range is spatially constrained to near nesting areas. Recent changes in marine environments may therefore be linked to changes in seabird productivity and population trends. Here, we assess causes of extensive Arctic Tern chick mortality across colonies on the Snaefellsnes peninsula in West Iceland during period of low productivity in 2008-2011 in relation to age, chick growth and survival probabilities. Overall, 46% of chicks died and 24% were assumed to have fledged, but 30% of chicks went missing without a known fate. Chicks of unknown fate tended to go missing at very young age and small size and were most likely undetected victims of starvation and/or predation. Proportion of chicks dying did not vary in relation to weather. Arctic Tern chick mortality was evenly distributed across colonies and across age stages suggesting chick starvation was occurring over a large spatial scale and was persistent through the breeding season. Daily changes in mass significantly influenced survival probabilities of Arctic Tern chicks across colonies and correctly predicted individual death in 80-95% of cases. Poor Arctic Tern productivity across colonies in W-Iceland in 2008-2011 was primarily caused by extensive chick mortality driven by starvation.

Keywords: Animal ecology, Demography, Breeding success, Chick mortality, Seabirds, Arctic Tern

Introduction

Seabirds are adapted to breeding on land and foraging in the highly variable marine environment with adaptations such as colonial breeding, small clutch size, prolonged incubation and chick rearing, delayed maturity and high adult longevity (Schreiber and Burger 2002). Among the main environmental constraints influencing seabird productivity are extrinsic factors such as food supply, predation and weather. These factors can influence breeding parameters such as clutch size and volume (Monaghan and Nager 1997; Ricklefs 2000; Martin 2000), laying date (Safina *et al.* 1988), chick growth (Massias and Becker 1990) and fledging success (Crawford and Dyer 1995). In addition, environmental stresses such as periods with limited resource availability can lead to trade-offs between resource allocations for possible future reproduction versus current breeding output (e.g. Williams 1966). A wide range of environmentally-driven impacts on breeding parameters have been described for seabirds, from adjustments in activity budgets (e.g. decreased attendance and increased foraging time) during periods of slight decreases in food availability to severe declines in chick survival (e.g. caused by starvation) during periods with poor foraging conditions (Cairns 1987). However, declines in adult survival are only predicted to occur when resources are extremely scarce, inhibiting adults to maintain their own body condition even after adjustments in breeding activity or output (Cairns 1987, Hamer *et al.* 1991, Davis *et al.* 2005).

Large-scale biological responses to climatic variability and global climate change have been observed to be particularly pronounced in marine ecosystems (Harley *et al.* 2006). As a result of past changes in air temperatures, ocean temperatures have risen in recent decades (Belkin 2009; Burrows *et al.* 2011) and this warming trend is amplified toward polar regions (Serreze *et al.* 2007; Graversen *et al.* 2008). Further ocean warming, along with other predicted physical changes such as sea level rise and declines in the extent of sea ice, are expected to have persistent and intensified effects on marine ecosystems in the future (Stenseth *et al.* 2002). Changes in the distribution of prey will affect seabirds directly through changes in bottom-up food web dynamics (Ware and Thomson 2005), as seabird population trends are strongly influenced by variation in prey abundance (Veit *et al.* 1996; Montevecchi and Myers 1997; Thompson and Ollason 2001; Frederiksen *et al.* 2006; ICES 2009; Jennings *et al.* 2012), which can in turn be influenced by fishing pressure (Frederiksen *et al.* 2004), and environmental conditions such as changes in sea temperature (Dulvy *et al.* 2008). Ongoing depletion of fishing stocks and observed, and future predicted, shifts in fish distributions in response to rising sea temperatures (Perry *et al.* 2005), may therefore have considerable and persistent negative effects on seabird populations (Burthe *et al.* 2012; Frederiksen *et al.* 2012), which are likely to be manifest in low chick survival, reduced productivity, decreased adult survival and possibly population declines (Szostek and Becker 2011; Sandvik *et al.* 2012).

In recent decades, breeding densities of several seabird species have decreased across the North Atlantic (Frederiksen 2010; Sydeman *et al.* 2012; ICES 2012). Reports of repeated annual breeding failures and chick mortality from most major North Atlantic seabird areas (Frederiksen 2010) coincide with measures of population declines for numerous species across the North Atlantic (Mavor *et al.* 2008; Barrett *et al.* 2012). Identifying the causes of these declines is complex but large-scale oceanic changes and climatic variability are suggested to underpin many of the changes (e.g. Sydeman *et al.* 2012). During the last 15 years, the waters around the South and West of Iceland have warmed by 1-2°C and many southern commercially fished species have extended their ranges further North, and northern species ranges have retreated further North (Valdimarsson *et al.* 2012). Further hydrographic changes with warming sea temperatures have been predicted in the future at high latitudes, including Icelandic waters (IPCC 2007). A key component of the diet of many of the fish species which seabirds consume is copepods, and a recent study exploring changes in copepod density in relation to climatic and oceanic changes suggests that seabird populations in the NW-Atlantic have been influenced by disruptions in this base of the food web, and that these changes will increase in ocean areas further North, including Iceland (Frederiksen *et al.* 2012).

Arctic Terns are relatively small seabirds that undertake an annual pole-to-pole migration, from breeding areas at high northern latitudes to winter areas in the South Atlantic Ocean (Egevang *et al.* 2010). During the breeding season, they have relatively short (~ 5 - 10 km) foraging ranges (Pearson 1968; Rock *et al.* 2007) and spend a large proportion of their time foraging during chick rearing (Pearson 1968). Additionally, their pole-to-pole migration (Egevang *et al.* 2010) and late arrival to the Icelandic breeding grounds (e.g. Gunnarsson and Tomasson 2011) mean that individuals are on a tight schedule for breeding. This may make them particularly sensitive to environmental stresses such as changes in food abundance or availability during chick rearing, as there is little time for re-laying following unsuccessful nesting attempts.

Although there is evidence for changes in sea surface temperatures (Valdimarsson *et al.* 2012) and associated food web dynamics in Iceland waters (Frederiksen *et al.* 2012), the impact of these changes on seabirds in Iceland is not known. However, we have previously shown that Arctic Tern productivity appears to have been very low on colonies across the Snaefellsnes peninsula in West Iceland during the years of 2008 to 2011 (Chapter 2) and that these breeding failures were primarily a function of high chick mortality (Chapter 3). In order to explore the causes of this high chick mortality, we explore whether the chick mortality in these colonies can be related to predation effects, weather conditions or food supplies. In particular,

we assess the variation in chick growth rates between colonies and the extent to which it determines chick survival.

Methods

Study area and species

The study was conducted on Snaefellsnes peninsula from 2008 to 2011. Snaefellsnes is situated in W-Iceland, and comprises a mountainous terrain surrounded by coastal lowlands. The peninsula stretches 100 km into the Atlantic Ocean, between the bays of Faxafloi and Breidafjordur (Fig. 4.1). The peninsula supports numerous seabird colonies, both of cliff breeders and ground nesters. Arctic Tern colonies are found along the whole coastline of the peninsula.

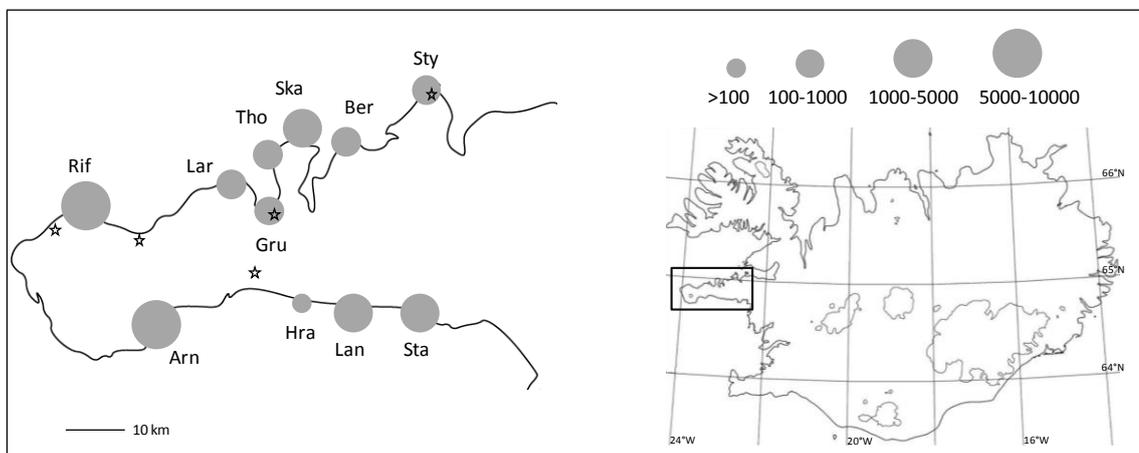


Fig. 4.1. Location and size (circle size: approximate number of pairs) of Arctic Tern study colonies on Snaefellsnes peninsula and the location of the peninsula in western Iceland (inset). Sty: Stykkisholmur, Ber: Berserkseyri, Ska: Skallabudir, Tho: Thordisarstadir, Gru: Grundarfjordur, Lar: Larvadall, Rif: Rif, Arn: Arnarstapi, Hra: Hraunsmuli, Lan: Langaholt, Sta: Stakkhamarsnes. Stars indicate locations of weather stations.

Nest monitoring and chick measures

In each colony, chick growth rates and survival were monitored throughout the breeding season by following nests and recapturing known (ringed) chicks. Between 15-148 chicks in each colony were ringed and re-measured every 3-5 days, and between four and 11 Arctic Tern colonies were monitored each year. Within each colony, nests were located during egg-laying, and egg floatation (Rahn and Paganelli 1989) was used to estimate egg incubation stages and predict hatching dates. Arctic Terns are semi-precocial and chicks typically remain in the nest for the first three days after hatching. Nests were visited every 1-3 days around the predicted hatching date to ensure date of hatching was known for as many nests as possible.

To aid nest and chick relocation, monitored nests were enclosed within low (30 cm high) chicken-mesh wire fences. At each recapture, to monitor growth rates, measurements of mass (measured to the nearest 0.1 g with electronic scales), wing length (measured to the nearest 1 mm with a wing ruler), and the combined head plus bill length (or skull) (measured to the nearest 0.1 mm with digital callipers) were recorded for each chick. Chicks were considered to have fledged successfully if they reached at least 80 g in mass and/or 100 mm wing length and were not relocated on subsequent visits (Drent *et al.* 1987; Klaassen *et al.* 1989a, 1989b).

On each visit to each colony, fenced areas were searched thoroughly for dead, ringed chicks. Dead chicks were placed in a zip-lock bag, stored in a 4°C cooler box in the field and put in a freezer within eight hours of collection. Estimation of date of death of these chicks was obtained via forensic techniques using length of blowfly larvae or eggs that had been laid on the carcasses (details in Chapter 3). Briefly, blowfly larvae growth rates are temperature-dependent so the accumulated degree hours (ADH) together with the length of the longest larvae on carcasses can be used to estimate the minimum time (here date) of death, by estimating the number of days since blowflies colonised the carcass and subtracting this from the date of collection. Age of later recaptured chicks was known for 192 of chicks as they were ringed and handled on the day of hatching. Age estimates for the remaining chicks were obtained using the relationship between skull length and age for chicks of known age (Chapter 3, Fig. 4.2).

Data analysis

The maximum known age (days) of chicks that are known to have died, fledged or that went missing were compared in a general linear model with a normal error distribution, with fate (died, fledged, fate unknown) and year as fixed factors. Arctic Tern chicks have been reported to experience higher mortality during bad weather, characterized by high wind speeds, high rainfall and low air temperatures (Robinson *et al.* 2002). In order to assess whether weather conditions may have influenced chick survival on these colonies, measures of high wind speeds (daily maximum wind (gust) speed), low temperature (daily minimum temperature), average wind speed (daily average wind speed) and humidity (daily average humidity) were explored in relation to number of chicks dying each day. Weather data were provided by the Icelandic Meteorology Office as hourly measures at five locations across the peninsula. Here, daily averages of weather parameters were used and the influence of daily weather conditions on daily chick mortality (arc-sin square root transformed percentage of chicks dying each day in each colony) was explored in general linear models with a normal error distribution, with year and colony included as fixed factors, and non-significant predictors were removed by backwards elimination.

As the rate of mass gain in chicks changes in a non-linear fashion through the pre-fledging period, the effect of growth rates on chick survival were explored during three periods with differing growth rates (0-5 days, 6-15 days and 16-33 days). These periods were defined visually and correspond to similar periods used in other studies (Suddaby and Ratcliffe 1997; Robinson and Hamer 2000; Stienen and Brenninkmeijer 2002). Age in chicks whose hatching date was not known was estimated from skull length after calibrating age against skull length in chicks of known hatching date. Logistic regression models of the influence of change in body mass (g/day) on the survival probability of Arctic Tern chicks during each pre-fledging growth period were constructed, with colony included as a fixed factor. Finally, the variation in body mass (g) and body size (skull length, mm) among chicks that did or did not survive each of the three growth periods was explored in generalized linear mixed models with a normal error distribution of individual body mass with fate (survived or died) and body size and their interaction as predictors, with individual included as a random factor.

Results

Arctic Tern breeding success

Between 2008 and 2011, Arctic Tern productivity on Snaefellsnes peninsula was very low, with none of the monitored chicks fledging in several colonies for several years, with fledging success in most of the remaining colonies ranging from 0.05 to 0.5 chicks per pair (Fig. 4.2). Only one colony in one year reached on average one fledgling per nest (Fig. 4.2). Fledging success in most colonies was higher in 2010 than in other years; in 2009, none of the measured hatchlings fledged in six out of ten colonies and in 2011 only two out of five colonies fledged any of the measured hatchlings (Fig. 4.2).

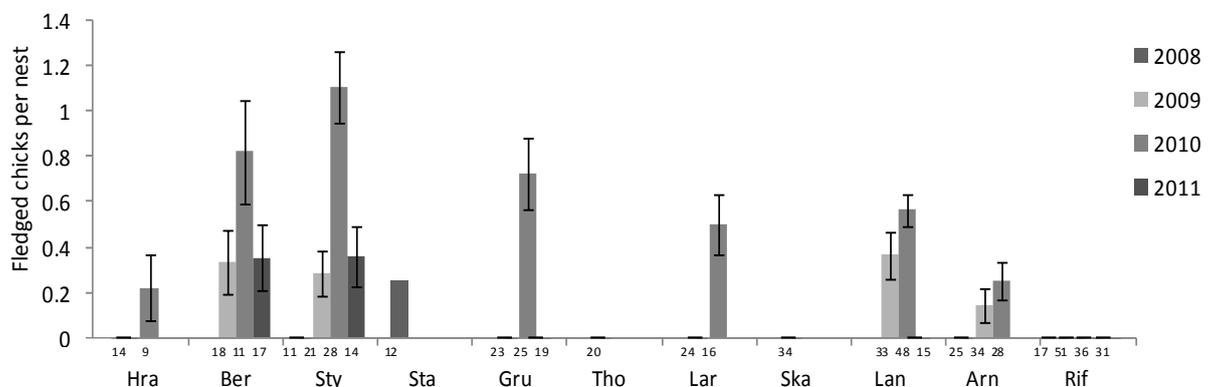


Fig. 4.2. Annual and between-colony variation in the mean (\pm SE) number of Arctic Tern chicks fledged per nest on the Snaefellsnes peninsula, W-Iceland. Colony order is presented according to colony size (from smallest (left) to largest (right)). Black dashed lines indicate zero values. Number of nests monitored in enclosures in each colony each year is indicated under the horizontal axis.

Chick fates

High levels of pre-fledging mortality can result from predator activities but, in semi-precocial species, predation impacts can be hard to measure because predation events are rarely observed and the fate of chicks preyed upon can rarely be confirmed. However, in each year of this study, between 50 and 80% of chicks within enclosures were assigned a final fate, i.e. found dead or reached a size where they were likely to have fledged (Fig. 4.3). Across all years, ~30% of ringed chicks from enclosures went missing before a final fate could be assigned to them, ~50% were confirmed to have died and ~20% were either confirmed or very likely to have fledged (Fig. 4.3).

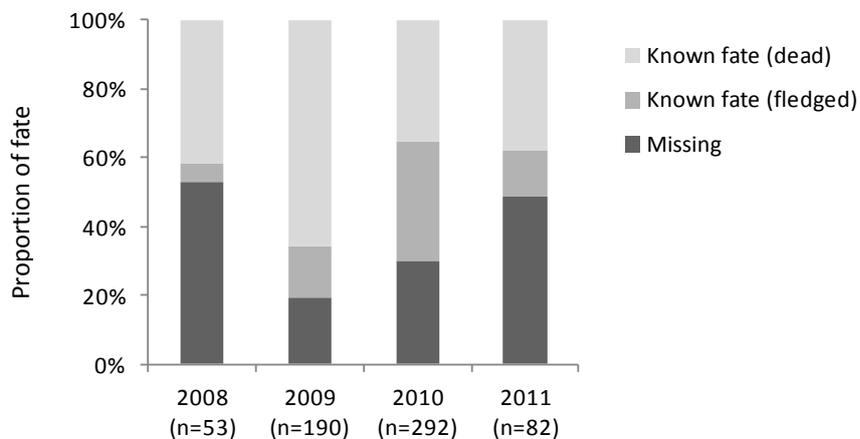


Fig. 4.3. The proportion of Arctic Tern chicks either known to have fledged or died or that went missing (fate unknown) prior to fledging from enclosures on colonies across the Snaefellsnes peninsula between 2008 and 2011. Numbers below bars indicate the number of chicks in each year.

Semi-precocial chicks can experience predation throughout the pre-fledging period and so, if missing chicks were preyed upon, they may be expected to go missing at all ages. However, while the mean age at last capture (either known from hatching date or estimated from skull length, see Methods) for chicks that subsequently died was 10.25 days (SE: 0.404), and for chicks that fledged was 23.20 (SE: 0.386), chicks that went missing tended to do so at a much younger age (mean age = 4.83 days (SE: 0.50), Fig. 4.4, fate: $F_{2,2175}=157.8$, $p<0.001$, year: $F_{2,2175}=39.04$, $p<0.001$). Thus if predation were the cause of mortality among these chicks, it would have to be biased towards very young chicks.

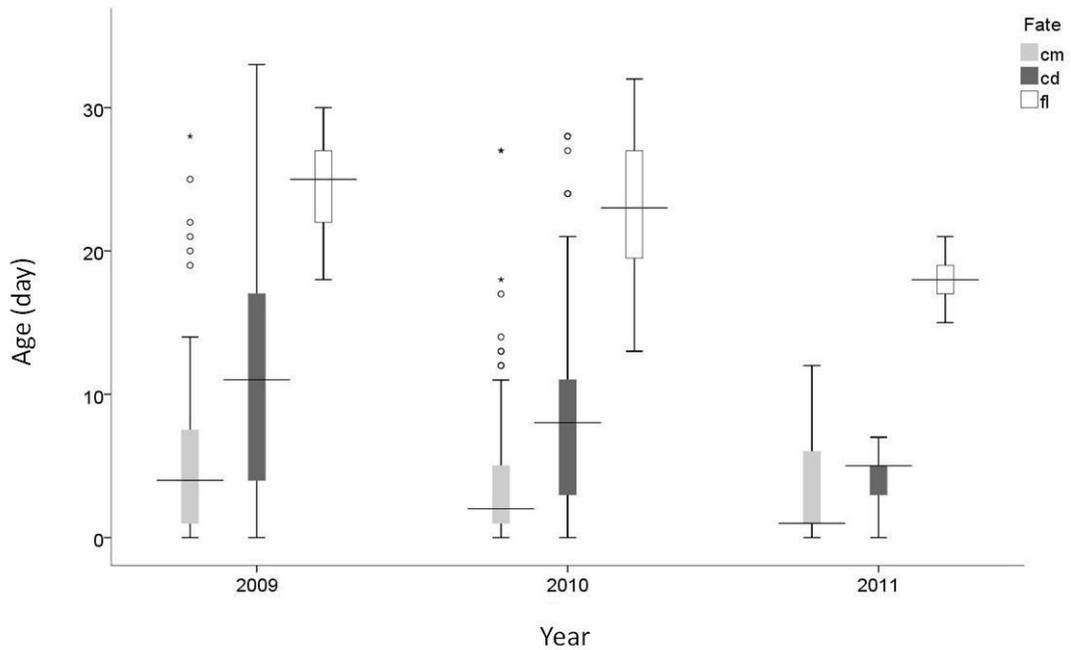


Fig. 4.4. The estimated age (median, inter quartile and outliers) at final capture of Arctic Tern chicks that subsequently went missing (cm), were found dead (cd) or fledged (fl) at colonies across the Snaefellsnes peninsula in 2009-2011.

Patterns of chick mortality during severe weather

Subarctic bird populations can be subject to severe weather conditions at their breeding grounds, which can influence survival probabilities of chicks (Robinson *et al.* 2002). However, the daily percentage of Arctic Tern chicks dying was not significantly related to any of the following weather conditions on those days; maximum wind speed ($F_{1,97}=2.8$, $p=0.10$), average wind speed ($F_{1,97}=1.6$, $p=0.22$), minimum temperature ($F_{1,97}=0.3$, $p=0.61$) and maximum humidity ($F_{1,97}=1.8$, $p=0.19$). There was also no evidence for greater chick mortality on days with particular combinations of different wind speeds, temperature and humidity, as days with low and high levels of chick mortality occurred throughout the recorded range of these weather variables (Fig. 4.5).

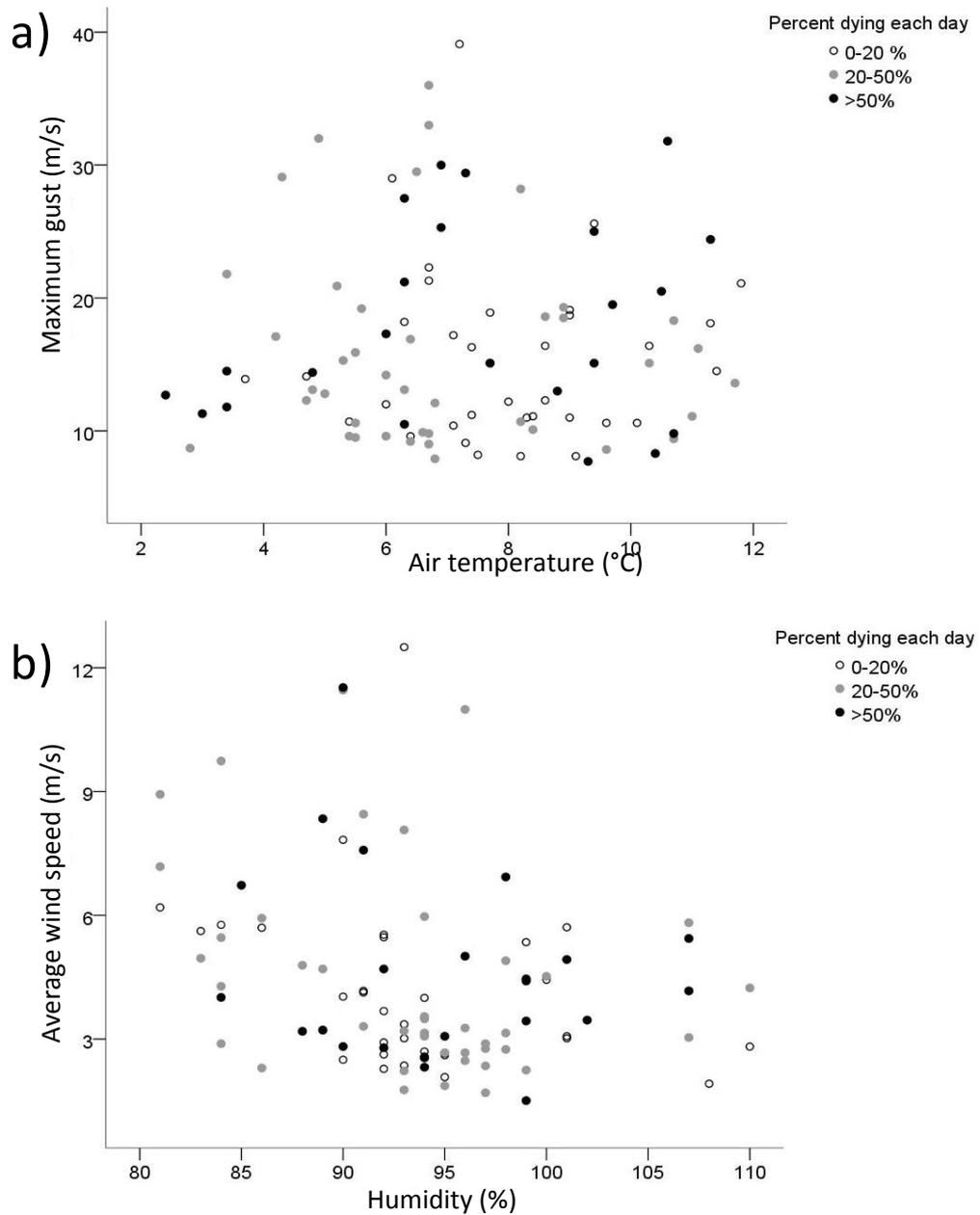


Fig. 4.5. Proportions of Arctic Tern chicks dying on days with differing a) minimum air temperatures and maximum wind speeds and b) maximum humidity and average wind speed on colonies across the Snaefellsnes peninsula.

Age-specific growth rates and survival

Arctic Tern chicks hatched at around 10-15 g and mass increased rapidly during the first two weeks after hatching (Fig. 4.6). The variation in mass increased with age and varied greatly among individuals, particularly among chicks older than 5 days.

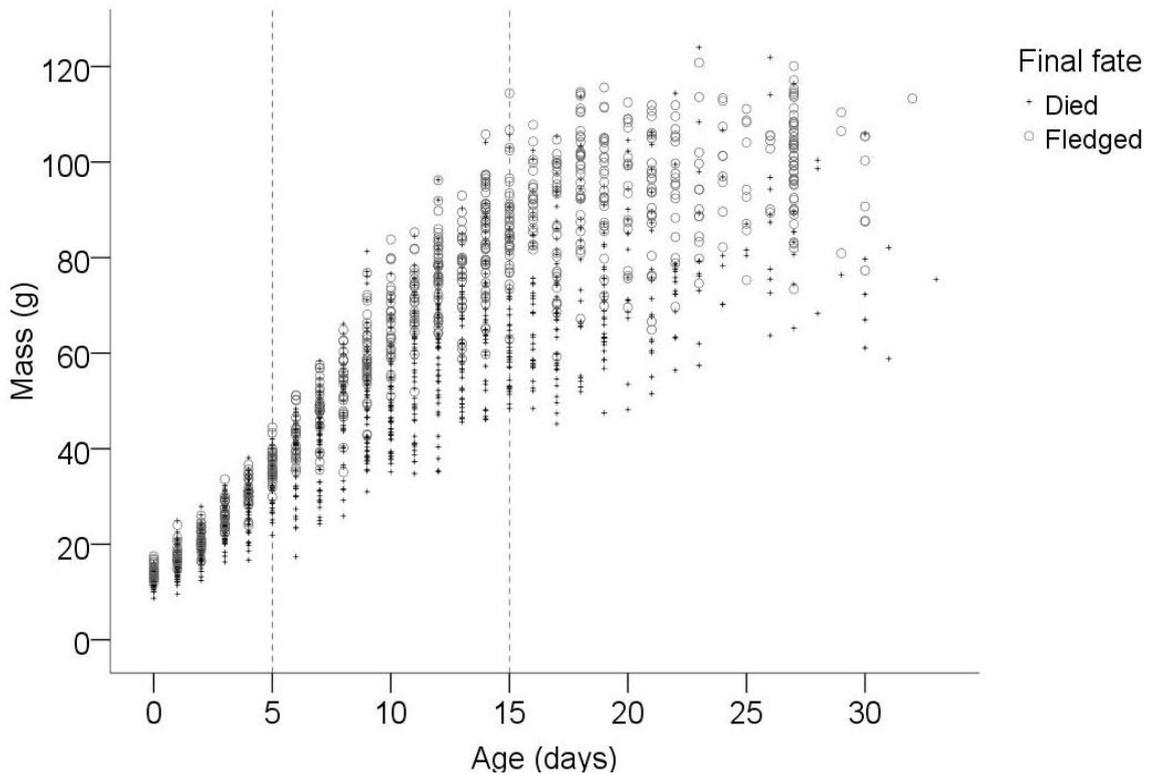


Fig. 4.6. The increase in mass of Arctic Tern chicks throughout the pre-fledging period, for 500 chicks hatched in colonies throughout the Snaefellsnes peninsula between 2009 and 2011. Vertical dashed lines indicate periods with differing rates of growth.

In all three periods of pre-fledging growth, chicks that died had shorter wing and skull lengths compared to those that survived, but the magnitude of these differences (2 - 7%) was always much smaller than the differences in mass 10 - 30%, Table 4.1). Thus individuals that died had similar rates of structural development but differed much more in rates of mass gain than those that survived in each growth period.

Table 4.1. Mean (\pm S.E.) mass, wing and skull (head+bill) measures, percentage differences and results of t-tests for Arctic Tern chicks that either died or survived during each of the three pre-fledging growth phases, for chicks hatched on colonies across the Snæfellsnes peninsula in 2009-2011 (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

	Age 0-5 days			Age 6-15 days			Age 16-33 days		
	Survived ($n = 137$)	Died ($n = 472$)	% t	Survived ($n = 280$)	Died ($n = 540$)	% t	Survived ($n = 261$)	Died ($n = 228$)	% t
Mass (g)	27.9 \pm 2.27	25.1 \pm 1.19	10 1.13	69.2 \pm 0.99	56.6 \pm 1.07	18 7.6***	108.2 \pm 6.32	76.1 \pm 1.08	30 5***
Wing (mm)	25.6 \pm 0.61	23.8 \pm 0.32	7 2.7**	80.6 \pm 1.50	75.3 \pm 1.05	6 2.8**	149.1 \pm 5.84	141.4 \pm 1.41	5 1.2
Skull (mm)	36.1 \pm 0.28	35.3 \pm 0.15	2 2.3*	49.2 \pm 0.23	48.2 \pm 0.16	2 3.6***	58.6 \pm 0.14	57.9 \pm 0.17	1 3.3**

Across all 11 colonies that were studied between 2009 and 2011, Arctic Tern chick mortality occurred throughout the pre-fledging period, with ~18% of chicks dying in the first 5 days, ~32% of the chicks that survived the first 5 days dying during days 6-15, and ~33% of the chicks that survived the first 15 days dying during the final period of growth (Table 4.2). The pattern of age-specific mortality of chicks was also similar across all colonies (Table 4.2).

Table 4.2. Numbers of Arctic Tern chicks measured and the percent dying during the three pre-fledging growth phases in each colony (see Fig. 4.1 for colony details).

Colony	Age 0-5 day		Age 6-15 day		Age 16-33 day	
	n	% dead	n	% dead	n	% dead
Arn	86	22	57	28	27	41
Ber	29	14	31	6	18	6
Gru	87	0	84	15	44	9
Hra	25	8	17	12	11	36
Lan	122	11	98	7	75	32
Lar	62	5	34	29	18	22
Rif	175	35	98	69	18	72
Ska	35	9	48	29	32	66
Sta	16	69	4	100		
Sty	83	18	58	2	47	6
Tho	23	13	25	56	9	44
	743		554		299	

Influence of chick body condition on survival probability

The survival probability of chicks during each of the three pre-fledging growth periods was significantly influenced by their growth rates during each period, with chicks with lower growth rates being significantly more likely to die during each period (Table 4.3, Fig. 4.7). However, the effect of change in absolute mass on survival probability was weaker in the older age groups, becoming proportionally smaller with age; an absolute change in mass of 1 g alters survival probability by 5.23 during the first five days, but by 2.25 during 6-15 days and by 1.90 at 16-33 days old. These models correctly predicted survival probability in more than 90% of cases during the first two growth phases, and in 70-80% for the final growth phase (Table 4.3). Survival probabilities did not differ significantly between colonies, except for 6-15 day old chicks on Langaholt, on which slightly fewer chicks died at this stage than in other colonies and Larvadall, on which slightly more chicks died at this stage (Tables 4.2 and 4.3b).

Table 4.3. Results of logistic regression models of the influence of change in body mass (g/day) on the survival probability of Arctic Tern chicks during each of the three pre-fledging growth periods, for chicks on ten colonies on the Snaefellsnes peninsula between 2009 and 2011.

Variable	a) Age 0-5 days				b) Age 6-15 days				c) Age 16-33 days			
	Wald	df	Sig.	Exp(B)	Wald	df	Sig.	Exp(B)	Wald	df	Sig.	Exp(B)
Change in mass	38.82	1	<0.01	5.23	44.52	1	<0.01	2.25	6.35	1	0.01	1.90
Arn	7.15	9	0.62		18.18	9	0.03		5.78	8	0.67	
Ber	0.06	1	0.80		0.22	1	0.64					
Gru	0.14	1	0.71		0.00	1	1.00		0.13	1	0.72	
Hra	0.00	1	1.00		1.37	1	0.24		0.00	1	1.00	
Lan	0.22	1	0.64		6.21	1	0.01		0.00	1	0.96	
Lar	0.27	1	0.60		7.11	1	0.01		1.35	1	0.25	
Rif	0.07	1	0.79		0.14	1	0.71		0.15	1	0.70	
Ska	0.15	1	0.70		0.00	1	0.96		0.62	1	0.43	
Sty	0.94	1	0.33		0.17	1	0.68		0.93	1	0.34	
Tho	0.20	1	0.65		3.61	1	0.06		0.00	1	1.00	
Constant	1.02	1	0.31		1.83	1	0.18		0.04	1	0.85	
Log likelihood ratio	76.44				167.51				44.30			
% correctly predicted dead	95.20				91.60				86.20			
% correctly predicted alive	94.40				90.00				72.00			
Overall % correctly predicted	94.70				90.60				79.60			

Chicks were more likely to survive the first five days of their life if they were able to gain more than 2.5 g per day (Fig. 4.7a). Chicks gaining less than 2 g per day or losing mass during these first days of life were most likely to die during that period. During the rapid growth period of 6-15 days old, all but two chicks that died gained less than 2 g per day (Fig. 4.7b). On average, the chicks surviving during this life stage gained ~5 g per day but the ones dying during this stage lost, on average, ~1.5 g/day. Change in mass was a weaker predictor of survival probabilities during ages 16-33 days, and a number of chicks predicted to survive had a negative change in mass during this final life stage. Surviving this period is defined by reaching a given size/mass (100 mm wing and/or 80g), whereas in the previous periods survival meant that chicks were recorded alive in subsequent periods, and so many of these chicks with low growth rates in the final period may not have fledged, or may have died soon after fledging.

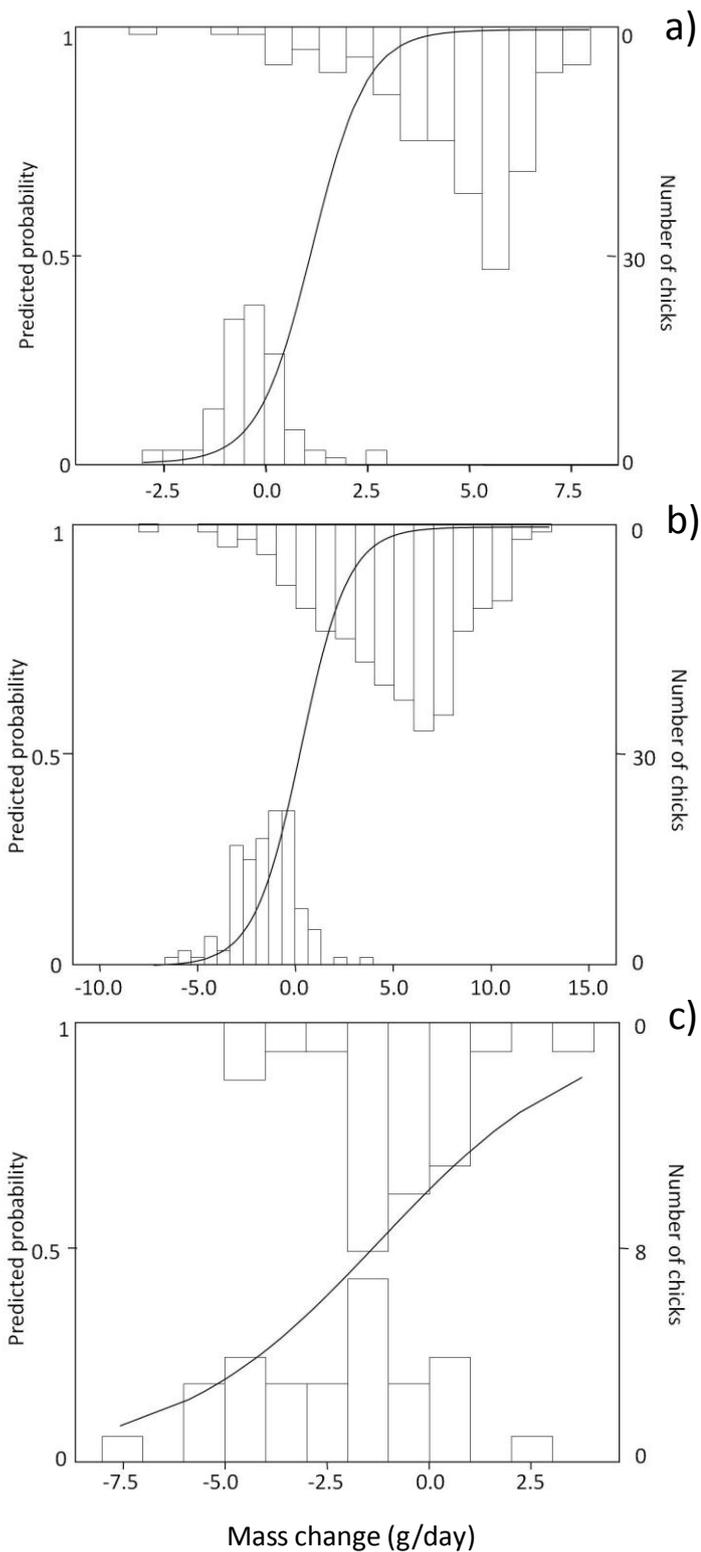


Fig. 4.7. The influence of change in body mass on the probability of survival in Arctic Tern chicks (0=dead, 1=alive) between the ages of a) 0-5 days, b) 6-15 days and c) 16-33 days. For statistics see Table 4.3. Bars show the frequency distribution of the observed data for number of chicks that survived (top) and died (bottom) and lines show the fitted logistic regression curves.

Influence of size and mass on final fate

During the first 5 days of life, there was a weak significant difference in mass between chicks that fledged and died, and chicks that survived were significantly larger in skull length (Table 4.4). In addition, there was a significant interaction between fate and skull length, such that mass increased more rapidly with skull length for chicks that survived (Table 4.4). The body mass of chicks of any given skull length was more variable in the later growth stages (Fig. 4.8), and the difference in mass between the chicks that survived and died was strongly significant during the 6-15 day old phase (Fig. 4.8b, Table 4.4). During this life stage mean mass was 55.51 g (SE: 1.50) for the ones that died and 70.12 (SE: 0.99) for those that fledged (Fig. 4.8b). After age of 16 days, there was no significant difference in mass between chicks that died and survived, but chicks with larger skull lengths were more likely to survive (Fig. 4.8c, Table 4.4).

Table 4.4. Generalized linear mixed models of the body mass of chicks with different fates (survived or died) and of different body sizes (skull length).

	Age 0-5 day			Age 6-15 day			Age 16-33 day		
	F	df; df	<i>p</i>	F	df; df	<i>p</i>	F	df; df	<i>p</i>
Fate	4.99	1; 423.704	<0.05	39.87	1; 628.321	<0.001	1.18	1; 476.718	ns
Skull	2330.43	1; 416.722	<0.001	1274.48	1; 622.535	<0.001	7.99	1; 478.634	<0.05
Fate * Skull	6.95	1; 416.722	<0.05	56.51	1; 622.535	<0.001	3.07	1; 478.634	ns

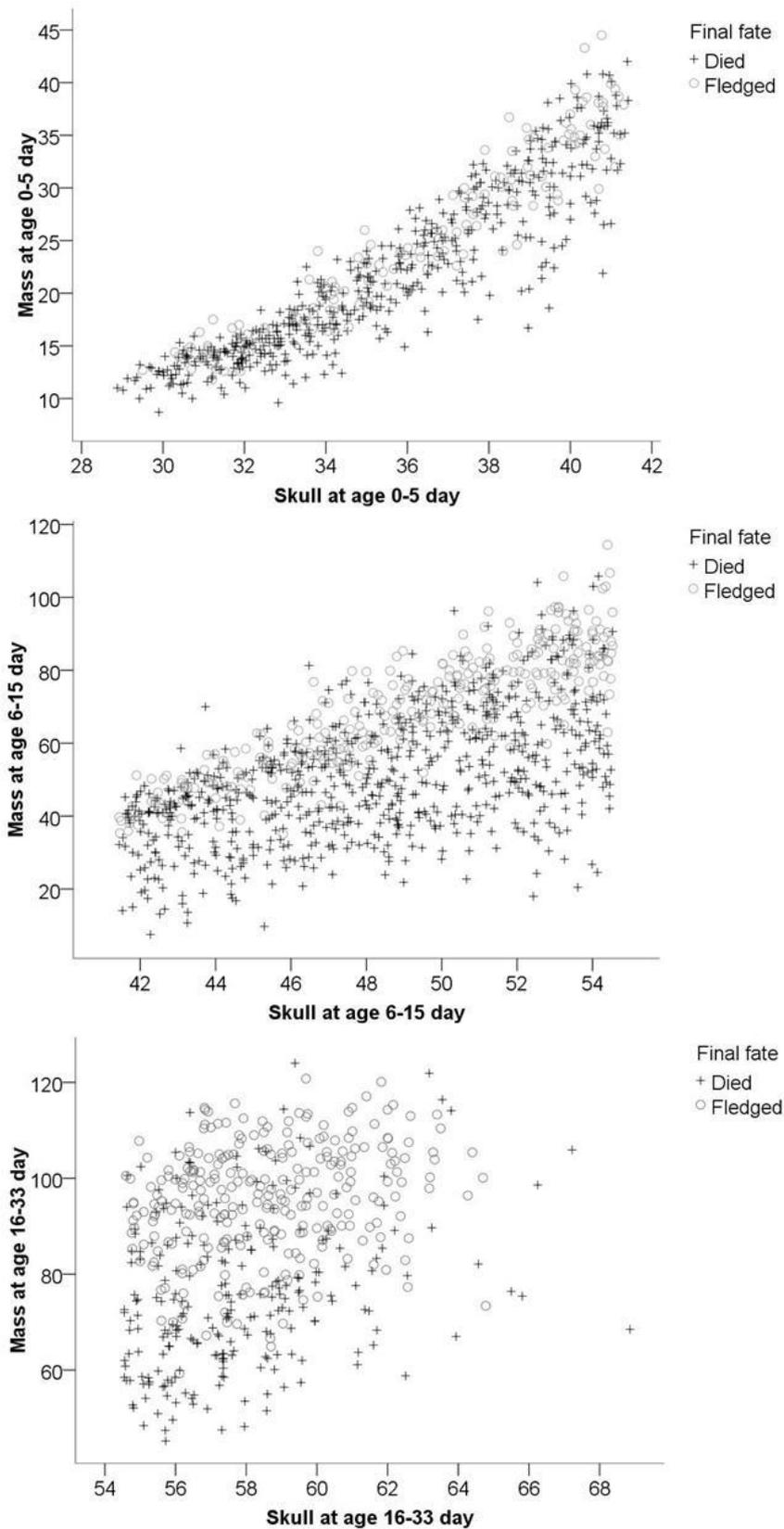


Fig. 8. Variation in mass (g) for a given skull (mm) size of Arctic Tern chicks at three life stages, a) 0-5, b) 6-15 and c) 16-33 day old. Markers differentiate between chicks that died (cross) and fledged (open circle).

Discussion

Arctic Tern productivity across all colonies on the Snaefellsnes peninsula, W-Iceland, was very low between 2008 and 2011, with only one colony in one year exceeding one chick per pair (Fig. 4.2). Over all colonies and years, 70% of chicks were assigned a final fate (46% died and 24% assumed to have fledged) but 30% of chicks went missing without a known fate (Fig. 4.3). Chicks that went missing could have been preyed upon, which could implicate predation as a cause of the low productivity on these colonies. However, the chicks of unknown fate tended to go missing at very young ages and small sizes (Fig. 4.4). These chicks may therefore have died and gone undetected, as such small carcasses can be very difficult to locate, particularly in vegetation. Additionally, only once was a predation event witnessed during the four years of studies, when a black-headed gull successfully caught one chick within one of the colonies (though not within our research area). Predators were seen approaching colonies but intense mobbing by adult Arctic Terns always chased the predator away, which is likely to prohibit predation taking place. Predation is thus unlikely to be the main driver of the low productivity experienced on these colonies in these years.

Poor weather conditions or extreme weather events have been described previously in other areas as a cause of an increased mortality or mortality events in terns (Robinson *et al.* 2002; Stienen *et al.* 2000). Although quite severe weather conditions are not uncommon in Iceland, there were no periods of particularly harsh weather during the four years of this study, and there was no apparent increase in the number of Arctic Tern chicks dying in days of poor weather conditions, characterized by strong winds, low air temperatures high levels of humidity (indicating rainfall) (Fig. 4.5). Weather conditions did not therefore seem to influence the rate of chick mortality or to be the main driver of the low productivity of Arctic Terns.

The non-linear growth pattern of Arctic Tern chicks during the pre-fledging period is typical of semi-precocial species (e.g. Drent *et al.* 1987; Massias and Becker 1990; Stienen and Brenninkmeijer 2006). Rates of mass change are low for the first few days of life, followed by a period of quite rapid growth and then a levelling-off of mass change prior to fledging (Fig. 4.6). While, in all three growth periods, the chicks that died had quite similar structural (wing and skull length) growth rates to those that survived or, in the final growth period, were assumed to have fledged, they were always lighter in mass (Table 4.1). The large difference in mass between these two groups suggests that the chicks that died were in much poorer condition and probably died of starvation. The mortality was quite evenly distributed across colonies and across age stages (Table 4.2), suggesting that chick starvation was occurring over a large spatial scale (i.e. across the whole peninsula) and was

persistent through the breeding season. Daily change in mass significantly influenced survival probabilities of Arctic Tern chicks across colonies (Table 4.3, Fig. 4.7), and correctly predicted individual mortality in 80-95% of cases, suggesting that starvation was the primary cause of chick mortality. During the last growth period of 16-33 days, body mass did not differ significantly between chicks that were found dead and those that were assumed to have fledged (Table 4.4, Fig. 4.8c). It is therefore possible that some of the chicks that were assumed to have fledged will have been in very poor condition and might not have survived despite being able to leave the enclosures.

Starvation as a driver of chick mortality and poor productivity has been observed in various seabird species across the North Atlantic (e.g. Ratcliffe *et al.* 1998; Stienen and Brenninkmeijer 2002; Davoren and Montevecchi 2003; Durant *et al.* 2004; Wanless *et al.* 2005; Szostek and Becker 2011; Burthe *et al.* 2012). Reduced food availability leading to chick starvation can be influenced by temporal and/or spatial displacement of food (e.g. Burthe *et al.* 2012). Reduced food availability may cause declines in food delivery rates (e.g. Jodice *et al.* 2006), increased parental foraging effort (e.g. Ronconi and Burger 2008) reducing nest attendance (Ratcliffe *et al.* 1998), which may increase predation and/or con-specific aggression (Ashbrook *et al.* 2010). Additionally, low nutritive content of prey has been observed to be linked to poor productivity in seabirds (Wanless *et al.* 2005), especially where alternative prey are either not available (Monaghan *et al.* 1989), of inappropriate size (Harris *et al.* 2008) or of too poor quality to sustain energetic needs (Massias and Becker 1990). For long lived species such as seabirds, adults have been shown to respond to a lack of resources by adjusting their breeding investment in relation to the level of constraints. Minor changes in food availability can lead to adjustments in activity budgets but severe reductions in food availability can impact chick survival, through changes in prey delivery rates, parental attendance and nest defence (Cairns 1987; Davis *et al.* 2005; Jodice *et al.* 2006; Ashbrook *et al.* 2010). However, seabird population trends are most sensitive to changes in adult survival (e.g. Ezard *et al.* 2006, Stahl and Oli 2006), and thus population declines may be most likely when either resources are so scarce that adult survival is reduced (Cairns 1987, Hamer *et al.* 1991, Davis *et al.* 2005), or when low productivity occurs for prolonged periods of time prohibiting recruitment (Ezard *et al.* 2006; Szostek and Becker 2011). Arctic Terns are known to respond to unfavourable breeding conditions, such as poor environmental conditions or disturbance, by redistribution of breeding sites and such redistribution can have substantial effects on local population sizes (Ratcliffe 2004; Devlin *et al.* 2008; Egevang and Frederiksen 2011).

The marine ecosystem is complex and dynamic, so causes of disruptions to food availability and lack of suitable prey for chick-rearing are difficult to identify, and long term studies and comprehensive data sets are typically required to quantify

causal effects (e.g. references in Sydeman *et al.* 2012). However, environmentally-driven changes in marine food webs, including seabirds as higher predators, have been described for marine ecosystems in Norway and the North Sea (see references in Frederiksen *et al.* 2012). For example, herring *Clupea harengus* dependent seabirds in Norway showed a change in breeding success with change in herring size and availability (Durant *et al.* 2003), which was tightly linked to ocean climate conditions, with a positive relationship between herring recruitment and sea temperature (Durant *et al.* 2006). Adult survival among these seabirds was also found to be positively associated with sea temperature (Harris *et al.* 2005; Grosbois *et al.* 2009), suggesting an association with herring recruitment and food availability. In the North Sea, most seabird species are heavily dependent on sufficient amounts of sandeel *Ammodytes marinus* for successful reproduction (Hamer *et al.* 1993; Furness and Tasker 2000; Frederiksen *et al.* 2006). Past local (Monaghan 1992; Hamer *et al.* 1993) seabird breeding failures have been associated with reductions in sandeel availability (Uttley, Tatner, and Monaghan 1994; Davis *et al.* 2005; Wanless *et al.* 2007; Furness 2007). However, the reasons for the sandeel decline (excluding fisheries) have been more difficult to describe (Frederiksen *et al.* 2007), although a recent study has shown a strong link between the abundance and distribution of copepods *Calanus finmarchicus* in relation to climatic and oceanic changes (Frederiksen *et al.* 2012), which may possibly be linked to a trophic mismatch across multiple levels of the North Sea pelagic food web (Burthe *et al.* 2012). As predicted by Frederiksen *et al.* (2012) these sort of trophic cascades may in the near future spread northward, including Icelandic waters. Those predictions of increased sea temperatures and disruptions in primary productivity are in an agreement with observed and predicted hydrographic (changes in ocean currents, temperature and salinity) and marine ecosystem changes (shifts in distributions and abundance of fish species) around Iceland (Valdimarsson *et al.* 2012). Observed population declines in a range of seabird species around Iceland (Gardarsson 2006; Gardarsson *et al.* 2011; A. Gardarsson pers. comm.), as well as the poor productivity and chick mortality described in this study, may therefore be linked to these changes in the marine environment.

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Chapter 5

Chapter 5

The influence of dietary composition and provisioning rates on Arctic Tern productivity in Iceland

Abstract

Many seabirds populations across the North Atlantic have been in decline and have been subjected to breeding failures. Many of these declines have been linked to local or large scale reductions in food availability during the breeding season. Arctic Terns *Sterna paradisaea* in W-Iceland have experienced very low breeding success in recent years, primarily driven by low chick fledging success as a consequence of low growth rates and starvation. In order to explore the factors contributing to these poor conditions for chick growth and survival, we quantify the types and size composition of prey delivered to chicks in colonies across the Snaefellsnes peninsula in W-Iceland, and relate between-colony variation in prey delivery rates to chick growth and survival. However, as the main marine prey resource in W-Iceland is sandeels, which are only present in the waters of S- and W-Iceland, we also quantify prey composition, delivery rates, chick growth rates and survival in colonies in NE-Iceland, in order to compare Arctic Tern success rates in areas with differing prey communities. Prey composition and size varied greatly between regions and colonies. In W-Iceland, higher delivery rates were associated with greater fledging success, but sandeels were delivered at low rates at all colonies. In NE-Iceland, capelin replaced sandeels as the main marine prey, but delivery rates of capelin were either very low or very inconsistent, and fledging success in NE-Iceland was similarly low.

Keywords: Animal ecology, Demography, Provisioning rates, Chick growth, Seabirds, Arctic Tern

Introduction

Food availability can strongly influence avian productivity, through impacts on adult condition for breeding and associated reproductive decision-making, and through impacts on offspring survival. Several studies have shown the influence of changes in food supply on seabird breeding parameters such as age and time of breeding (Safina *et al.* 1988; Ratcliffe *et al.* 1998), clutch size and egg volume (Monaghan and Nager 1997; Martin *et al.* 2000; Ricklefs 2000; Stienen and Brenninkmeijer 2006), chick growth and fledging success (Monaghan *et al.* 1989; Hamer *et al.* 1991; Crawford and Dyer 1995; Stienen and Brenninkmeijer 2002; Davis *et al.* 2005). Food resources in the marine environment can be highly variable and unpredictable, which may explain some aspects of seabird life histories like longevity, delayed maturation and slow reproduction (Furness and Monaghan 1987; Gaston 2004). Limited resources can lead to trade-offs between resource allocations for possible future reproduction versus current breeding output (e.g. Williams 1966), and the degree to which such trade-offs are expressed may be indicative of the level of constraints to which the individuals are subjected. Many studies have described how seabirds respond to changes in food availability and have consequently proposed using seabird abundance and demography as indicative signals of marine food supplies (e.g. Cairns 1987; Furness and Camphuysen 1997; Durant *et al.* 2009). Positive relationships have been found between fledging success of many seabird species and food availability (Ronconi and Burger 2008; Burthe *et al.* 2012) and food quality (Massias and Becker 1990; Wanless *et al.* 2005; Jodice *et al.* 2006), although other factors can also influence productivity, such as predation and severe weather conditions (Cairns 1987; Becker and Specht 1991; Thompson and Furness 1991; Becker 1995).

Marine ecosystems are complex but often dominated by few and abundant mid-trophic pelagic fish species (Rice 1995). Although seabirds can exploit a wide range of oceanic food resources, pelagic fish species are the dominant food among most seabird species (Boyd *et al.* 2006). Additionally, for successful chick rearing, food items have to be of high nutritive value and delivered at high enough rates to be sufficient for chick growth requirements throughout the pre-fledging period (Klaassen *et al.* 1992). In the North Atlantic, sandeel *Ammodytes spp.* and capelin *Mallotus villosus* are the most common fish species in seabird diets (Lilliendahl and Solmundsson 1998, 2006; Thompson *et al.* 1999; Furness 2002; Carscadden 2002; Wanless *et al.* 2005; Barrett *et al.* 2006; Lilliendahl 2009), as these species are of particularly high nutritive value and naturally occur in shoals that are accessible to seabirds (Pearson 1968; Furness and Tasker 2000).

Iceland is surrounded by cool currents from the Arctic Ocean at the North coast which meet warmer boreal waters from the Gulf Stream off the West and the East

coast. Over the last 15 years, the waters in the South and West of Iceland have warmed by 1-2°C and many southern commercially fished species have extended their ranges further north, and northern species ranges have retreated further north (Valdimarsson *et al.* 2012). Further hydrographic changes with warming sea temperatures are predicted for the future at high latitudes, including Icelandic waters (IPCC 2007). Interactive links between seabird populations and prey abundance in Icelandic waters have not been described directly but many seabird species have declined in numbers (Gardarsson 2006a; Gardarsson *et al.* 2011) and/or experienced poor breeding success in recent years (Gardarsson 2006b; E. S. Hansen pers.comm.). Populations to the South and West of Iceland seem to have experienced particularly poor breeding success, but some studies indicate better breeding success among seabirds breeding on the North coast (Gardarsson 2006a; Gardarsson *et al.* 2011; E. S. Hansen pers. comm.).

In Iceland, studies have shown pronounced geographical differences in seabird diet during the breeding season, with seabirds breeding in the south and west primarily exploiting sandeel populations, and seabirds breeding in the north and east exploiting capelin (*Mallotus villosus*), as well as krill (Euphausiacea) (Lilliendahl and Solmundsson 1998; Thompson *et al.* 1999). In contrast to the North Sea (Furness 2007), sandeel populations are not harvested in Icelandic waters, but capelin populations, the largest pelagic fish stock in Icelandic waters (Astthorsson *et al.* 2007), are heavily exploited, with average annual total landings of 824 thousand tons since 1984 (Anon. 2012). Seabird responses to over-harvesting and depletion of fish stocks have been described in the many areas, e.g. the North Sea (Furness 2002; Frederiksen *et al.* 2004), Barents Sea (Barrett *et al.* 2006; Barrett 2007) and Newfoundland (Davoren and Montevecchi 2003; Davoren *et al.* 2007). Additionally range shifts and population changes of marine prey species in response to past and predicted climatic and oceanic changes have been described for some areas in the North Atlantic (Perry *et al.* 2005; Dulvy *et al.* 2008), and these changes have been linked to declines in productivity and abundance of several seabird populations (Sydeman *et al.* 2012; Frederiksen *et al.* 2012).

Arctic Tern breeding colonies are distributed around Iceland, primarily along the coastline but also inland by freshwater lakes and in terrestrial habitats. Arctic Terns therefore have access to a wide range of foraging habitats, although the availability of different habitats and prey resources can vary locally and regionally. Depending on their location, colonies may have access to differing amounts of marine, freshwater and estuarine resources, and the distance to and availability of these different resources may result in different foraging decisions for individual Arctic Terns (Rock *et al.* 2007). We have previously shown that Arctic Tern fledging success in colonies across the Snaefellsnes peninsula in western Iceland was very

low between 2008 and 2011 (Chapter 2), and that the low breeding success was mainly a result of high chick mortality (Chapter 3). Chick mortality was greatest among chicks with very low growth rates, suggesting that starvation was the cause of the high mortality (Chapter 4). These patterns suggest that prey resources for chicks were likely to have been limited during these years. In order to explore the nature of these resource limitations, and the extent to which they may vary in different parts of Iceland, in this chapter, we explore (1) the variation in chick dietary composition and prey delivery rates to chicks among colonies in West and North Iceland with access to differing resources, (2) the relationships between prey delivery rates and chicks growth rates and fledging success among colonies and (3) the level and consistency of delivery of the main high quality prey (sandeel and capelin) among colonies with differing resource availability and breeding success.

Methods

Study area

The study was conducted on the Snaefellsnes peninsula in W-Iceland in 2010 and on Melrakkasletta in NE-Iceland in 2011 (Fig. 5.1). Both study areas are peninsulas comprising a mountainous terrain surrounded by coastal lowlands. Snaefellsnes stretches 100 km into the Atlantic Ocean, between the bays of Faxafloi and Breidafjordur (Fig. 5.1) and is surrounded with waters of boreal origin. Melrakkasletta stretches into the cold water masses just beneath the Arctic Circle and is surrounded by waters of polar origin. Both areas support numerous seabird colonies, both of cliff-breeding and ground-nesting species, and Arctic Tern colonies are found along the coastline of both peninsulas. On the Snaefellsnes peninsula, the habitats available within the estimated 5-10 km foraging range of breeding Arctic Terns (Pearson 1968; Rock *et al.* 2007) vary from solely marine habitats surrounding the westernmost colonies of Rif and Arnarstapi (as this area is primarily glacial and rocky) to marine, estuarine and freshwater (lakes and rivers) habitats near the more easterly colonies (Fig. 5.1a). On Melrakkasletta, the southernmost colony (Valthjofsstadir) has access to marine resources only, while the more northerly colonies have marine and estuarine habitats, freshwater lakes and the rocky shoreline along the North side of the peninsula (Fig. 5.1b) which has extensive areas of tide wrack and associated insect prey.

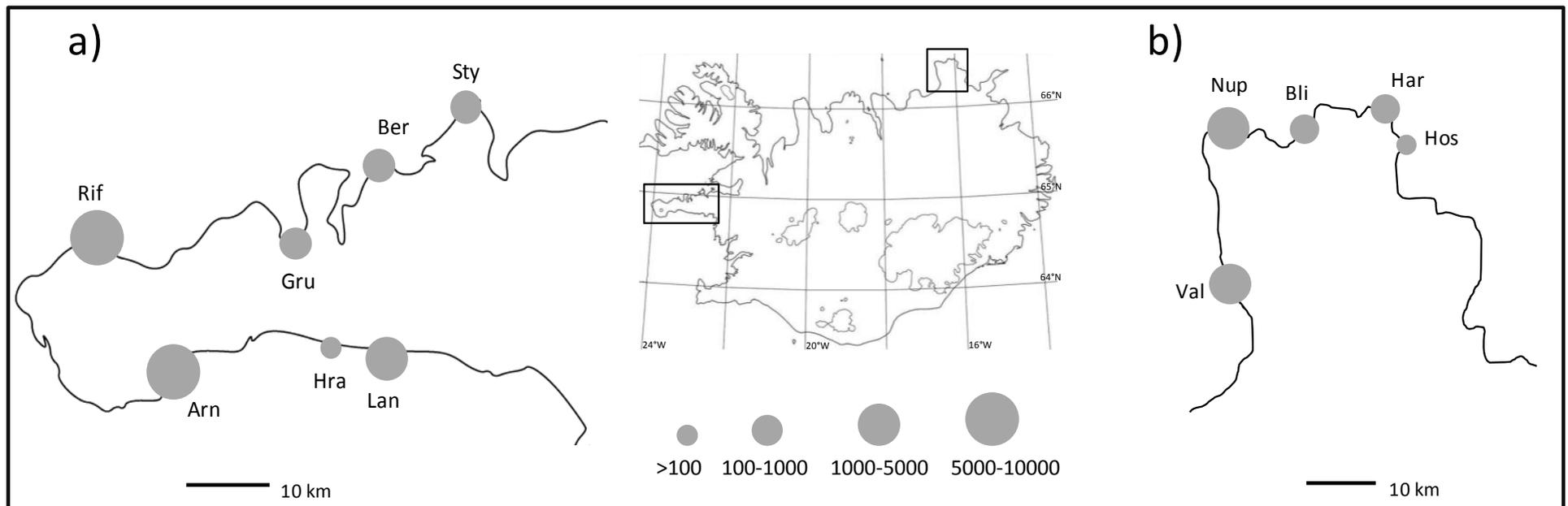


Fig. 5.1. Location and size (estimated number of pairs) of Arctic Tern study colonies on a) Snæfellsnes peninsula, W-Iceland and b) Melrakkasletta, NE-Iceland. Location of both study areas are indicated (inset). Sty: Stykkisholmur, Ber: Berserkseyri, Gru: Grundarfjörður, Rif: Rif, Arn: Arnarstapi, Hra: Hraunsmúli, Lan: Langaholt. Val: Valthjofsstaðir, Nup: Nupskatla, Bli: Blikalon, Har: Hardbakur, Hos: Hoskuldarnes.

Nest monitoring and chick diet

Chick growth rates and survival were monitored throughout the breeding season across 12 colonies, by following nests and recapturing known (ringed) chicks within enclosures (see Chapter 4 for enclosure details). Between 14-46 chicks in each colony were ringed and re-measured every 3-5 days in seven colonies on Snaefellsnes peninsula (Fig. 5.1a) and five colonies on Melrakkasletta (Fig. 5.1b). At each recapture, to monitor growth rates, measurements of mass (measured to the nearest 0.1 g with electronic scales) and wing length (measured to the nearest 1 mm with a wing ruler) were recorded for each chick. Chick growth rate measures were conducted after observations of prey deliveries to minimize disturbance during food provisioning. Chicks were considered to have fledged successfully if they reached at least 80 g in mass and/or 100 mm wing length and were not relocated on subsequent visits (Chapter 4; Drent *et al.* 1987; Klaassen *et al.* 1989a, 1989b).

Prey delivery rates

Prey deliveries to chicks at enclosed nests were observed from the beginning of the hatching period until chicks were either fledged or dead in each colony (28th June to 29th July on Snaefellsnes peninsula in 2010 and 2nd June to 26th June on Melrakkasletta in 2011). Depending on survival rates of chicks (number of chicks left alive) and nest density between different colonies, between 1 and 32 chicks were observed by 1 or 2 observers in a vehicle parked no more than 7 m away from the enclosures. Enclosures were observed for between 1 and 6 hours per day, and each colony was observed at least every 2 to 4 days (with observations at different hours of the day at each visit to avoid any systematic bias from time of day). During each observation period, the total number of prey items delivered to chicks within the enclosure was recorded and, where possible, each prey item was identified and prey length was estimated (most deliveries were photographed for further identification using digital photography (Canon EF 400mm f/5.6L lens mounted on a Canon 1D Mark III). At the end of each observation period, all chicks within the enclosure were captured and measured, allowing prey delivery rates for each observation period to be calculated as number of prey items per chick per hour.

Energy value of food items

The length of each prey item delivered was estimated in relation to the bill length of the adult Arctic Tern and assigned to the following size categories: <3 cm, 3.1-6 cm, 6.1-9 cm and >9 cm (following Robinson *et al.* 2001). Conversion factors from

length to weight and calorific values for appropriate species and size classes were collated from a range of published sources (Table 5.1). Estimated energy values were obtained for dry weight as recommended by (Montevecchi and Piatt 1987) and used previously by Massias and Becker (1990), Wanless *et al.* (2005) and Harris *et al.* (2008). Prey of unknown species were assigned the average energy content for all prey of that size class, and unidentified fish prey species were assigned the average energy content for fish items of that size class.

Table 5.1. Estimated energy content (kJ g^{-1} dry weight) of prey items in different size classes (cm) delivered to Arctic Tern chicks in Snaefellsnes and Melrakkasletta, and the published sources from which energy content estimates were collated.

	Energy density (kJ g^{-1} dry wt) for different size classes (cm)			
	<3	3.1-6	6.1-9	>9
Sandeel	0.25 ¹	4.79 ²	25.99 ²	46.78 ^{2,3}
Capelin		4.88 ⁴	29.11 ⁴	51.67 ⁴
Stickleback	8.40 ³	17.64 ³	25.20 ³	
Gadidae	4.26 ⁵	14.09 ⁵	61.00 ⁵	
Fish larvae	4.84 ⁶	9.68 ⁶		
Crustacea	4.40 ³	17.37 ³		
Insect	0,40			
Unknown*	2.40	11.41	35.33	49.23
Unidentified fish [†]	4.33	10.21	35.33	49.23

Sources: 1 = Wanless *et al.* 2005, 2 = Hislop *et al.* 1991, 3 = Massias and Becker 1990, 4 = Montevecchi and Piatt 1987, 5 = Harris & Hislop 1978, Weslawski *et al.* 1994. *Assigned a size specific mean value accordingly to the type of item. [†]Assigned mean value of all fish items.

Data analysis

In order to compare the different types of prey delivered to Arctic Tern chicks between the two regions, Snaefellsnes peninsula and Melrakkasletta, and between colonies within the regions, the proportions of prey species recorded during all prey delivery observations were calculated. Fish species were identified as sandeel *Ammodytes marinus* (on Snaefellsnes only), capelin *Mallotus villosus* (on Melrakkasletta only), three-spined stickleback *Gasterosteus aculeatus* and lump sucker *Cyclopterus lumpus*. Other fish types were not identified to species but, for the purposes of estimating their energetic value, they were differentiated as: gadidae, fish larvae and un-identified fish. In diet composition analyses, these were grouped as unidentified fish.

Variation between the regions in the size distribution of prey items delivered was explored with a chi-square test of the number of prey in each of the four size categories. General linear models were used to relate average productivity (no. of fledged young per pair) and chick growth rates (g day^{-1}) to prey provisioning rates (delivery $\text{chick}^{-1} \text{ hour}^{-1}$) and estimated energetic intake rates ($\text{kJ chick}^{-1} \text{ hour}^{-1}$) across colonies, with region (Snaefellsnes or Melrakkasletta) included as a fixed factor and the interaction between region and provisioning rates/intake rates also included.

Finally, the variation among colonies and regions in delivery rates of the main marine prey species (sandeel in the West and capelin in the North) in comparison to delivery rates of all other prey species combined was explored by calculating prey-specific delivery rates (e.g. number of sandeel delivered per chick per hour during each observation period).

Results

Chick diet

The dietary composition of prey delivered to Arctic Tern chicks varied between colonies and between regions (Fig. 5.2). Both regions, Snaefellsnes peninsula (W) and Melrakkasletta (NE), had a mixture of marine fish items and estuarine or terrestrial crustacea or insects delivered, although in differing proportions. The majority of the identified prey delivered on Snaefellsnes was sandeels but the proportion of sandeels delivered varied among colonies. The proportion of prey of estuarine and terrestrial origin was low in the two most westerly and largest colonies (Rif and Arnarstapi) and greatest in the north-eastern colonies of Stykkisholmur and Berserkseyri (Fig. 5.2). On Melrakkasletta, capelin comprised a substantial (> 20%) proportion of the diet in the southern colony (Valthjofsstadir) and, in the other colonies, prey of non-marine origin were generally present in higher proportions than in the Snaefellsnes colonies (Fig. 5.2).

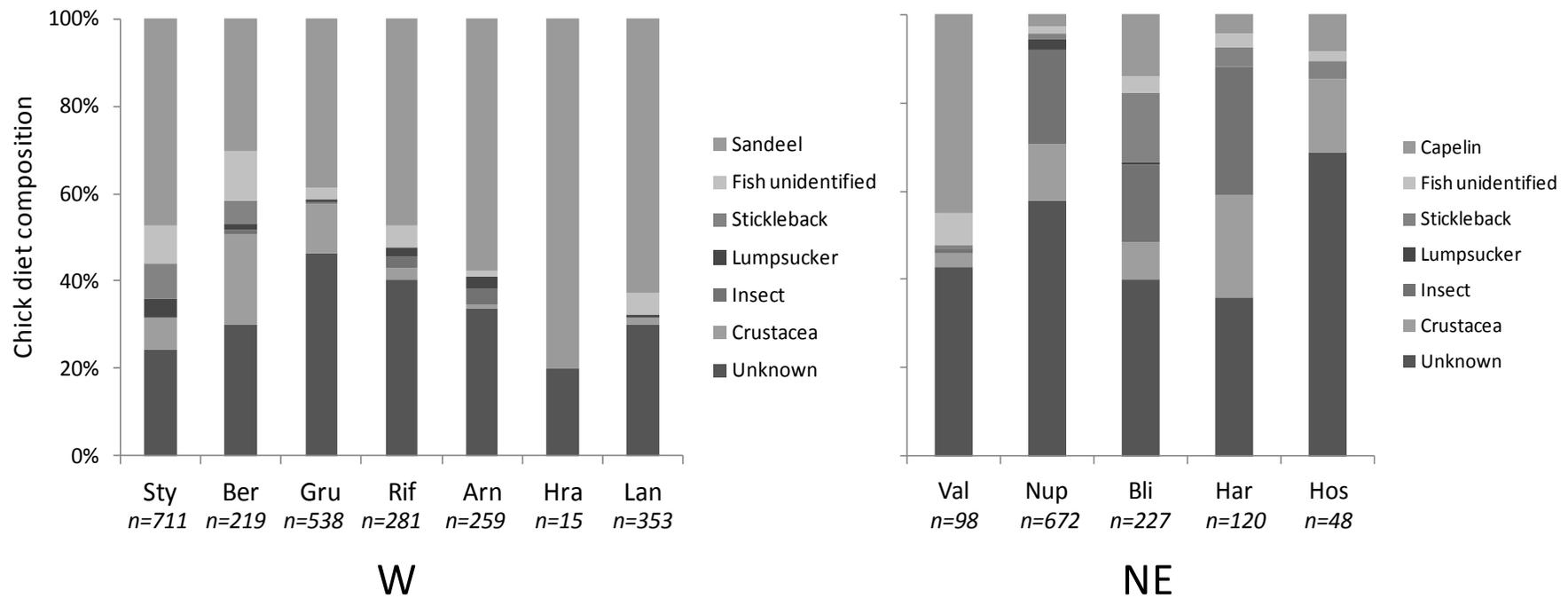


Fig. 5.2. Dietary composition (%) of food items delivered to Arctic Tern chicks in colonies at Snaefellsnes peninsula (W) and Melrakkasletta (NE). Colony order is geographical, for details see Fig. 5.1. The total number of prey items recorded in each colony is shown below colony names.

Energetic value and size distribution of chick food

The estimated energetic value of different prey items delivered to chicks varied greatly, with large fish items of marine origin having the highest values and small insects of terrestrial origin having the lowest values (Table 5.1). The size distribution of prey delivered to Arctic Tern chicks during chick rearing differed significantly difference between Snaefellsnes and Melrakkasletta regions ($\chi^2 = 1650.42$, d.f. = 3, $p < 0.0001$, Fig. 5.3). Almost 90% of the prey items delivered on Snaefellsnes peninsula were in the intermediate two size classes (3.1-6 cm and 6.1-9 cm), but 82% of items delivered on Melrakkasletta were smaller than 3 cm (Fig. 5.3).

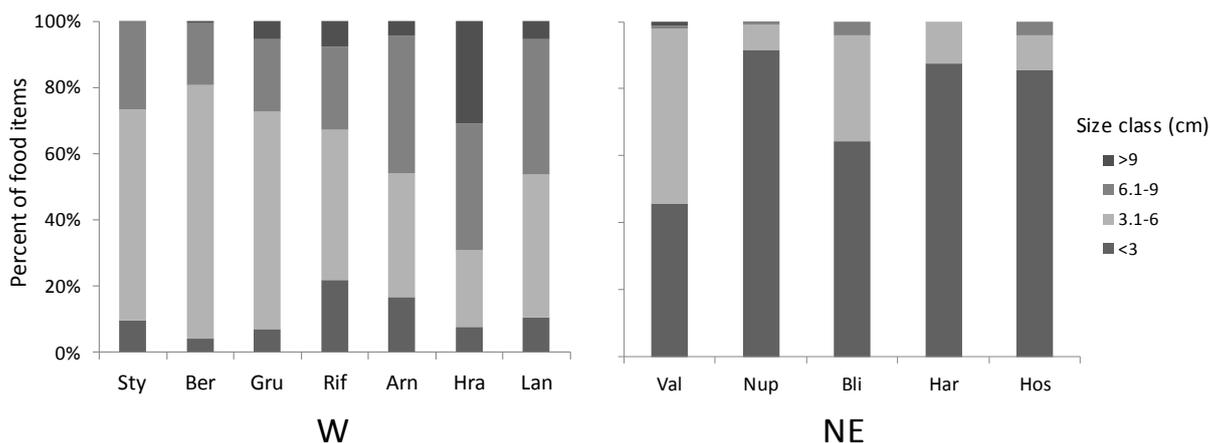


Fig. 5.3. The proportion of different size-classes of food items delivered to Arctic Tern chicks at Snaefellsnes peninsula, W-Iceland, and Melrakkasletta, NE-Iceland.

Prey delivery rates, chick growth rates and fledging success

Mean prey delivery rates varied greatly between colonies, from ~1 to 6 items per hour per chick (Fig. 5.4a). On the Snaefellsnes peninsula, chick growth rates were generally higher in colonies with higher prey delivery rates and estimated energy intake rates, but this relationship was not significant, and there was no such relationship in colonies at Melrakkasletta (Fig. 5.4, Table 5.2a,b).

Table 5.2. Results of general linear models of the variation in Arctic Tern chick (a and b) growth rates ($\text{g chick}^{-1} \text{day}^{-1}$) and (c and d) fledging success (chicks fledged per pair) in each region (Snaefellsnes peninsula, W-Iceland and Melrakkasletta, NE-Iceland) in relation to (a and c) prey item delivery rate (feeds $\text{chick}^{-1} \text{hour}^{-1}$) and (b and d) estimated energy intake ($\text{kJ chick}^{-1} \text{hour}^{-1}$).

<i>Dep. var.</i>		F	df; Df	p
a)	g day^{-1}			
	Region	0.12	1; 8	0.74
	Delivery rate	0.90	1; 8	0.37
	Delivery*Region	4.73	1; 8	0.06
b)	g day^{-1}			
	Region	0.00	1; 8	0.99
	kJ	1.31	1; 8	0.22
	Region*kJ	2.08	1; 8	0.14
c)	fledged pair ⁻¹			
	Region	3.20	1; 8	0.11
	Delivery rate	18.18	1; 8	<0.01
	Delivery*Region	24.57	1; 8	<0.001
d)	fledged pair ⁻¹			
	Region	4.53	1; 8	0.07
	kJ	29.06	1; 8	<0.001
	Region*kJ	28.81	1; 8	<0.001

Mean colony fledging success (number of fledged chicks per pair) did not vary significantly between regions overall but did increase significantly with increasing prey delivery rates (Table 5.2c) and estimated energy intake rates (Table 5.2d). However, these patterns varied significantly between the regions (Table 5.2c,d), with colonies on Melrakkasletta showing no significant increase in fledging success with prey delivery or energy intake rates (Fig. 5.3a). In particular, two colonies on Melrakkasletta (Valthjofsstadir and Nupskatla), had much lower fledging success than colonies on Snaefellsnes with similar delivery and energy intake rates (Fig. 5.3).

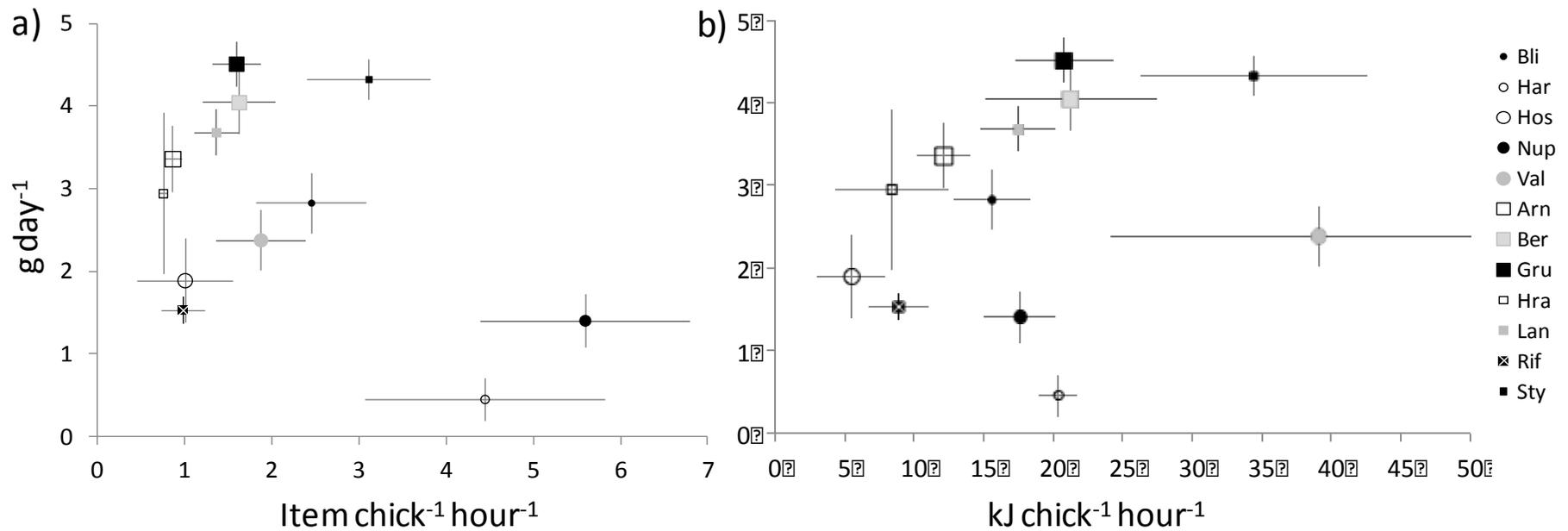


Fig. 5.4. Relationships between mean (\pm SE) chick growth rates (g day^{-1}) and a) mean (\pm SE) prey item delivery rates ($\text{item chick}^{-1} \text{ hour}^{-1}$) and b) mean (\pm SE) estimated energy intake rates ($\text{kJ chick}^{-1} \text{ hour}^{-1}$) across colonies on Snæfellsnes in W-Iceland (squares, a) $y=0.77x+2.35$, $R^2=0.37$, b) $y=0.09x+1.99$, $R^2=0.57$) and Melrakkasletta in NE-Iceland (circles, a) $y=-0.30x+2.73$, $R^2=0.39$, b) $y = 0.01x+1.61$, $R^2 = 0.02$). Locations of colonies can be seen in Fig. 5.1 and results of statistical analyses in Table 5.2.

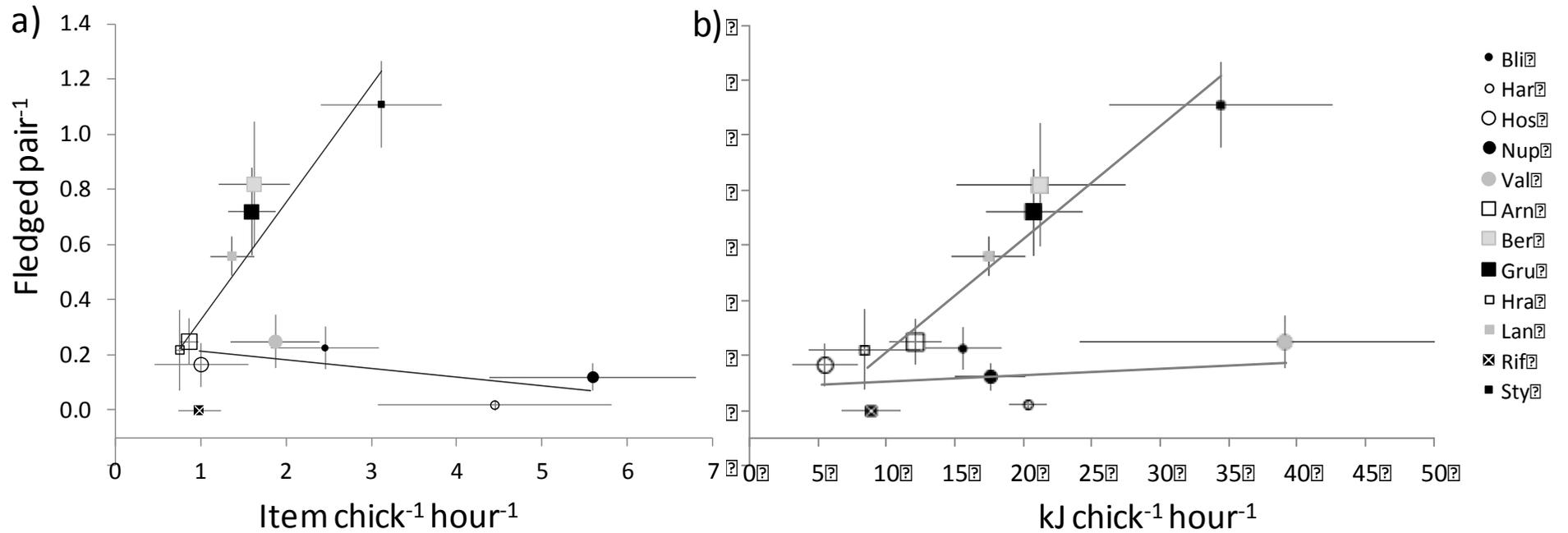


Fig. 5.5. Mean (\pm SE) productivity (number of chicks fledged pair⁻¹) in relation to a) mean (\pm SE) food item delivery rate (item chick⁻¹ hour⁻¹) and b) mean (\pm SE) estimated energy intake rate (kJ chick⁻¹ hour⁻¹) across colonies on Snaefellsnes in W-Iceland (squares, a) $y=0.43x-0.11, R^2=0.79$, b) $y=0.041x-0.198, R^2=0.92$) and Melrakkasletta in NE-Iceland (circles, a) $y=-0.03x+0.25, R^2=0.43$, b) $y=0.0023x+0.11, R^2=0.09$). Location of colonies can be seen in Fig. 5.1 and results of statistical analyses in Table 5.2.

Item specific delivery rates

There were fundamental differences between the two regions, Snaefellsnes peninsula and Melrakkasletta, in prey composition, prey size and, to some degree, in chick fledging success. In particular, prey items were typically larger at colonies on the Snaefellsnes peninsula (Fig. 5.2) and sandeels were the main large prey item at these colonies, while capelin were the main marine fish prey item on Melrakkasletta (Fig. 5.3). On the Snaefellsnes peninsula, sandeel delivery rates were highly consistent between different colonies, but the provisioning rate was low, with daily delivery rates of sandeel generally less than one item delivered chick⁻¹ hour⁻¹ (Fig. 5.6a). Delivery rates of alternative prey (other than sandeel) were more variable between colonies and higher than sandeel delivery rates in the three innermost colonies on Snaefellsnes peninsula (Stykkisholmur, Berserkseyri and Grundarfjordur; Fig. 5.6a). Delivery rates of 'other' (non-capelin) prey items were higher in some colonies in NE-Iceland on Melrakkasletta but delivery rates of capelin were very low in most colonies (Fig. 5.6a).

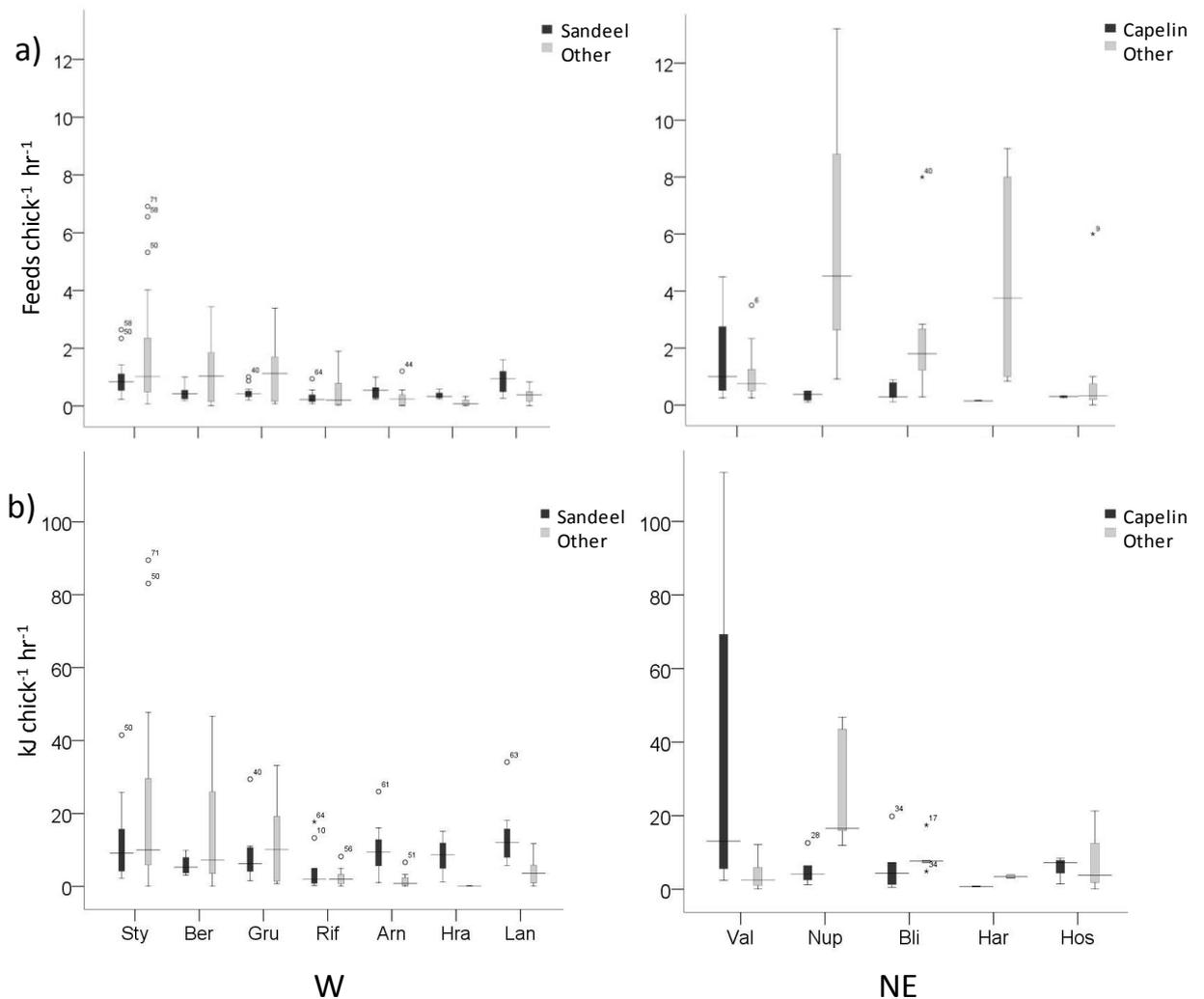


Fig. 5.6. Species-specific prey delivery rates in colonies on Snaefellsnes peninsula (W) and Melrakkasletta (NE) measured as a) items delivered (items chick⁻¹ hour⁻¹) and b) estimated energetic value (kJ chick⁻¹ hour⁻¹). Colonies are presented in geographical order (Fig. 5.1).

On the Snaefellsnes peninsula, rates of estimated energy intake of sandeels and other, alternative prey were similar on the north-eastern colonies of Stykkisholmur, Berserkseyri and Grundafjordur, but the West and South colonies of Rif, Arnarstapi, Hraunsmuli and Langaholt had lower intake rates of non-sandeel prey (Fig. 5.6b). Chicks in the Rif colony experienced low estimated energy intake rate of both sandeel and other food items (Fig. 5.6b). On Melrakkasletta in NE-Iceland, the rate of estimated energy intake was by far the highest in Valthjofsstadir (Fig. 5.6b), where 45% of items were capelin (Fig. 5.2) and where size of items delivered was higher than in other colonies on Melrakkasletta (Fig. 5.3). However, this rate of energy supply varied greatly, with estimated capelin intake rates ranging between <10 to >100 kJ chick⁻¹ hour⁻¹ on different days (Fig. 5.6b). Rates of energy supply from alternative prey to chicks in this colony was always low (Fig. 5.6b), and the inconsistent capelin delivery and lack of alternative prey sources is likely to have contributed to the low breeding success at this site (Fig. 5.5). Interestingly, the opposite pattern was observed in Nupskatla, where the rate of energy supply to chicks from capelin was consistently low, but other prey items provided much more of the chick energy intake rate at this site (Fig. 5.6b). As breeding success at this site was similar to Valthjofsstadir (Fig. 5.5) it appears that, at both sites, prey sources were either too low in quality or too inconsistently available to support chick growth and survival. Chicks in the other colonies on Melrakkasletta experienced consistently low rates of energy intake from capelin and other prey sources (Fig. 5.6b), which is likely to contribute to the low breeding success on these colonies (Fig. 5.5).

Discussion

The dietary composition of prey delivered to Arctic Tern chicks varied between colonies and between the two regions (Fig. 5.2). Both regions had a mixture of marine fish items and estuarine or terrestrial fish, crustacea or insects delivered, although in differing proportions. The majority of the identified prey delivered on Snaefellsnes was sandeels but the proportion of sandeels delivered varied among colonies. Colonies in the western part of the peninsula (Rif and Arnarstapi) appear to be almost entirely restricted to marine resources while colonies in the north-eastern part of the peninsula (Stykkisholmur and Berserkseyri) appeared to use a mixture of marine, estuarine and freshwater prey resources (Fig. 5.2a). On Melrakkasletta, only one colony (Valthjofsstadir) had relatively high delivery rates of energy rich marine fish, (capelin), and the other colonies had large proportions of insect and crustacean prey being delivered (Fig. 5.2). The size distribution of prey delivered to Arctic Tern chicks during chick rearing also differed significantly difference between Snaefellsnes and Melrakkasletta regions; almost 90% of the

prey items delivered on Snaefellsnes peninsula were of intermediate length (3-9 cm), but 82% of items delivered on Melrakkasletta were smaller than 3 cm (Fig. 5.3).

Provisioning rates, measured as items delivered per hour, varied greatly between colonies and were highest on Melrakkasletta, in Nupskatla and Hardbak colonies, where small crustacean and insect prey were delivered at average rates of $\sim 4-6$ items hour⁻¹ chick⁻¹ (Fig. 5.4a). However, these high delivery rates did not result in higher chick growth rates or fledging success, suggesting that the prey were too small to facilitate chick growth and survival. At the Snaefellsnes peninsula, mean colony fledging success increased significantly with increasing prey delivery rates and estimated energy intake rates (Fig. 5.5). The colonies with lowest chick growth rates and fledging success were those at which the great majority of the identified prey were of marine origin (Fig. 5.2).

Sandeel were delivered at consistently low rates to chicks in the Snaefellsnes peninsula colonies but, at colonies where alternative prey were delivered at higher rates than sandeels (Stykkisholmur, Berserkseyri and Grundafjordur, Fig. 5.6), chick growth rates and productivity were higher (Figs. 5.4 and 5.5). However, these colonies were all small (Fig. 5.1a) so the absolute number of chicks produced will not contribute substantially to future population growth. Non-sandeel prey may therefore have facilitated better fledging success when and where they were available. The variation in chick diet among colonies was greater at Melrakkasletta in NE-Iceland, than on Snaefellsnes, both in type of prey as well as delivery rates (Fig. 5.6). In the one colony (Valthjofsstadir) where energy-rich fish (capelin) were delivered at higher rates than alternative prey, the delivery rates varied greatly between days, and were very low on some days and not replaced by alternative prey (Fig. 5.6a). Thus, capelin availability appeared to vary substantially throughout the pre-fledging period, and the availability of this high quality prey source appears not to have been sufficiently consistent to facilitate chick survival to fledging. Other colonies on Melrakkasletta had much lower rates of capelin delivery, and the composition of alternative prey also varied greatly between these colonies, with insects and crustaceans being common in Nupskatla and Hardbakur, but, sticklebacks also being commonly delivered in Blikalon (Fig. 5.2). The unidentified prey items that were delivered were predominantly small (<3 cm) and likely to have been small crustaceans or insects (Fig. 5.3).

Sandeel has been identified as the main prey item for a range of seabird species breeding along the South and West coasts of Iceland (Lilliendahl and Solmundsson 1998; Thompson *et al.* 1999). Repeated annual poor breeding success since 2005 (Gardarsson 2006b; G.T. Hallgrimsson pers. comm.; E.S. Hansen pers. comm.), and growing evidence of population declines in many of these seabird populations

(Gardarsson 2006a; Gardarsson *et al.* 2011) is thought to be related to a lack of food resources. A monitoring programme on sandeel abundance along the South and West coast of Iceland, initiated in 2006 by the Icelandic Marine Research Institute, suggested an annual low recruitment of 0-group sandeel up to 2011 (Bogason and Lilliendahl 2008; Anon 2012). Dietary studies of Northern Gannet *Morus bassanus* chicks in South Iceland (Vigfusdottir *et al.* 2009) showed that sandeel was the main prey in chick diets in 1973 and again in 2004-2005, but was absent and replaced by mackerel *Scomber scombrus* in the diet in 2006-2007. It is likely that the lack of the main prey, sandeels, may be linked to the observed population decline and breeding failures of many seabird populations in West Iceland. The study reported here suggests that limited availability of sandeels, and consequent low rates of delivery of sandeels to chicks, are also likely to be contributing greatly to the low productivity of Arctic Terns in West Iceland.

Capelin has been described as the main prey item exploited by seabird populations breeding in the North and East of Iceland (Lilliendahl and Solmundsson 1998; Thompson *et al.* 1999). Capelin was indeed the main marine fish species delivered to Arctic Tern chicks in colonies at Melrakkasletta in NE-Iceland. However, only in one colony (Valthjofsstadir) was capelin the most common prey species delivered to chicks (Fig. 5.2). Items of estuarine or terrestrial sources comprised a higher proportion of the chick diet (Fig. 5.2), and were delivered at much higher rates, in most colonies on Melrakkasletta (Fig. 5.6a). Seabird populations breeding in North Iceland have been reported as experiencing better breeding success in recent years than individuals of same species breeding along the West and South coast (Gardarsson *et al.* 2011; A. Gardarsson pers. comm.; E.S. Hansen pers. comm.). However, this study suggests that Arctic Tern chick growth and fledging success were similarly low in most colonies in both Snaefellsnes and Melrakkasletta areas (Figs. 5.4 and 5.5).

Arctic Terns appear to have limited access to capelin at most colonies at Melrakkasletta, and the majority of prey at several colonies were small items from estuarine or terrestrial sources. Similar findings have been reported for Common Tern *Sterna hirundo* chicks in colonies on the Lower Saxon Wadden Sea (Massias and Becker 1990), where herring *Clupea harengus* and other marine fish were the most favoured diet, but three-spined sticklebacks and common shrimps *Crangon crangon* were an important additional energy source in times of low availability of main prey. In the Common Tern study, the availability of the alternative prey resources facilitated maintenance of chick body mass and growth, and prevented chick starvation during periods of when marine fish resources were scarce. However, despite being of relative high nutritive value, the alternative prey were likely to have been of lower energetic value for chicks, because their exoskeletons are not digestible by the chicks (Massias and Becker 1990). Similar digestive

constraints may influence the value of the estuarine and freshwater prey delivered to Arctic tern chicks in our study.

Many seabird populations across the North Atlantic have been declining in recent years, and breeding failures are increasingly reported (Frederiksen 2010). Many of these declines have been linked to local or large scale reductions in food availability (Wanless *et al.* 2005; Frederiksen *et al.* 2006), influenced by over fishing and/or environmental changes (Anker-Nilssen *et al.* 1997; Wanless *et al.* 2004; Frederiksen *et al.* 2004, 2012; Furness 2007). Effects of depletion of fish stocks on seabird populations have been well documented in West Norway where population of Atlantic puffins *Fratercula arctica*, dependent on young herring as chick food, declined by 65% during decades of low productivity, after an over-fishing and consequent collapse of the spring-spawning herring stock (Anker-Nilssen *et al.* 1997; Barrett *et al.* 2006). The breeding success of a surface-feeding seabird, Black-legged kittiwakes *Rissa tridactyla*, was also depressed during a period of intensive sandeel fishing off the east coast of Scotland during the 1990s, while no negative effect was apparent on productivity of four species of diving seabirds (Frederiksen *et al.* 2004, 2008; Wanless *et al.* 2007). Sandeels are not fished in Iceland and, in the absence of effects of fisheries, the cause of declines in the availability of such prey to seabirds is less clear, but is most likely linked to environmental changes (Frederiksen *et al.* 2007b). Sandeel recruitment is highly variable between years, and seems to be affected by climatic conditions, either directly or through the availability of their copepod prey *Calanus finmarchicus* (Arnott and Ruxton 2002; Frederiksen *et al.* 2006; van Deurs *et al.* 2009). Several studies have quantified associations between changes in environmental conditions, e.g. sea temperature, and seabird productivity and population trends, suggesting an indirect link via changes in resources availability. Studies on the Isle of May in East Scotland have shown that several aspects of seabird demographic performance were negatively correlated with sea temperature: breeding success of black-legged kittiwakes (Frederiksen *et al.* 2004), adult survival of Atlantic puffins (Harris *et al.* 2005; Grosbois *et al.* 2009) and black-legged kittiwakes (Frederiksen *et al.* 2004). For black-legged kittiwakes, the negative relationship between breeding success and sea temperature was consistent across colonies in East Scotland (Frederiksen *et al.* 2007c) and Orkney (Frederiksen *et al.* 2007a), suggesting effects beyond the areas being intensively fished. Demographic modelling of this population indicated that continued population declines are likely if sea temperatures continue to increase, even if sandeel fisheries remain closed (Frederiksen *et al.* 2004), highlighting the important role of environmental conditions on sandeel availability. More recently, Frederiksen *et al.* (2012) demonstrated a strong link between the abundance and distribution of copepods *Calanus finmarchicus* in relation to climatic and oceanic

changes, which may possibly be linked to a trophic mismatch across multiple levels of the North Sea pelagic food web (Burthe *et al.* 2012).

As predicted by Frederiksen *et al.* (2012) these sorts of trophic cascades may spread northward in the near future, including Icelandic waters. Predictions of increased sea temperatures and disruptions in primary productivity are in an agreement with observed and predicted hydrographic (changes in ocean currents, temperature and salinity) and marine ecosystem changes (shifts in distributions and abundance of fish species) around Iceland (Valdimarsson *et al.* 2012). Range shifts of fish species have already lead to changes such as marked increases in numbers of mackerel in the South and West of Iceland (Astthorsson *et al.* 2012), a species which is known to predate sandeel in the North Sea (Furness 2002). In contrast, sandeel are not yet present in the waters of North and East Iceland, but excessive capelin fisheries in the North of Iceland (Astthorsson *et al.* 2007; Anon. 2012) may be influencing seabird populations in those areas through resource depletion (Furness 2007). Observed population declines in a range of seabird species around Iceland (Gardarsson *et al.* 2011; A. Gardarsson pers. comm.), as well as the poor productivity and chick mortality described in this study, are therefore likely to be linked to these ongoing, complex changes in the marine environments in Icelandic waters.

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Chapter 6

Chapter 6

General Conclusions

Changing environmental and climatic conditions in the marine environment

In recent years, understanding the impacts of global changes in environmental and climatic conditions has become one of the principal challenges facing the scientific community (Salinger 2005; IPCC 2007). Climate-driven environmental changes are predicted to be particularly severe at high latitudes (IPCC 2007), where fragile ecological systems may be severely disrupted by changing temperatures, sea level rise and glacial retreat. In terrestrial environments, numerous studies have indicated climate-related shifts in species distribution, range size and demography (Parmesan and Yohe 2003), but the effects of climate change on the world's largest ecosystem, the marine pelagic realm, are less well understood. The effects of climatic variation on marine ecosystems are complex to unravel because of their large scale and dynamic complexities (Richardson and Schoeman 2004; Richardson *et al.* 2012), and because ocean research is costly and time consuming. Consequently, most reports on climate-related changes in marine systems have focussed on commercially-exploited species and related subjects (e.g. Perry *et al.* 2005). Identifying ecological systems and species that operate as indicators of environmental changes in the marine realm can provide opportunities to understand the impact of changes to these environments. Higher predators are often of particular value as indicator species, as they are sensitive to changes throughout the ecosystem (Boyd *et al.* 2006).

Seabird populations have provided some of the clearest evidence for changes in marine ecosystems, and many breeding populations of seabirds have declined in productivity and abundance in recent decades (Frederiksen *et al.* 2006; Frederiksen, Furness, and Wanless 2007; Barrett 2007; Piatt and Sydeman 2007; Heath *et al.* 2009). Iceland supports a very large proportion of the breeding seabirds of the North Atlantic region (Gardarsson 1995; Asbirk *et al.* 1997) and, while there are no regular and systematic surveys of seabird abundance and demography in Iceland, there is evidence of recent declines in several species (Gardarsson 2006a; b), particularly those dependent on small, high energy fish species such as sandeels (Lilliendahl and Sólmundsson 1998; Thompson *et al.* 1999).

In this study I have shown that, on colonies right across the Snaefellsnes peninsula in western Iceland, Arctic Tern productivity was very low between 2008 and 2011 (Chapter 2), and that the low productivity was primarily the result of high chick mortality (Chapter 3). Chick mortality was greatest among chicks with very low growth rates, and in colonies at which the prey delivered to chicks was of low energetic value and/or delivered at very low rates, suggesting that starvation was the cause of the high mortality (Chapter 4). These patterns indicated that prey resources for chicks were likely to have been limited during these years. However, as the main marine prey resource in West Iceland was sandeels, which were only present in the waters of South and West Iceland, we also quantified prey composition, delivery rates, chick growth rates and survival in colonies in North East Iceland, in order to compare Arctic Tern success rates in areas with differing prey communities. Prey composition and size varied greatly between regions and colonies. In West Iceland, higher prey delivery rates were associated with greater fledging success, but sandeels were delivered at low rates at all colonies. In North East Iceland, capelin replaced sandeels as the main marine prey, but delivery rates of capelin were either very low or very inconsistent, and fledging success in North East Iceland was similarly low (Chapter 5).

This evidence suggests that sandeel availability in West Iceland was not sufficient to fuel high productivity during these years, but also that capelin abundance in the North East was similarly low, in 2011 at least. Seabird populations around Iceland therefore appear to be facing changes in prey abundance and availability, although the causes of these changes may vary regionally. Sandeels are not fished in Icelandic waters, but are known to be influenced by changing sea temperatures (Arnott and Ruxton 2002; Heath *et al.* 2012), perhaps directly but also through changes in their own prey distribution (Frederiksen *et al.* 2012). However, capelin is fished very intensively around Iceland, and this study suggests that capelin may be of limited availability to Arctic Terns, at least in 2011.

Wider consequences of poor prey resources for Arctic Tern chicks

In this study, low prey delivery rates were associated with low chick growth rates and high levels of chick mortality. However, low prey abundance may not have been the only reason for the chick mortality, as indirect consequences of low prey abundance were also recorded, including apparent behavioural responses to resource limitations. Low food availability can result in parents increasing their foraging time, leading to less frequent nest attendance, which may in turn leave chicks more exposed to predation (Davis *et al.* 2005) or conspecific attacks (Ashbrook *et al.* 2010). Some evidence of this was observed during this study as, on

Snaefellsnes in 2010, all nests in the two colonies with higher prey delivery rates and productivity (Stykkisholmur and Berserkseyri) had at least one parent present during observations, while most nests at other colonies were frequently unattended by adults (Fig. 6.1).

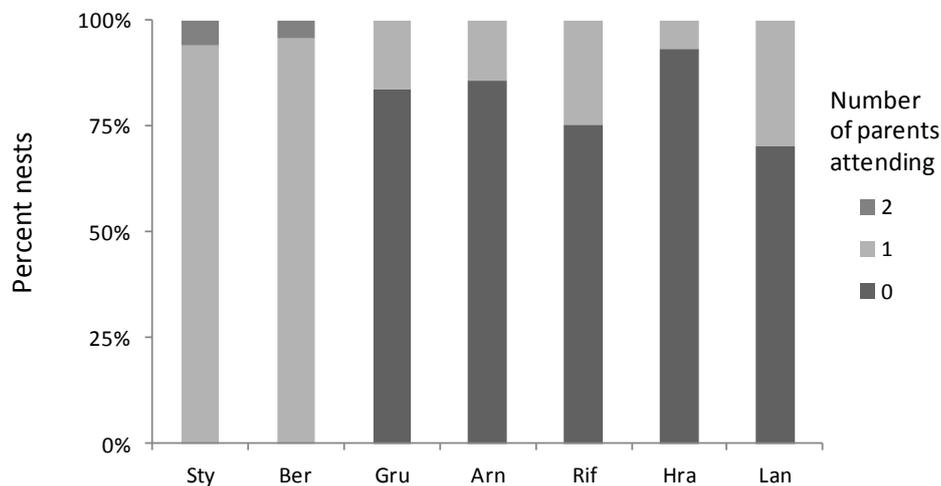


Fig. 6.1. Proportion of nests attended to by no (0), one or two parents across colonies on Snaefellsnes peninsula in 2010.

Additionally, kleptoparasitism has been documented in populations as a behavioural response to limited food availability (Ratcliffe *et al.* 1997; Stienen *et al.* 2001). Here, conspecific kleptoparasitism, typically by neighbouring Arctic Terns, was observed quite frequently within study areas during provisioning observations (Fig. 6.2). These events were most commonly observed in the largest colony (Rif) where fledging success and chick growth rates were also the poorest (Chapter 5), and thus there were particularly large numbers of failed adult breeders present. Kleptoparasitism has been recorded as being more frequent when prey are of greater value and require greater handling times (Steele and Hockey 1995; Ratcliffe *et al.* 1997; Stienen *et al.* 2001). Kleptoparasitism may therefore have had a negative influence on chick survival by reducing food delivery rate through disturbance of provisioning events and/or through robbing of food items.

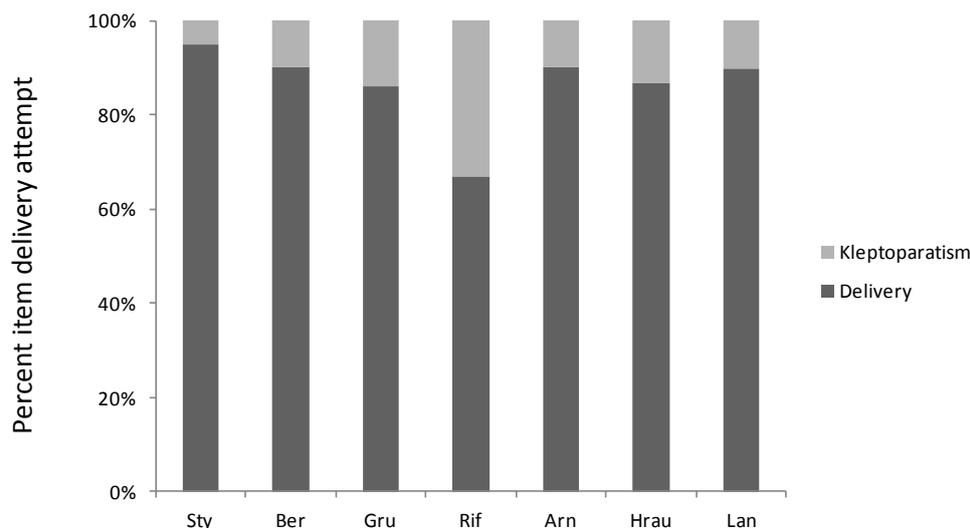


Fig. 6.2. Percent of food items presented to Arctic Tern chicks on colonies across the Snaefellsnes peninsula that were either successfully delivered or robbed by conspecific kleptoparasites.

Another response to low resource availability and a lack of preferred prey types can be for adults to search for alternative prey sources, for example from different foraging habitats (Massias and Becker 1990). Alternative prey may be of poorer nutritive quality than preferred prey types (e.g. Massias and Becker 1990; Harris *et al.* 2008; Chapter 5) and/or of less appropriate shape or size for chicks to handle, which may lead to high prey refusal rates (Stienen *et al.* 2001). In this study, although not quantified systematically, prey items with external defence structures, such as the spikes on sticklebacks, and large, difficult to handle items such as lumpsuckers were often found uneaten around nest bowls of monitored chicks and, during provisioning observations, chicks were seen struggling to swallow or rejecting such items. In these cases, alternative prey of this sort may lead to poor energy intake by chicks which may also increase the risks of starvation.

Additionally, during examination in the field and dissections of dead chicks (Chapter 3), gut parasites were found in chicks from colonies where alternative prey, in particular sticklebacks, had been delivered at high rates (Larvadall, Skallabudir, Nupskatla and Blikalon) (Chapter 5). The parasites were identified as tapeworms (K. Skirnisson, pers. comm.), and the tapeworm *Scistocephalus solidus*, is a common gut parasite in sticklebacks in Iceland (Richter 1982). Before these tapeworm-infected chicks died, they were often observed with to have a swollen gut, leaking faecal matter and to be in very poor condition. It is therefore likely that these parasitic infestations may have had direct negative effects on chick condition and survival, in addition to the overall low food availability. Parasites have also been reported having negative effects on body condition and consequent survival and recruitment probabilities of other tern species (Monticelli and Ramos 2012).

Arctic Tern 'super-colonies' in Iceland

Although food supply is widely viewed as having an important role in regulating seabird colony size (Furness and Birkhead 1984), the direct mechanism for such regulation is unclear. Cairns (1989) proposed an alternative model of population regulation of size of seabird colonies, based on the notion that colony size was related to the amount of foraging habitat used by the colony, that neighbouring colonies occupy non-overlapping feeding zones and that colony population was a function of the size these zones. However, these effects may not be apparent for species with particularly long foraging ranges, which can exploit additional resources, or those with very short foraging ranges, for which resources may be replenished from the surrounding habitat (Cairns 1989). The influence of colony size and resource availability on seabird populations is therefore not always clear. However, in agreement with previous studies (Massias and Becker 1990; Anker-Nilssen, Barrett, and Krasnov 1997; Wanless *et al.* 2005; Frederiksen *et al.* 2007; Burthe *et al.* 2012), the results of this study stresses the importance of adequate availability (quality and quantity) of nutrient rich food items, here primarily of marine sources, for successful rearing of Arctic Tern chicks. Interestingly, the largest colonies on Snaefellsnes peninsula are also the colonies where alternative prey items were not delivered, and possibly not available, to the chicks (Chapter 5). The individuals in these colonies seem to depend primarily on marine food resources which in turn may explain why these colonies are so large in the first place. For long-lived species with high natal philopatric behaviour, the resource quality and abundance required to fuel high annual productivity and consequent recruitment that lead to very large colony sizes may only be available from marine ecosystems. Historically, the very large colonies in this study (Rif and Arnarstapi), have been very large for at least a century (S. Kristjansson, pers. comm.) indicating that favourable conditions for these colonies to become and persist at these sizes must have been present in previous decades. However, these conditions were not present during the period of this study, as the breeding success in the largest colonies was among the poorest in the area (Chapter 2). This is in agreement with density studies of the marine prey, sandeel, in this area, that has been measured in very low numbers and with poor recruitment annually since 2006 (Bogason and Lilliendahl 2008; Anon. 2012).

Such very low fledgling success in the largest colonies is clearly of concern in relation to the overall population status of Arctic Terns in Iceland. The only colonies with fledging success in excess of 0.5 chicks per pair were small colonies (hundreds of pairs), and the 'super-colonies' with > 5000 pairs fledged only 0 - 0.2 chicks per pair in all years of the study. In absolute terms, the higher fledging success at smaller colonies is likely to have resulted in approximately half the number chicks fledging than in the larger colonies with lower per capita fledging success (assuming

~0.5 chicks per pair in colonies of 500 pairs and ~0.1 chicks per pair in colonies of 5000 pairs, Chapter 2, Figs 6.1 and 6.2). Small colonies with these levels of fledging success cannot therefore compensate for the losses at larger colonies, and it seems likely that total number of breeding Arctic Terns in Iceland is in decline. However, a decline in numbers in colonies comprising many thousands of breeding pairs can be very hard to detect, while detecting population change in colonies of tens to hundreds of pairs is much easier. It may therefore be that population declines have already taken place and gone undetected, as there are no systematic monitoring programs in action for Arctic Terns in Iceland. Our results suggest that the productivity that these populations have experienced in recent years is very poor and, if this continues, these populations are likely to decline rapidly as a consequence of low productivity and recruitment. Increases in adult survival rates could potentially reduce the impacts of low productivity on overall population size, but the high annual survival rates of such long-lived species may mean that the necessary increases in survival rates are unlikely (e.g. Klok *et al.* 2009).

The importance of Iceland for Arctic Terns

Around 20-30% of the world's Arctic Terns breed in Iceland (Asbirk *et al.* 1997), and their breeding status in Iceland is therefore a key issue for the global conservation of the species. Additionally, the waters surrounding Iceland support one of the richest marine ecosystems in the North Atlantic region and are consequently of huge biological and economical importance, hosting a wide range of sea life, including large commercial fish stocks as well as huge populations of seabirds, (Astthorsson *et al.* 2007). However, in the past decade, the waters around Iceland are warming and many fished species have extended their ranges northward (Valdimarsson *et al.* 2012) and further hydrographic changes with warming sea temperatures are predicted for Icelandic waters (IPCC 2007). Understanding the dynamic and complex marine environment is therefore of great value, and seabird research may be of help in assessing the nature and extent of the current changes. Arctic Terns are conspicuous and easily accessible and distributed all around the Icelandic coastline in colonies that are exposed to range of environmental conditions, allowing multi-colony studies that can have advantages over single colony studies in allowing a wider range of conditions to be assessed (Jennings *et al.* 2012).

Many other seabird species breeding around Iceland depend on the same resources as Arctic Terns. Some recent studies indicate that these productivity in these species has not been as low on the North coast as on the South coast (Gardarsson *et al.* 2011; E. S. Hansen pers. comm.). However, the results of this study indicate that the breeding conditions for seabirds on the North coast may not be as

favourable (at least in 2011) as previously suggested. This might be a recent trend and/or a temporary lack of resources, which surface feeding, short distance foraging species (like the Arctic Terns) are known to react to sooner than long distance diving species (Wanless *et al.* 2007; Frederiksen *et al.* 2008). Given the importance of the North of Iceland for seabird populations, it will clearly be important to identify whether this is part of a longer-term, and perhaps larger-scale, decline in availability of food resources.

Future perspectives for Icelandic Arctic Terns and the importance of seabird conservation in Iceland

Species that can act as indicators and integrate signals from a range of complex processes can be extremely effective in allowing rapid exploration of the implications of environmental changes (Furness and Camphuysen 1997; Boyd *et al.* 2006; Piatt and Sydeman 2007; Parsons *et al.* 2008). Although many factors may influence seabird demography (Cairns 1987; Piatt *et al.* 2007), seabirds can act as useful sentinels of the marine environment (Furness and Camphuysen 1997; Furness and Tasker 2000; Boyd *et al.* 2006; Heath *et al.* 2009).

Population monitoring of Arctic Tern in Iceland is currently non-existent and given the evidence for widespread productivity failure and the huge numbers of Arctic Terns breeding in Iceland, it is clearly needed. However, Arctic tern colonies are spread throughout Iceland, which present considerable logistic challenges and, given the potential problems with detecting changes in breeding numbers in very large colonies, simple estimates of annual changes in colony size may not be sufficient to identify population changes. Monitoring programmes may also therefore need to consider methods for quantitatively assessing both abundance and breeding demography of Arctic Terns. Rapid measures of productivity may be possible for a sample of colonies by surveying each colony during incubation, to measure nesting density, clutch size variation and estimate laying dates (from egg floatation methods), and again during chick-rearing, to measure chick mortality (from carcass counts), and potentially also to measure fledging success (within enclosures for larger colonies) .

In relation to habitat conservation, it is important to bear in mind that the main prey of seabirds in South and West of Iceland is sandeel, a fish species that is not harvested in these waters. Any, changes relating to abundance and/or distribution of these species is therefore likely to be linked to complex issues such as trophic changes operating through the marine food web that may be influenced by larger scale oceanic or climatic changes. On the North and the East of Iceland, the main prey of seabirds is capelin which is heavily fished in these areas and thus reducing

fishing pressures on capelin may be beneficial for seabirds breeding in these areas. Exploring the role of capelin abundance for seabirds in these areas may prove to be an important opportunity for improving seabird conservation in Iceland. Iceland supports 30 million seabirds and 300 thousand people, and so the task of seabird monitoring and conservation is not straightforward, but is clearly very important for these vast and internationally important seabird populations.

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