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The use of eggs and diet of great skuas as biomonitors in the Faroe Islands

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Declaration

I declare that, except where explicit reference is made to the contribution of others, that this dissertation is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

The following chapters have been published in co-authorship with my supervisors and others:

Chapter 4: Hammer, S., Nager, R. G., Alonso, S., McGill, R. A. R., Furness, R. W., Dam, M., Legacy Pollutants are Declining in Great Skuas (Stercorarius skua) but Remain Higher in Faroe Islands than in Scotland (2016), Bulletin of Environmental Contamination and Toxicology, DOI: 10.1007/s00128-016-1856-x

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Signature ____________________ Printed name __________________________

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I won’t be the last
I won’t be the first
Find a way to where the sky meets the earth
It’s all right and all wrong
For me it begins at the end of the road
We come and go…

Eddie Vedder

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1. General Introduction

All biological life needs energy for survival, growth and reproduction. Numerous morphological, physiological and behavioural adaptations have arisen for organisms to acquire the necessary resources of energy and nutrients. For free-ranging animals, this generally involves foraging behaviours (Levin 2009). While some organisms are able to utilise energy and elements directly from the environment - autotrophs, most animals are heterotrophs and acquire these resources from autotrophs. Resources can be broadly categorised as substitutable, essential or hemi-essential, and these vary in the degree that they influence the rate of population growth of the consumer (Tilman 1982). Resources in this regard are typically considered in pairs. Substitutable resources can be replaced with one another without loss of time or nutritional value. Essential resources are necessary for life, and if a pair of essential resources are considered, the maximum growth rate of a species will be determined by which resource is more limiting. Hemi-essential resources can be where one resource is nutritionally complete, and others may lack key elements. From these general categories of resources, there are numerous constellations of resource pairs, and these can be divided as linear, concave or convex (Tilman 1982). However, resources shall not be considered solely for their nutritional value, as there are many other factors, which influence the access and suitability of resources at any given time. Resource acquisition or foraging can for many animals be limited spatially and temporally, for example in order to avoid predators, or socially learned behaviour from conspecifics (Brown 1999). So the value of resources is relative to their accessibility. Optimal foraging theory proposes that organisms will search for and consume food which is optimal relative to the time and energy it has spent finding and digesting it (Begon *et al.* 2006).

One important feature of resources is that they are consumable. If, as it frequently is in nature, resources are limited in supply consumption of it makes a resource unavailable for others, which gives rise to resource competition. David Tilman (1982) proposed that if two or more species require the same resource, the one which has the highest rate of per capita growth at the lowest resource level, will exclude all other species, and this became known as the R* rule (Tilman 1982). In other words competition under the R* rule will favour one until the other is extinct. However, in the natural environment competing species are widely observed, so there are apparently other mechanisms, which allow for coexistence of competing species.

How a species' population exists and is limited to its environment can be generally described as a niche. Niches can have four dimensions: resources, natural enemies, space and time (Chesson 2000) – this is also recognised as "n-dimensional niche space" (Cohen 1978). The two important parameters to consider in this context are the niche distance (d) – the between species difference and niche width (w) – the within species difference. The degree of coexistence with other species is determined by niche overlap. Similarly to the R* rule, the resource-utilization niche theory by MacArthur and Levins (1967), also suggests that two species which have a high degree of similarity cannot co-exist. The resource-utilization niche model can characterize species as generalists (large w) or specialists (small w). However an increasing body of evidence suggests that considering species as uniform in this regard presents a simplified view of individuals within a population (reviewed in Bolnick *et al.* 2003). Individuals within a population can indeed use different subsets of resources within the same niche (Bolnick *et al.* 2002), and this can vary across sex, age and morphology (Bolnick *et al.* 2003). One implication is that a generalist population can be composed of specialist individuals, i.e. different individuals specialise on different resources. Examples of individual niche specialisation (INS) are sharks, alligators and gulls (Pierotti & Annett 1991, Munroe *et al.* 2014, Rosenblatt *et al.* 2015). With a growing, amount of evidence for individual variations across a wide taxa of for example diet, some studies have begun exploring the mechanisms behind this, and the general ecological implications of this (Araújo *et al.* 2011).

INS is not independent of habitats or population size. Rosenblatt et al. (2015) found lower INS of American alligator *Alligator mississippiensis* found in lakes compared to coastal individuals. In a study of southern sea otters (*Enhydra lutris nereis*), Tim Tinker *et al.* (2012) found the degree of INS to be greater in dense populations. In testing for different explanatory models for prey preference in otters, they found best support for a model called "competitive refuge model" – which suggests that individuals have a similar core diet, but differ hierarchically in their preference for sub optimal food (Tim Tinker *et al.* 2012). In other words, competition for the optimal resources may make the less capable competitors chose sub-optimal prey

A predicted advantage of specialisation is in relation to optimising resource acquisition. Terraube *et al.* (2014) showed that the foraging success of Montagu's harrier (*Circus pygargus*) was highest for the most specialised individuals. Short term pay off from specialisation has also been seen in black-tailed godwits (*Limosa limosa islandica*) which specialised on bivalves (Catry *et al.* 2014). There were significant sex differences in the degree of specialisation, and this is likely due to sexual dimorphism. However, the study also found evidence for specialisation independent on morphology and sex, and found that specialist feeders had a higher intake rate than non-specialists (Catry *et al.* 2014)

The degree of specialisation can have implications for the extinction risk of some species to environmental change (Colles *et al.* 2009). The relative quantification of specialisation is receiving increased attention. For example a recent study created a community specialisation index and applied it to a spatial scale (Vimal & Devictor 2014). The loss of habitat heterogeneity in Europe would for example has been predicted to result in fewer specialists and more generalists, but this is not found to be the case universally (Sullivan *et al.* 2016). Sullivan et al. (2016) showed a slight increase in UK specialist populations over the past two decades, and propose that the decline in habitat heterogeneity has resulted in declines of moderate generalists.

Most seabird species are colonial, and during the breeding season they are central place foragers (Gaston 2004). This can result in a progressive depletion of local food resources – “Storer-Ashmole’s Halo” (Storer 1952, Ashmole 1963). As the breeding season progresses, intraspecies competition for food may increase. Since 2000 a number of published studies have shown individual specialisation among seabirds (reviewed by Ceia & Ramos 2015). While most studies have focused on testing a null hypothesis of whether the diets of individuals differ significantly from niche width, many studies have shown an increased breeding performance due to dietary specialisation (Annett & Pierotti 1999, Votier *et al.* 2004). This could be due to numerous factors such as nutritional value, but one important factor is the reduction of foraging time and effort (Wakefield *et al.* 2015). Votier *et al.* (2007) hypothesised that competition for food among great skuas (*Stercorarius skua*) resulted in specialisation of seabird prey, and this was generally seen with larger colonies where most feed on fish, while smaller colonies, a greater portion feed on seabirds.

Studies have shown that dietary specialisation can improve the breeding performance of individual organisms, less attention has been paid on potential negative effects from dietary specialisation. A specialized diet can differ in various aspects such as trophic level, physiology or life-history of the prey, and this can lead to differences in pollutant exposure (Anderson *et al.* 2009, Newman 2010). Bearhop *et al.* (2000) showed that trophic level as inferred from stable isotope analysis correlated with an elevated concentration of mercury in great skuas. So dietary specialisation can in some cases result in increased exposure to pollutants, and the research challenge is to evaluate the relative weighing of two factors which can potentially influence the breeding performance of individuals - dietary specialisation and pollutant exposure.

Biomonitoring in the Northeast Atlantic

Chemical compounds, whether they are designed with specific purposes such as pesticides or flame retardants or secondary emissions or by-products from industrial production, enter into the environment, where they can have unforeseen detrimental effects on a wide ranging scale from the cellular to ecosystem level within the system in which they are released (Peakall 2007). Detrimental effects of chemical pollution include suppression of the immune system, hormonal disturbance, and serious neurological and kidney damage (Wolfe *et al.* 1998, de Wit *et al.* 2002). Due to these detrimental effects of chemical pollutants, there is concern not only about hazards to human health through consumption, but also about their possible toxic effects on wildlife (Muir & de Wit 2010). The main chemical pollutants which have attracted concern are known as persistent organic pollutants (POPs) (Newman 2010). Although in Europe and North America the use of some pollutants has been banned or is restricted (e.g. organochlorine insecticides) (Lead *et al.* 1997) other emerging pollutants (e.g.brominated flame retardants, perfluorinated substances (PFAS) and dioxin-like PCBs) are generally found to increase and present a threat to human and wildlife (Lindström *et al.* 1999, Lavoie *et al.* 2010, Muir & de Wit 2010).

Pollutants can accumulate in the environment and be transported away from the site of use or emission and various different physical properties determine the transport and persistence of chemical pollutants in the environment. POPs that are released into the environment in relatively warm climates, can be transported over large distances towards the poles via atmospheric circulation, before being deposited (Muir & de Wit 2010). Due to this many pollutants have been found to accumulate in the polar areas (de Wit et al. 2002). Most POPs are lipophilic and as a result are concentrated in lipid where they bioaccumulate (Newman 2010) and bio magnify in food chains, so that they reach highest concentrations in top predators (Lavoie et al. 2010). Marine food webs accumulate higher levels of POPs than terrestrial food webs (Newman 2010), which makes seabirds particular useful monitors of chemical pollution. Although an overall reduction in legacy POPs has been apparent in eggs of some seabirds in some ecosystems, levels in seabird eggs have shown little or no decrease or have continued to increase. For example, concentrations of certain PCB congeners continued to increase in gannet *Morus bassanus* eggs from the Bass

Rock, east Scotland from 1990 to 2004 (Braune *et al.* 2007, Helgason *et al.* 2008, Pereira *et al.* 2009). Because of global spread of POPs to the Arctic, much of the emphasis on monitoring trends in legacy POPs has focused on Arctic marine ecosystems, while few data are available from lower latitudes. In the context of the marine ecosystem around the British Isles for example, Pereira et al. (2009) concluded "The lack of any decline in some contaminants, for example some of the heavier PCB congeners in gannets at Bass Rock, highlights a need for further monitoring to determine future risk". In recent decades, new "emerging" POPs have also appeared in seabird eggs, including PBDEs and PFAS (Lavoie et al. 2010). For example in an environmental report by the Nordic Ministers council there were detectable concentrations of PFOS in fulmar *Fulmarus glacialis* eggs sampled in the Faroes (Kallenborn *et al.* 2004).

In many pollutant monitoring programmes birds eggs are used, as they are generally easier to sample and standardise, and they require less destructive sampling than sampling for internal tissues. Many studies have quantified the correlation between egg concentrations and other tissues of birds (reviewed in Beyer & Meador 2011). For many seabird species such sampling has been undertaken in the past which allows for examining temporal differences. Collecting eggshells post hatching may also provide for suitable samples, as eggshell thickness, pigmentation and the chorioallantoic membranes (CAMs) have all been used as pollutant indicators in various bird species (Blus *et al.* 1972, Cobb *et al.* 2003, Jagannath *et al.* 2008). Using eggs also allows for examining maternal transfer of pollutants, directly and indirectly. Lipophilic compounds are transferred along with fat into developing eggs, and concentrations in eggs reflect the contaminant burden of the female at the time of laying, especially the uptake of contaminants from food recently ingested around the colony (Braune & Norstrom 1989, Becker *et al.* 2001).

Natural history and ecology of the great skua in the Faroe Islands

Great skua is the only species of the genus *Catharacta* which breeds in the Northern hemisphere. Their breeding distribution stretches from Bear Island to the British Isles from Jan Mayen to north Russia (Furness 1987).

Not much is known about the great skua before 200 years ago. In early 1800 great skuas were only known to breed in Iceland, Faroes and at two locations in Shetland (Foula and Unst) (Furness 1987). This would suggest that the great skua distribution has expanded quite markedly southwards in mid 20th century, most likely due to a decline in persecution. Also their expansion has been northwards over the past 40 years (Furness 1987).

The Faroese great skua population has undergone significant changes over the past 200 years. Such as in Shetland the main driver of this change can be assumed to be persecution (Furness 1987). From 1742-1881 the bill-tax obliged any man in the Faroes to annualy submit one beak of raven (*Corvus corax*), or two of crow (*Corvus cornix*), greater black-backed gulls *(Larus marinus*) or great skuas. The tax was repealed in 1881, but continued as a reward scheme until 1934 (Bloch 2012). This resulted in a great population decline of great skuas, who reached as few as four pairs left in 1896 (Salomonsen 1935a). In 1897 a ban to kill great skuas was passed , and this lasted until 1972 (Bjørk 1963, Føroya Løgting 2014). Following the ban, the general population in the Faroes steadily recovered as seen with the population on one traditionally large colony - Skúvoy (fig. 1.1). However following the law change in 1972 which removed the protection of great skuas, there was a slight dip in the population on Skúvoy, likely due to persecution. The two consequtive population estimates for Skúvoy (2010 and 2012) suggest that the marked population growth from 2001 until 2010 has stalled. With no protection, it is quite likely that persecution may be an important driver of population changes in the Faroes. Anecdotal evidence would suggest that local persecution increases when the population increases.

The great skua as a species is a generalist feeder. Because it has such a broad repertoire of strategies such as scavenging, predation or kleptoparasitism, there is a great level of spatial variation in their primary diet (Furness 1987). The great skuas on the world's largest colony on Foula, Shetland live primarily on fish discards (Phillips *et al.* 1997). Further North, on Bear Island and Faroes there is a greater proportion of great skuas that prey upon other seabirds such as black-legged kittiwakes (*Rissa tridactyla*), common guillemots (*Uria aalge*) and Atlantic puffins (*Fratercula arctica*) (Bayes *et al.* 1964, Knutsen 2010), while the Iceland population appears intermediate (Bourgeon *et al.* 2012). Although great skuas have been known to prey on terrestrial animals such as rabbits and hares, it is clear that their primary diet is marine which they acquire directly or indirectly. Votier et al. (2008) found that seabird predation was density dependent in UK colonies.

Although some historical descriptions have been done of the Faroese great skua, their diet was not been described in much detail until mid 20th Century. Faroese naturalist Hans-Christian Muller wrote in 1862 that great skuas feed on herring (*Clupea harengus*), which they kleptoparasitise from other birds or which they catch themselves. Further he notes that they feed on whale carcasses, steal eggs, and kill geese, ducks and other birds (Müller 1862). Mikkjal á Ryggi (1978) wrote in 1951 that great skuas pursue lesser black-backed gulls (*Larus fuscus*) to get them to regurgitate fish, and it also catches saithe *Pollachius virens* and herring itself . He also notes that it is a threat to all seabirds, especially puffins *Fratercula arctica*, of which it steals eggs and kills the adults (Ryggi 1978). The first detailed description of the diet of the Faroese great skua population was done in 1961 by Bayes *et al.* (1964).The study which was mainly based on observations, prey remains and pellets from Svínaskoradalur (N61°15'41 W07°12'15) (fig 1.2b), showed that the majority of their diet constituted adult kittiwakes and fish. There was a high rate of predation of adults, eggs and chicks of various seabirds, although they were also observed following fishing boats for offal or bycatch (Bayes *et al.* 1964). Pellets collected both at the clubsite (which typically is close to the colony, where immature individuals and territories was mostly kittiwake – e.g. all 76 pellets collected early in the breeding season at the clubsite had kittiwake remains. Eggshells could be found at 13 territories, the great majority from kittiwake. One territory had as many as 200 kittiwake egg remains. Eight chicks regurgitated during handling and all but one contained kittiwake liver, one contained sandeel *Ammodytes spp*. They also noted observations of chick predation of kittiwake (12), guillemot (30), fulmar (2), great skua (10), arctic skua (2).

Anders Holm Joensen who did work on Skúvoy (N61°45'57 W06°49'23) (fig 1.2a) also in 1961 noted that great skuas are frequently seen stealing eggs from kittiwakes, guillemots and Northern fulmars *Fulmarus glacialis*, and carcasses of these species were also found around great skua territories (Joensen 1963), but he did not produce an estimate of relative abundance. As a testimony to the great skuas opportunistic foraging habits, Joensen also notes that he found the remains of a whimbrel egg, and the great skuas were frequently seen chasing whimbrels (*Numenius phaeopus*) and Eurasian oystercatchers (*Haematopus ostralegus*) (Joensen 1963).

From the historical accounts of the diet of great skuas in the Faroes, it is worth noting that they differ in time, but there are also potential small-scale regional differences within the Faroes. For example Mikkjal á Ryggi's (1978) note that great skuas are a particular threat to puffins, could potentially have been biased by observations in the area he was most familiar with on West-Vágoy and Mykines, where there are large puffin colonies. Indeed great skuas are still controlled on Mykines for the sake of protecting puffins (Esbern í Eyðanstovu pers.comm.). Another example of regional variation in great skua feeding strategy are observations by Alwin Pedersen in 1935 of great skuas kleptoparasitising

Northern gannet *Morus bassanus* on Mykines (Pedersen 1935). The older historic accounts and the study from 1961 suggest that great skuas in the Faroes predate to a higher extent on other seabirds compared to Shetland which feed mainly on fish (Furness 1987).

From historic studies on the diet of Faroese great skuas, it appears that they may be feeding at a higher trophic level than the Shetland population (Bayes *et al.* 1964, Furness 1979). Due to the great skua's opportunistic nature, variation in diet can be expected between colonies in the Faroes and Shetland, and will give an opportunity to examine whether a high pollutant load reflects predatory specialisation. The Faroese great skua population has three main colonies with approximately 100-200 pairs each: Skúvoy (which will be the main study site), Saksun and Svínoy, with numerous smaller sub-colonies of 5-20 pairs. Although the monitoring on Skúvoy has shown an overall decline in seabird numbers, prey availability for skuas can be considered still to be relatively abundant (Olsen 2011b).

Studies of the great skua in Shetland, Iceland and Bear Island, have shown that those closest to the Arctic (Bear Island) are most polluted with POPs, and the Shetland population least polluted (Bourgeon *et al.* 2012). Whether this is due to a difference in diet or the geographical variation of POPs remains uncertain.

Due to the Faroese great skua's diet of predominantly seabirds, they can be expected to accumulate pollutants (heavy metals and POPs) predominantly from marine sources. A study on pollutant load of Faroese great skuas from 1977 has reported levels of total mercury, dieldrin, DDE and ∑PCB in 19 great skua eggs (Bloch *et al.* 1987). These levels were higher than found in great skuas in Scotland (Leat *et al.* 2011), presumably at least in part due to the higher trophic level of great skuas in the Faroes. Although Bourgeon *et al.* (2012) did not detect an elevated stress level associated with the high pollutant load in the Bear Island great skuas, a combined effect of reduced food and high pollutant load, resulted in reduced reproductive success in great skuas (Bustnes *et al.* 2015).

Due to the significant spatial variation of great skua diet, gaining more insight into the diet of Faroese great skuas is important in relation to their pollutant exposure. In addition, the link between diet specialisation and pollutant load deserves more detailed study.

Globally the great skua population at 16.000 pairs is of "least concern" (BirdLife International 2012). However its geographically limited distribution means that local threats at colonies can have disproportionally high impact on the population. An overall decline in productivity in UK colonies since 2000 (JNCC 2016), will likely result in population declines over the next decade, and this has been observed for the larger colony on Shetland and Orkney (Furness, pers. comm.,Meek *et al.* 2011). The population trends in Iceland remain largely unknown, but in Bear Island, there is a continued population growth and its breeding range is expanding eastwards towards Russia (Hallvard Strøm pers. comm.).

In the Faroe Islands, the population has increased markedly between 2000 and 2014. There exist only regular counts of the colony on Skúvoy (fig 1.1,1.2a), but this increase has by own observations been observed throughout the Faroes. Ring recoveries suggest that this population growth could be due to immigration, as there are some spring recoveries of mature Scottish ringed great skuas (Hammer *et al.* 2014). Another likely cause of the increase is likely a reduction in persecution, although there exist no public statistics on culling. A higher rate of Faroese ring recoveries (5%) compared to Scottish ringed great skuas (3%) (Wernham *et al.* 2002), and the fact that 56% of Faroese recoveries are of shot or otherwise hunted birds (Hammer *et al.* 2014) would suggest that the degree of persecution in the Faroes can be relatively high. Great skuas are in the Faroes generally not hunted for food, but controlled as they are considered a menace to sheep, inland birds and seabirds, and they are currently not legally protected. Considering recent population growth, it is therefore likely that there will be an high rate of persecution in the Faroes. Outside the Faroes, great skuas are not legally killed, so the persecution risk can be considered rare and sporadic.

For some great skua populations which depend to some extent on fishing activity and discarding, the recent EU policy to reduce fish discarding can potentially result in population declines (Bicknell *et al.* 2013). The fisheries in the Faroes, Iceland and Norway are separately managed, and have in various ways ensured a lesser degree of discarding (Johnsen & Eliasen 2011, Gullestad *et al.* 2015), so the impact of great skua populations outside the EU can be assumed to be less influenced negatively by a reduction in fish discards.

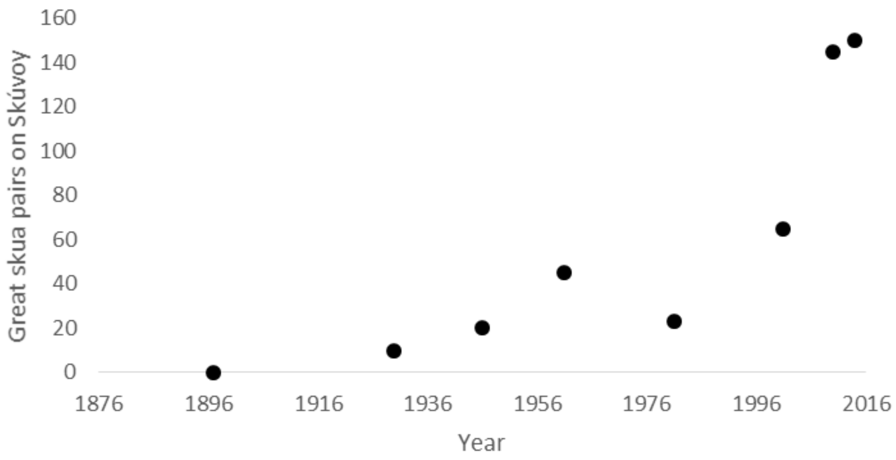

Fig.1.1 The great skua population on Skúvoy (Salomonsen 1935b, Ferdinand 1947, Joensen 1963, Bloch 1981, Olsen 2003, 2011a).

Fig 1.2 Map of the Faroe Islands showing the sites of the three largest great skua colonies a. Skúvoy, b. Svínaskoradalur, c. Svínoy

Aims

The initial aim of the thesis is to establish baseline information about diet and pollutant load of great skuas in the Faroe Islands. With reference to historical accounts, it is possible that the diet of great skuas in the Faroes differs greatly in relation to the diet of great skuas in Shetland. If this is found to be so, it opens up an additional avenue of investigation of diet’s influence on breeding performance and pollutant pathways, An extensive temporal and spatial analysis of great skua egg sizes will be investigated with these ecological differences in mind. Also if a significant ecological dissimilarity between great skuas breeding in Shetland and Faroes can be established, this will allow for a disentanglement of different pollutant pathways, and in this regard the great skua as a biomonitor is discussed.

Chapter 2.

Is the breeding benefit of dietary specialisation context specific? Most of the research done on great skua dietary specialisation has been undertaken in Shetland and Orkney, where the main diet constitutes of fish. In chapter 2 the aim is to explore if the general diet is different in the Faroes, and if it is, to test if predating on other seabirds results in improved breeding performance as has been found in Shetland colonies. If dietary specialisation results in improved breeding parameters due to meeting a higher nutritional demand, I would predict that a supplementary feeding experiment should result in improved breeding performance.

Chapter 3.

Average egg sizes have in some seabird species been found to correlate with food availability. Egg sizes of great skuas have in the literature been noted to be significantly smaller now than they were 30 years ago. This led me to explore if this was an overall declining trend as has been seen in other colonies where food availability has been declining. By acquiring egg measurements from the field and museum collections this study can explore long term trends and wide spatial scale of egg sizes of great skuas and two other seabird species in the Faroes.

Chapter 4.

Last time great skua eggs were analysed for persistent organic pollutants was in 1977, they showed some of the highest concentrations in Faroese avian biota. While there is good reason to study pollutant loads of top predators, there is further insight to gain from comparing the pollutant loads of great skuas from the Faroes with those of published values from Shetland. Although not a long distance away, great skuas in Shetland may differ trophically compared to the Faroese great skuas, so this study may give insight into the importance of diet and bio accumulation as a mechanism of transfer of persistent organic pollutants. The relationship between trophic level and POPs is also demonstrated with a correlational relationship between nitrogen isotope ratio and POPs concentrations.

Chapter 5.

Plastic is an emerging pollutant in the world's oceans. My study is the first to observe plastic in great skua pellets in the North Atlantic. The ratio of pellets which are found corresponds to seabird prey species which are known to accumulate plastic. This implies that the plastic found in great skua pellets, is not from direct consumption, but is likely secondary consumption of the plastic load which the prey carried. While there is no indication of long-term accumulation of plastic in great skuas, the findings suggest that great skuas specialising on fulmars, will be exposed to more plastic than generalist feeders or individuals specialising in other seabird species. The aim of this study is to evaluate if plastic found in great skua pellets corresponds to the type of prey which is known to accumulate plastic, and thereby assess the suitability of great skuas as biomonitors of secondary consumption of marine plastic.

2. Diet of great skua in the Faroe Islands

Abstract

Acquiring sufficient food during the breeding period represents a challenge for many seabird species, since the food is patchily distributed at sea while the birds are spatially restrained to stay close to their terrestrial breeding territory. For a generalist opportunistic forager such as the great skua nearby seabird colonies offer access to marine food resources which they either predate or steal fish from, or they forage for fish out in the sea. I investigated the diet of a great skua colony in the Faroe Islands during breeding with two different methods to establish what was their diet, using pellets and stable isotopes of great skua tissue, and if the diet influenced their breeding performance. Their diet consisted to a greater extent of seabird species such as kittiwake, Atlantic puffin and fulmar than elsewhere, but I found no evidence for individual specialisation on seabirds vs fish as had been demonstrated in other great skua populations. There was no significant correlation between the occurrence of seabirds in the diet and egg size or clutch size but there was a relationship with laying date. I also experimentally increased terrestrial food near the nest by supplementary feeding great skua pairs during the pre egglaying period to see if a ready supply of nearby terrestrial foods influenced their breeding performance compared to a control group. I found that the supplementary feeding did not influence egg size or laying date, but it did reduce the within clutch egg size dimorphism. These results suggest that there is some breeding benefits of specialising on bird predation, but the relationship does not appear to result in larger eggs in Faroese great skuas.

Introduction

Food is one of the most important resources for free ranging animals providing the necessary nutrients and energy for self-maintenance and reproduction (White 2008). Where resources are limited, the potential for competition with conspecifics arises, and for animals that breed colonially such as seabirds, this can strengthen the competition (Furness & Birkhead 1984).Individual specialisation on different resources can be a mechanism to reduce conspecific competition. However, food items can vary in quality and availability and specialising on different food types may have fitness consequences(Pierotti & Annett 1990, O’Hanlon *et al.* 2017). Through the discovery of individual specialisation of generalist predators (Pierotti & Annett 1991), seabirds have emerged as highly suitable study models for studying dietary impact on reproduction. Although generalists such as gulls and skuas benefit from a wide choice of potential prey, they will also display signs of reduced reproductive output such as reduced clutch or egg size during periods of low food availability or quality (Pierotti & Annett 1987). Some studies have shown evidence of reproductive consequences for individual dietary specialisation (Votier *et al.* 2004), while other have not found support for any clear advantage to specialising or generalising (Woo *et al.* 2008).

For many birds, the breeding period can be a particular challenge to mobilise suitable nutrients and energy to produce eggs. For most seabirds, the breeding period represents the only period when they are bound to a terrestrial area, and this central place foraging is another challenge to efficient resource acquisition. Specialisation can be therefore be expected to occur for high quality food (e.g. high calorific content). However, in addition to food quality, availability should be considered. For example, the great skua population on Foula has seen a steady population growth over the past century which is generally assumed to be associated with high fish availability (Furness 1987). However Phillips *et al.* (1997) showed that the great skua population on Hirta, which lacks a similar abundance of fish showed similarly improved breeding parameters as Foula. Phillips *et al.*(1997) found that great skuas, which mainly feed on other seabirds had shorter foraging trips, allowing more time to defend their territory and offspring. The implication of this would be that there may be a trade-off between food quality and foraging trips for great skuas.

The great skua displays a rich variety of potential feeding strategies such as generalist predator, scavenger and kleptoparasite, and their diet is accordingly very varied between regions. The great skuas can also have very variable foraging trip lengths, ranging from offshore to coastal foraging. At the larger colonies in Shetland and Orkney, the diet of great skuas is mainly fish, and fishing discards. In smaller colonies, the greater proportion of individuals are seabird predators. This density dependent relationship with resource use was described in Votier *et al.* (2008a), and suggested that competition and intraspecific conflict might be an influencing factor in driving larger colonies to feed predominantly on fish. A study from 1961 on the diet of Faroese great skua, indicated the majority of the great skua diet to be seabirds (Bayes *et al.* 1964). Historical notes preceding the diet study in 1961 (Bayes *et al.* 1964) suggest that great skuas in the Faroes fed on offal from fisheries and whaling, and could also be seen fishing at herring shoals (Müller 1862). But Müller (1862) also notes that they are a threat to other seabirds, which they kill with a single hit to the head. Although great skuas have always bred in the Faroes, there is no reliable information about their population size prior to its near extinction due to culling at the end of the 19th Century (Salomonsen 1935a). The population of great skuas appears to have increased markedly in the Faroes between 2001 and 2011. For example, on Skúvoy the breeding population has increased from 65 pairs in 2001 (Olsen 2003) to 145 pairs in 2011 (Olsen 2011a). Hence, if there is a density dependent relationship we should expect a higher proportion of fish consumption compared to the historical information we have on the Faroese great skua diet.

The historical accounts, and the small scale local differences in diet, illustrates well that the diet of great skuas is largely opportunistic and therefore diet and feeding strategy can be influenced by nearby seabird colonies (Furness 1987). However there may also be inter-pair differences that suggest behavioural foraging specialisation. By collecting remains from 30 territories, Bayes *et al.* (1964) found that 10 territories had only kittiwake remains, 15 had only fish, and 5 which had both kittiwake and fish. They also reported, citing a local source, that around some pair's territory, there would be a high number of kittiwake eggs, suggesting that some pairs specialised on egg stealing for a limited period. It is thought that specialising to forage on seabirds can have reproductive benefits for great skuas (Votier *et al.* 2004) because seabirds are either of better nutrition or more readily available near the skuas' breeding territory. This is usually investigated by correlating diet and breeding parameters, although this will not distinguish between effects of nutrition and availability. Some studies have tested effects of food on breeding parameters experimentally by supplementary feeding. There are various approaches to test the effect of nutrition, where the supplementation is based on calorific measures or qualitative supplement (protein, micronutrients etc) (Nager 2006). One supplementary feeding study on great skuas showed that it had a detectable effect on egg size of younger breeders (5-10 years) but not of older breeders (11-29 years) (Ratcliffe 1993). Here I quantified diet of individual breeding pairs using pellet and stable isotope data and supplementary fed a subsample of these pairs. The supplementary feeding was of a low nutritional quality, in order to test if availability, more than nutritional quality, influenced breeding parameters. I want to test whether diet correlates with reproductive traits and whether supplementary feeding differentially affects pairs with different feeding specialisations.

Method

Fieldwork was carried out on the island of Skúvoy (61°46′N 6°49′W) in the Faroe Islands (Faroes hereafter). The island hosts approximately 150 great skua pairs in total. During the breeding season of 2012 territories on the entire island were visited, while during the season of 2013 the focus was mainly on the territories on the southernmost region of the island, named “Bergið”, which has the most densely populated area (with approximately 100 great skua nests). Territories or apparently occupied territories (AOT) were identified based on signs of activity such as trampled grass, guano or brood patch feathers (Furness 1987). After a territory has been located, the GPS location was recorded for re-visits.

The first aim was to assess the pairs’ diet in both years using collection of pellets. Each territory was visited frequently and at each visit all pellets were collected to be analysed back in the lab. Territories were visited at different frequencies between the two seasons of 2012 and 2013. In 2012 the frequency of visits was on average every 5-8 days, and in 2013 on average every 3-5 days, but each nest was visited at least every 10 days.

After egg laying, a remote controlled noose trap was fitted to trap the breeding adults. During handling biometrics were measured and blood samples were taken (n=21). In 2012 and 2013, 61 adult breeding great skuas were captured. The biometric measurements taken were body weight (g) and head+bill (mm). In order to calculate a condition index that takes into account scale, I use the Scaled Mass Index designed by Peig & Green (2009). Blood samples were collected for molecular sexing.

After hatching (2-20 days post-hatching), down feather samples were taken from the great skua chicks with scissors (n=51). Since the down feathers were grown pre-hatching, they should represent maternal nutrient transfer into egg production (Klaassen *et al.* 2004).

Supplementary feeding

To test if increasing the accessibility of food resources of some pairs would influence breeding parameters, I undertook a feeding experiment in 2013. After a territory had been established, I selected 42 territories to supplementary feed and 52 controls to visit every second day; experimental and control territories were allocated approximately equal number of control and feeding territories every day. The defining of clusters of 5-20 territories was done to minimize the possibility of “spill-over” effect from supplementary fed pairs to control pairs (fig 2.1). Supplemented pairs were fed 200g cat food every second day during the afternoon at their territory[control territories were visited with the same frequency and the same routine was done except the dropping of a food supplement. The cat food used was from a terrestrial food source – “beef”, in order to isotopically distinguish it from a more typical marine diet of the great skua. And thus being able to quantify their uptake of supplementary food by the experimental pairs. The amount supplemented corresponded to 7.5% of their daily energetic requirement (Kalmbach *et al.*

2001), and the protein content was 7 per 100 g, which is low compared to their typical diet. Feeding was continued until clutch completion, or at least two days after the first egg was found. The analysis included only pairs which had been visited or fed at least six times or more. The prediction was that if the great skuas are constrained by the availability of food, then a supplementation should have a detectable influence on breeding parameters such as clutch size, laying date and egg size.

During feeding events, notes were taken where I observed other great skuas stealing food supplement from the experimental birds and assessed how many thieves fed, and how much of the feeding portion was taken up by the territorial pair. Control territories were visited the same way and at the same frequency as treatment territories. The behavioural notes were then used to assess how well the experimental pairs were capable or motivated to defend their territory during feeding (1-5), and hence how much of the supplement they acquired. The score was given as follows: 1- Target pair ate none of the food, 2- pair ate some of the food, 3-pair ate half of the food, 4-pair ate the majority of the food, 5-pair ate all the food. At every feeding event, this score would be noted, and we used the mean of these scores to assess the success rate of each pair defending their food. The observations were transformed into a continuous variable from 0-1 of how successful the experimental pairs were at defending and acquiring the food, with 0 the target pair never ate any of the supplement and 1 when the target pairs always ate all the supplement..

To measure a proxy of the amount of supplementary food actually consumed by the target pair and was used in egg formation, we located the chicks after hatching. Down feathers are formed while the chick is in the egg, and therefore they will carry a stable isotope signature reflecting the diet of the female while she was forming the egg, and if an experimental bird had access to the food supplement (Klaassen *et al.* 2001). As the supplement was intended to have different $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios than the great skuas natural prey, the uptake of food supplement can also be inferred from the stable isotope signature of chick down. Out of the pairs which successfully reared one or two chicks that could be located between 2 and 20 days post hatching were measured and a sample of down feathers was collected (n=51, 29 experimental, 22 control).

Assessment of Diet

Pellets

In the study of generalist seabird diets, pellet collection has been an often-used tool . Numerous studies have used this method to evaluate between pair differences (Resano-

Mayor *et al.* 2014). In my study of great skua diet in the Faroes, pellets are also used. These pellets are found on territories, and give a good representation of diet during the breeding season, but since different prey result in different number of pellets this is a qualitative rather than quantitative assessment (Votier *et al.* 2001). Experimental feeding of great skuas has showed that the rate of production differs notably between types of prey (Votier *et al.* 2001).

The diet of the great skuas was firstly assessed using pellets and other prey remains that were found by searching in a circle approximately 5-10 meter radius from the centre of the territory. During the first territory visit, any pellets found would be collected and discarded. The pellets were then collected at each territory visit. Using features such as feather colour, smell and hard material, the prey species were identified to nearest possible taxa and categorised. All hard material such as fish otoliths, bones, plastics (see Chapter 5) and unidentified feathers were kept. It was for example not possible to distinguish guillemots, puffins and razorbills, unless the skulls or whole wings were found, and they were therefore pooled as auks. It is important to note that pellets are only pair-specific so there is a potential for underrepresenting specialists since the two parents may have different specialisations.

Stable Isotope Analysis

Carbon and nitrogen isotope analysis of feathers or blood provides another method of evaluating diet (Hobson *et al.* 1994). However, different tissues will reflect different time-scales of formation. Isotope samples of chick tissue will generally indicate the diet of great skuas during the breeding season post hatching, however samples of chick down feathers will indicate the stable isotope signature of the female that went into egg production. Another well established way to assess diet is through the use of stable isotope analysis (SIA). This is based on the fractionation rate of different isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) that can leave a dietary signature in the consumer during tissue formation. C reflects a terrestrial/marine gradient, and N can be used as a proxy of trophic level of the prey (Hobson & Welch 1992). For this study I analysed blood samples (red blood cells only), homogenized egg content, and chick down feathers. Knowing the turn-over rate of tissues all three reflect a similar time scale, namely 2-3 weeks before egg laying (Inger & Bearhop 2008). Also samples of reference material of typical prey items were collected: 10 kittiwakes, 10 puffins were sourced from local hunters, and 10 fish muscle samples were acquired from great skua regurgitation during handling. I was unable to identify all the fish taxa of the samples, but they were all pelagic, mostly mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*). Also 10 samples of catfood from supplementary feeding (see below) were included in the analysis. Prior to analysis the samples were prepared (Bond & Jones 2009); the chick down feathers were washed using washing up liquid, and rinsed thoroughly in deionised water. Since lipid fractionation can potentially influence the carbon ratio, the lipid-rich samples (puffin, kittiwake, fish and catfood) were lipid extracted using a ethanol:chloroform 2:1 solution in a Soxhlet apparatus. After several full cycles, the samples were dried in an oven at 40 °C >24 hours.

The analyses of the samples for stable isotopes ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ was undertaken at the NERC Life Sciences Mass Spectrometry Facility in East Kilbride, Glasgow. The analysis was performed by continuous flow isotope ratio mass spectrometry (CF-IRMS) on an average of 0.8 ± 0.1 mg of sub-sampled material loaded into tin cups and combusted in a Costech ECS 4010 elemental analyser coupled to a Thermo Finnigan Delta Plus XP mass spectrometer. Lab standards (gelatin, alanine and glycine) were run between every 10 samples to correct for instrument drift. Isotope ratios are expressed as parts per thousand (‰) according to the equation $\delta X = [(R_{sample}/R_{standard})-1]$ x1000, where X is ^{15}N or ^{13}C, R is the corresponding $^{15}N/^{14}N$ or $^{13}C/^{12}C$, and $R_{standard}$ is the ratio in the international references (air for nitrogen and belemnite for carbon). Lab standards were calibrated with these international reference standards and the measurement precision is calculated as the standard deviation of multiple measurements of internal lab standard material (tryptophan) which was ±0.209‰ for N and ±0.151 for C.

It is important to note the difference between these two methods of assessing the diet. Stable isotope analysis reflects individual diet, while pellets are pair specific. The pellets were collected throughout the season, but for the sake of testing comparability of the two methods only pellets sampled during the period that was also sampled by the stable isotope analysis were used, i.e. pellets collected prior to egg-laying.

For the purpose of analysing the diet over the breeding season, the periods were split up into: pre-laying, incubation, and post-hatching. The diet relationship with egg production included only pellets collected during the pre-laying period.

Reproductive Traits

Egg Volume

Breeding parameters which I was interested in measuring were egg size, clutch size and laying date. Egg volume was measured as their maximal length and width and from those a volume calculated using Hoyt’s equation and a taxa-specific constant (length x width^2 x *Kv*) (*Kv*=0.507)(Hoyt 1979).

Laying date

Bird’s eggs lose mass through waterloss during incubation (Rahn & Ar 1974), which will change the ratio between egg mass to egg volume as the latter will not change through incubation. This makes it possible to predict hatching date of great skuas with egg volume and egg mass (Furness & Furness 1981). Egg mass was measured using a digital pocket scale, to the nearest 0.01g. Egg density was calculated as egg mass (g)/egg volume (cm^3). By observing hatching date of 32 eggs which I had measured the mass of (some measured more than once - 100 measurements in total), I calculated a quadratic regression with “days until hatching” as response variable and egg density as explanatory variable and eggID as random factor, using R’s package lmer4 (Bates *et al.* 2014) and calculated an r^2 value for the model using the method described by Nakagawa & Schielzeth (2013). The quadratic regression was then fitted to all the other measurements to predict hatching date, and laying date was assumed as 29 days (the average incubation period of great skuas, Furness 1987) before hatching date.

Egg size dimorphism

Great skuas typically lay two egg clutches. For testing the prediction that some females may be food limited to produce a full clutch, I analysed the egg size difference in two egg clutches (Vallarino *et al.* 2011). If the egg size of the second laid egg is smaller due to depletion of energy reserves, we would predict the within-clutch dimorphism to be negatively correlated with % of bird pellets or successful supplementary feeding (quantified as low δ^{13}C of chick down feathers).

The statistical analysis for this study was done using the core package of R software, and linear mixed effects models with R package “lme4” (Bates *et al.* 2015a).

Results

A total of 2323 pellets were collected over the seasons 2012 and 2013. Despite the differences in frequency of territory visits between the years (described in the methodology), the ratio of bird and fish pellet occurrence at territories did not differ significantly between years: (Binomial GLM, $Z = 0.164$, $p = 0.87$). The majority of pellets contained kittiwakes (Table 2.1).

Considering the total amount of pellets collected from 322 territories over the two seasons, including only those territories where we had collected 5 pellets or more, 119 pairs had over 70% of pellets with bird remains (Fig. 2.2). No pairs consumed predominantly fish or other prey types. Only three pairs had 40-50% fish pellets around their territory. Among the pairs that consumed predominantly birds, 22 pairs ate mainly kittiwakes, 2 mainly fed on fulmar, and 1 on auks. A biomass conversion also supports the greatest proportion of consumption to be kittiwakes and secondly fulmars. Assuming fish biomass to be 300 grams suggests that skuas consume an approximate equal mass of fish as auks,

Interestingly, there were significant positive correlations between both δ^{15}N and δ^{13}C in parent blood or egg material with number of pellets collected prior to egg laying, but not with the proportion of different pellet types (Table 2.2). Due to the relative high occurrence of bird pellets throughout the colony I used the proportion of bird pellets out of the total number of pellets produced by that pair as a proxy for a pair's diet.

To predict the hatching date of all the eggs in my dataset, I calculated a quadratic regression of the density of the eggs of a known hatching date (Fig 2.3). I estimated laying dates of 916 eggs with the median laying date being 24 May (± stdev 11).

Pairs visited only five times or less before egg laying were excluded from the subsequent analyses. All remaining pairs were visited on average 22 ±11 times during the pre-laying period. There was no significant relationship between nitrogen isotope profile of chick down feathers and the feeding success on supplementary food (Pearson's -0.282 t=1.67 df=32 p=0.1051). There was a strong negative correlation between observations of supplementary feeding success and chick down feather δ^{13}C isotope profile (Pearson's -0.609 t=4.34 df=32 p<0.001) with catfood having lower δ^{13}C values than natural prey types (Fig 2.4). Thus carbon isotope ratio was used further as a proxy for supplementary feeding.

A linear mixed effect model was run with Laying date, Clutch size, average egg size, egg size dimorphism as response variables, experimental feeding, proportion of bird pellets, and their interaction as explanatory variables, and experimental zone (fig. 2.1) as random effect (table 2.3 & table 2.4). There was a weak negative but non-significant influence of occurrence of bird pellets on laying date (table 2.3), but no effect from observed supplementary feeding success. There was no relationship between the proportion of bird pellet or supplementary feeding and average egg size or clutch size.

Another linear mixed effect model was with the same breeding parameters, but with chick δ^{13}C isotope profile as the proxy for supplementary feeding, and the interaction between both explanatory variables, and experimental zone (fig. 2.1) as a random effect (table 2.4). This model showed a significant relationship between occurrence of bird pellets and laying date (table 2.4). There was no significant relationship between diet and average egg volume or clutch size, but there was a strong relationship between chick carbon isotope ratio and egg size dimorphism (table 2.4). This was a positive correlation suggesting the supplementary resulted in less egg size dimorphism.

Discussion

The diet of Faroese great skuas is in this study found to differ markedly from the diet at other areas such as Shetland. The diet of great skuas on Skúvoy is dominated by seabirds, primarily kittiwake, fulmar and auks (table 2.1). There is however also a significant amount of fish, however we found no evidence of specialisation on a fish diet only. This relative high occurrence of seabird predators corresponds well with historical notes and anecdotes. The feeding experiment gave some unpredicted but important insight. Although we were not able to accurately assess the degree of supplementary feeding observationally, using stable isotope (especially carbon) we were able to assess the effect of supplementary feeding on breeding parameters, albeit on a much reduced sample size. What these results showed were that supplementary feeding did not significantly influence the clutch size or average egg size, or the laying date. The experiment did however find strong support for the occurrence of bird pellets has an effect on laying date (table 2.4), suggesting that bird predatory pairs have an earlier laying date. Also we found that supplementary feeding negatively influenced the egg size dimorphism, so supplementary feeding reduced the egg size difference in two egg clutches.

The diet study resulted in a high number of pellets found and analysed, and there was not a significant difference between the two years, so the pellet data can be assumed to be well representative for the contemporary diet of great skuas on Skúvoy. However, using pellets to infer diet must be done with a cautionary interpretation. Since it is possible that some types of pellets will break up and be less detectable than others, so territory visit frequency can bias the ratio of pellets found. It should however be noted that we have clear indications from fresh regurgitates that fish are highly underrepresented in our pellet samples, and that fish whether it is through kleptoparasitism or scavenging from ships will likely remain a significant portion of their diet.

Due to its opportunistic lifestyles, it is not unexpected that the diet of great skuas can vary significantly between regions. A study by Votier *et al*. (2008a) found that small colonies feed on a greater proportion on seabirds, while larger colonies depend on fish and discards. This appears to be due to a density dependent competition relationship (Votier *et al.* 2008a). The Faroese colonies of great skuas have not grown beyond the approximately 200 pairs each. This has been mainly due to persecution, but fish discarding has not happened around Faroese waters to the same extent as North Sea fisheries, so possibly there is also a bottom up limit to the Faroese population. It should therefore not be unexpected that a relative high proportion of the Faroese great skua diet, has and continues to be mainly on other seabirds.

However in the case of the Faroese great skua colony, bird specialisation at the level of pairs does appear to be particularly prevalent. In this study 119 pairs out of 322 were found to have a high occurrence of bird pellets >70%. This would suggest that the probability of both individuals of 322 pairs are 119 bird specialists, which is 119/322=0.37. The square root of 0.37= 0.61 suggests as many as 61% of individuals are seabird specialists. Such a high occurrence of seabird specialists is unusual and unique compared to other colonies in Shetland and Orkney. But it has been suggested that great skuas to some extent feed on whatever is available locally, and as such this could signify that despite significant declines in seabird populations (Olsen 2011b) there are still enough for it to be viable to breed and feed chicks.

Some studies have shown that dietary specialisation can improve breeding performance (Votier *et al.* 2004). In that context I wanted to explore if diet could play a role in breeding effort. No clear correlation was found between either pellets or stable isotope to suggest a relationship with breeding parameters such as egg size, clutch size and egg size dimorphism. However in a subset of samples (table 2.4) there was significant relationship between bird pellets and laying date, showing that bird specialists have an earlier laying date. This relationship was also found by Votier *et al.* (2004), however Votier *et al.* also found a relationship with egg volumes, and other studies have shown similar findings in other birds (Sorensen *et al.* 2009).

Dietary specialisation does not only influence the pairs, and can in some cases become a conservation concern for the prey species. For example on Hirta, St. Kilda it has been noted that some great skua pairs have begun nocturnal foraging of Leach's storm petrels *Oceanodroma leucorhoa* (Votier *et al.* 2006), and that these specialists can have a disproportionally high influence on prey populations. This has also been raised as a point of concern in Skúvoy where locals have noted an increase in Manx shearwater carcasses found near the southern fringe of the great skua colony "Bergið" (Harry Jensen, pers.comm.).

There were some detectable biases in the observed laying date between the two years. The laying date was significantly different between the years (GLM t=2.54 p=0.012), but this difference is likely due to differences in frequency of territory visits and range, which may have influenced the likelihood of detecting late (second clutch) breeding attempts. The laying date differed significantly between the two years 2012 and 2013 (p=0.012), with a mean laying date in 2012 was 20 May (Stdev 12), and in 2013 it was 25 May (Stdev 10). Due to the experimental work done in 2013 which focused on a very limited area (fig. 2.1), compared to the entire island of Skúvoy, in 2013 the likelihood of finding late breeding pairs and potentially re-laying pairs is higher, and may have skewed the mean laying date.

Dietary specialisation is found to have reproductive consequences for seabirds as some studies have suggested (Votier *et al.* 2004). In contrast to other great skua colonies, the diet of Faroese colony studied was a relatively high ratio of bird prey, and less of fish. Here I explored whether the different diet between different nests of Faroese great skuas was correlated with breeding parameters, and I found a relationship between bird specialisation and laying date.

In 2013 an experiment was designed and carried out to test if food supplementation would influence the breeding parameters such as average egg size, egg size dimorphism and laying date. The supplementary feeding experiment did not show a significant difference of laying date, clutch size, and mean egg size between supplementary fed pairs and control pairs. However stable isotope analysis of chick down feathers showed a significant correlation between δ^{13}C of chick downfeathers and the within-clutch egg size difference of those clutches. This contradicts Catry & Furness (1997) which found that within-clutch difference of great skua eggs was not a reliable measure of individual quality. There are two likely, and possibly interacting, drivers behind this finding: parental breeding strategy or energetic/nutrient limited. Great skuas show a degree of egg size dimorphism (Catry & Furness 1997), and there is a wealth of research trying to disentangle the factors influencing this dimorphism in various bird species (Badyaev 2002). The parents may enforce a certain evolutionary strategies in egg size dimorphism (Székely *et al.* 2000).

Alternatively the dimorphism can be due to the second laid egg being smaller as female nutrient or energy reserves get depleted. However, an experimental removal of great skua first laid eggs by Kalmbach *et al.* (2004), found that the second laid clutch was not significantly smaller, which would suggest that great skuas have normally no trouble mobilising enough nutrients or compounds to produce a second or even third clutch. Although the relationship between supplementary feeding and egg size dimorphism is intriguing, it is not possible in this study to disentangle this relationship much further, however the feeding experiment clearly suggests that the suppelementary food, albeit relatively low in protein, did reduce the difference in within clutch egg sizes. Whether it was the food itself or our feeding activity that resulted in this remains unknown, but would certainly deserve further study.

This study has shown that the diet of great skuas in the Faroes is to a great proportion other seabirds – mainly kittiwakes. I found some support for previous studies that bird specialisation results in earlier laying dates, however I did not detect similar relationships with other breeding parameters such as egg size or clutch size. In order to test the impact of diet on these breeding parameters, I carried out a supplementary feeding experiment, in which we found no support for that the feeding influenced breeding parameters such as laying date or egg size, but there was a strong negative relationship between supplementary feeding and egg size dimorphism. This is a first indication that egg size dimorphism can be influenced by food, but whether this is due to nutritional or energetic properties of the food, or the experiment influenced female egg investment remains unknown.

Table 2.1: Types of pellets, categorised as birds, egg, fish, and other. In order to correspond pellets to meals a correction factor (Votier *et al.* 2001) was applied. Body mass of birds was calculated from mean species specific body masses (Dunning 1992) and average fish size assumed to be 300 g.

Recorded food items in great skua diet 2012-2013 on Skúvoy

			Pellets	%	Correction	Meals	Biomass (kg)
Birds				68			
	Kittiwake		702		1.9	369	150.4
		Chick	16				
	Gull		7		1.7	4	
	Great skua		3		2.6	1	
	Arctic skua		2		1.9	1	
	Tern		3		4.8	1	
	Shag		1		1.8	1	
	Auk		326		1.8	181	69.0
	Puffin		59		1.8	33	12.5
	Guillemot						
		Chick	1				
	Razorbill		1		1.8	1	
	Fulmar		354		2.6	136	74.1
		Chick	1				
	Manx shearwater		13				
	Petrel		3				
	Snipe		3				
	Starling		3				
	Raven		1				
	Wheatear		2				
	Gannet		1		4	0.3	
	Greylag goose		6		4	1.5	
	Unknown		65				
Eggs				16			
	Kittiwake		319				
	Fulmar		6				
	Guillemot		2				
	Great skua		3				
	Unknown		38				
	Wren		1				
Mammals				2			
	Hare		28				
	Sheep		10				
		Lamb	2				
Fish			185	8	0.8	231	69.4
Other				1			
	Squid		1				
	Insect		1				
	Crab		1				
	Vegetation/moss		5				
	Pebbles		12				
	Unknown bones		11				
Mixed pellets				4			
	Fish:Bird		56				
	Mixed bird pellet		17				
	Bird:Vegetation		20				
	Other mixed		7				
Unknown			25	1			
Total			2323				

Table 2.2: Spearman ranked correlations between number of pellets collected (pre-egglaying) per territory and proportion of pellets with bird, fish or other remains against stable isotope signature from egg content or adult blood samples.

	C	p-value	N	p-value
Number of pellets	0.444	<0.001	0.299	0.007
% Bird	0.397	0.202	0.261	0.413
% Fish	-0.325	0.302	-0.198	0.537
Other	0.1101	0.733	0.079	0.808

Table 2.3 Linear mixed effects model with territory cluster as random effect. Various dietary parameters against breeding parameters.

	Laying date (n=61)			Average egg volume (n=56)			Clutch size (n=56)			Egg size dimorphism (n=46)		
	chi-sq	df	p	chi-sq	df	p	chi-sq	df	p	chi-sq	df	p
Supplementary feeding (continous variable of experimental treatment and success of retrieving the supplementary food	0.877	1	0.349	0.877	1	0.349	0.001	1	0.975	2.7067	1	0.099
Proportion of bird pellets in diet	2.879	1	0.089	0.805	1	0.369	0.024	1	0.876	0.789	1	0.374
Bird pellet * supplementary feeding	0.086	1	0.769	0.063	1	0.801	0.124	1	0.725	0.051	1	0.821

Table 2.4 Linear mixed effects model with territory cluster as random effect. Various dietary parameters against breeding parameters.

	Laying date (n=34)			Average egg volume (n=34)			Clutch size (n=34)			Egg size dimorphism (n=34)		
	chi-sq	df	p	chi-sq	df	p	chi-sq	df	p	chi-sq	df	p
Chick Carbon isotope ratio	1.295	1	0.255	1.158	1	0.282	0.316	1	0.574	7.5085	1	0.006
Bird pellets	4.972	1	0.026	0.560	1	0.454	0.0012	1	0.972	0.314	1	0.575
Bird pellets * Chick C ratio	1.321	1	0.250	0.671	1	0.413	0.4267	1	0.514	1.9521	1	0.162

Fig 2.1 Showing experimental setup at the great skua colony on Skúvoy. The green points are experimentally fed pairs, and red are control pairs, A-D annotate the experimental zones (Google Earth, Kortal.fo).

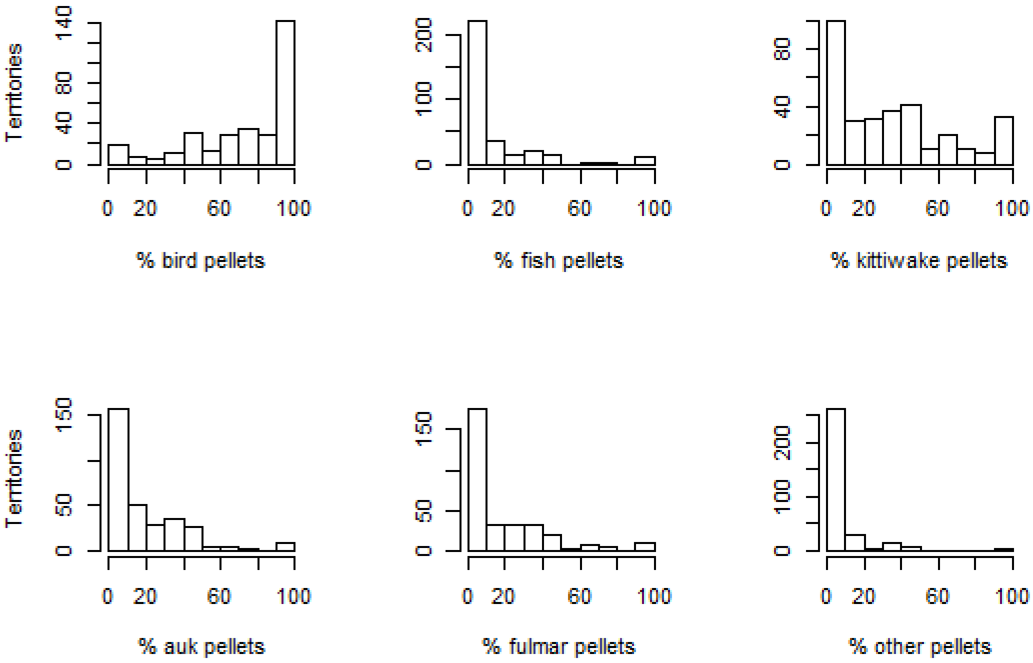

Fig. 2.2: Number of territories' percentage occurrence of different types of pellets. These histograms include all territories where pellets were found (including those where fewer than 5 pellets were found).

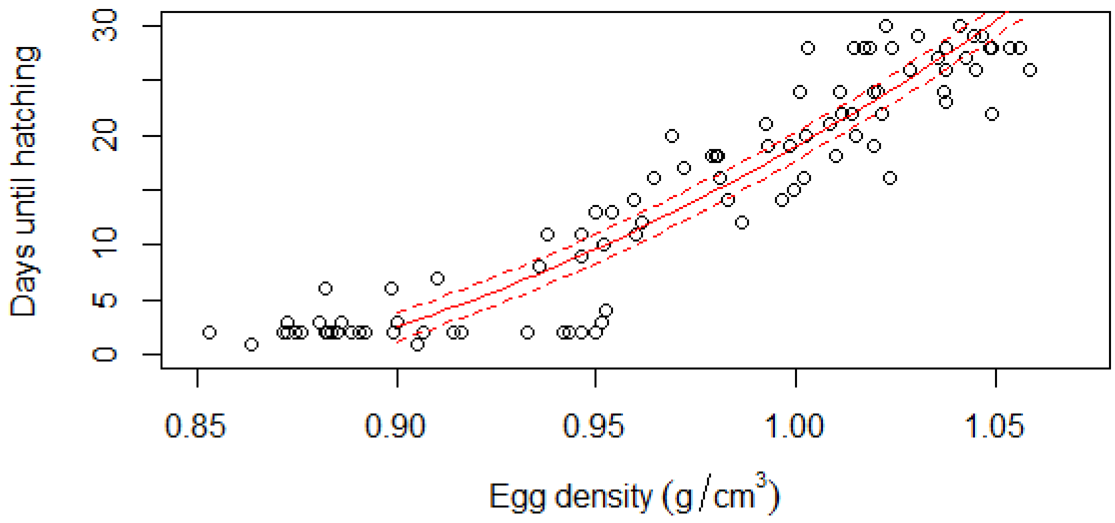

Fig. 2.3: Quadratic regression through egg density measurements of eggs of known hatching dates. Marginal r^2 is 0.8865 and conditional r^2 is 0.9850. The solid line shows the quadratic regression line and the dotted lines represent the 95% confidence interval.

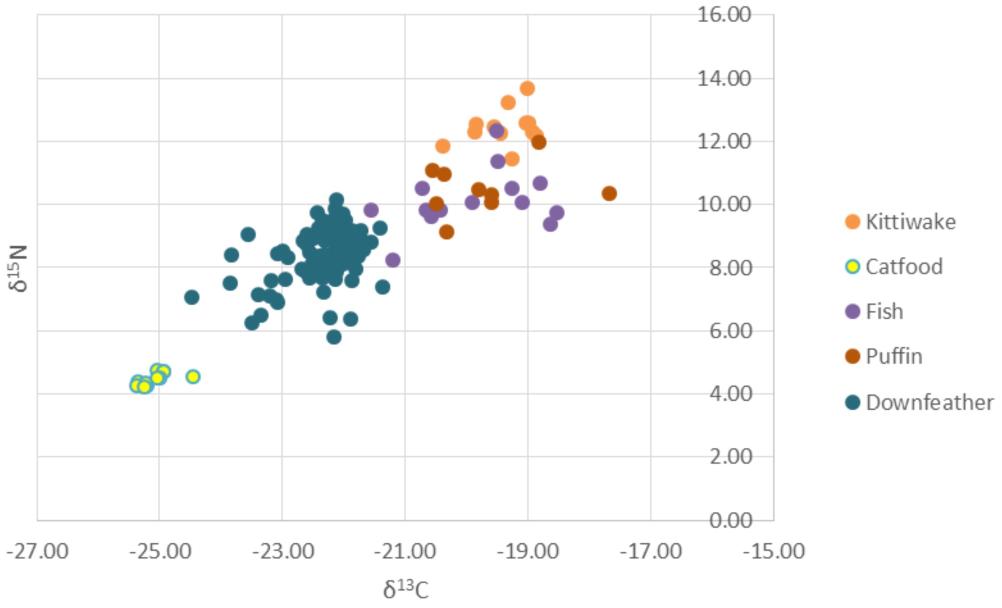

Fig 2.4 Stable isotope ratio of chick downfeathers and dietary reference materials

3. Temporal and spatial variation in seabird egg sizes

Introduction

In all populations of vertebrate organisms, there is a wide range of body sizes. However some spatial and temporal trends in vertebrate body sizes have also been observed, and are frequently interpreted by intrinsic or extrinsic factors (Yom-Tov & Geffen 2011). One spatial trend that animals in colder or higher latitude areas tend to have a greater body size has been formulated as Bergmann's rule (Blackburn *et al.* 1999). Temporal variation is also evident, and have been interpreted as environmental variability or climate, which may influence food availability (Yom-Tov & Geffen 2011).

For many animals the breeding period is a challenging time in terms of resources and time. It is well established that breeding is a demanding period for birds, and that in particular egg production can be a costly process (Monaghan & Nager 1997). To meet the energetic need for egg production is further complicated due to birds laying during a period of food constraints. If food constraints early in the season are too great then this can result in a delay in laying date or in smaller eggs (reviewed in Nager 2006). The energetic limitation of individuals resulting in smaller eggs may be particularly apparent in colonial birds where there is a strong selection towards having a synchronised start of laying (Nager 2006, Votier *et al.* 2009, Verboven *et al.* 2010), but it is also recognised that intrinsic factors such as female mass, age and experience may influence egg size (Christians 2002). Egg size can also influence offspring survival (Krist 2011), and may therefore have direct ecological implications.

Two recent studies have found a long term decline in egg size in glaucous gull *Larus hyperboreus* and Atlantic puffin *Fratercula arctica*, and have hypothesised the cause of this change to be related to food availability (Blight 2011, Barrett *et al.* 2012). A study of great skuas on Foula, Shetland have noted that the eggs measured in 2008 were significantly smaller than the eggs measured at the same colony in 1980 (Leat *et al.* 2011). This reduction in egg sizes coincides with a change in the Shetland great skuas' diet from sandeel *Ammodytes* spp. to less energy-dense fish discards (mainly haddock *Melangrammus aeglefinus* and whiting *Merlangius merlangus*) (Leat *et al.* 2011). This change in egg sizes also coincides with a decline in the great skua population on Foula (reviewed in Furness 2015). Compared to the population in Shetland, the great skuas in the Faroes feed and are thought to have done so also in the past to a larger extent on other seabirds such as black-legged kittiwake *Rissa tridactyla*, Atlantic puffin, guillemot *Uria aalge*, and Northern fulmars *Fulmarus glacialis*.

Few temporal studies of wild bird populations have been ongoing longer than 4-5 decades, so in particular field measurements on egg size have only been done in recent decades. However, eggs had been collected for much longer (about 150 years). So in order to study long-term trends in egg sizes, museum egg collections have become an important resource (Suarez & Tsutsui 2004). Egg collection began as a respectable past time for naturalists resulted in extensive private collections built up from 19th Century throughout Europe and North America in particular (Joseph 2011). Since ethical and ecological concerns grew around egg collecting, most countries banned egg collecting and most private egg collections have since been transferred to public natural history museums (Scharlemann 2001, Cole 2016). Museum birds eggs have been used in various ecological studies (Green & Scharlemann 2003, Pyke & Ehrlich 2010). Most famously museum eggshells were used to establish the pollutant effect on eggshell thinning (Ratcliffe 1967). Although seabird eggs are also found in museum collections, few studies have been done with historical collections of seabird eggs. There can be qualitative differences and biases between egg measurements taken from museum eggs and field measurements so comparison and interpretation of these needs critical evaluation. However museum collections allow us to study longer temporal scales than would otherwise be possible, and will therefore provide important insights in long-term variation in egg size over large geographical scales.

Museum eggs hold a number of uncertainties and potential biases in how they were collected and traded, and incorrect metadata which may or may not be intentional (Storer 1930). Depending on the individual collector eggs may have been collected for aestetic or curisity appeal or general naturalistic interest, but it is unknown if the collectors intent was to collect typical or atypical eggs. An indication that museum collections may contain some atypical eggs is exemplified in a higher ratio of “runt” or dwarf eggs in egg collections than you would otherwise expect to find in the field. Field data, while generally being undertaken by trained specialists, holds less bias, although there can be biases in how and when nests are located. For colonial species, perhaps by measuring eggs along the edge of a colony to minimise disturbance, this introduces possibly a bias towards younger or poorer quality birds that nest at the periphery of colonies (Wittenberger & Hunt 1985) and because they are young and lay smaller eggs (Hipfner *et al.* 1997). If colony visits are done only once, the date of when the measurements were taken can also bias the size of eggs, since it has been shown that eggs laid later in the breeding season of colonial birds are smaller (Birkhead & Nettleship 1982).

Bergmann's rule states that endothermic organisms tend to be larger at higher latitudes, and some studies have found this to be the case for eggs too. Eggs of Brunnich's *Uria lomvia* and common guillemot were bigger further north (Hipfner *et al.* 2005) and a geographic gradient was also found of tropical/subtropical songbirds (Martin 2008), and among new world flycatchers (Heming & Marini 2015). Although Bermann's rule explains the spatial variation to be due to thermal preservation of endothermic organisms or fasting endurance, the underlying mechanisms behind this spatial variation remains unknown (Ashton 2002). The most prevalent hypothesis explaining spatial trends in egg size is similarly related to temperature and parent attendance, but Heming & Marini (2015) emphasise that environmental temperature also influences parent investment in egg size.

Few studies have looked into temporal variation between different populations, and there is a growing realisation that inter-colony differences can be very informative in assessing environmental influence on population demography and growth (Dhondt 2001, Bairlein 2003, Frederiksen *et al.* 2005, 2010). In this study I aim to describe spatial and temporal trends in egg sizes of three seabird species. Firstly I compare the pattern of temporal variation in egg sizes between three different seabird species (great skua, fulmar *Fulmarus glacialis* and guillemot *Uria aalge*) in one region (the Faroes). Secondly I compare spatial trends of great skua eggs in six different regions, and I also provide a detailed analysis of temporal variation of great skua egg sizes at three important regions (Iceland, Faroe Islands and Shetland) with combined use of museum eggshells and field measurements, and analyse geographic variation of contemporary field measurements across the a wide breeding range.

Method

Eggs of great skuas, fulmars and common guillemot were sourced from any known published and unpublished records of field measurements of egg size (Table 3.1) as well as museum collections (Table 3.2). The field measurements were generally collected as a standard feature during fieldwork for individual projects in Shetland and the Faroes, or as part of ongoing population monitoring of populations such as Handa (RSPB) and Bear Island (NPI). Egg size measurements (length and width) were taken by Vernier calipers to a precision of 0.1 mm. Egg volume index (EVI) calculated as (length x width^2) was calculated for the between species comparison only, as the three species have very different shape constants. The metric volume of great skua eggs was calculated using Hoyt's equation and a taxa-specific constant *Kv* (length x width^2 x *Kv*) (*Kv*=0.507) (Hoyt 1979). Unlike guillemot and fulmar that only have single egg clutches, great skuas typically have two egg clutches. However a large number of great skua museum specimens were single eggs, although typical clutch size is two eggs with the first-laid egg being larger than the second-laid one (Furness 1987). I therefore averaged the egg volumes of the two eggs when measurements from both eggs of a clutch were available. Museum eggs were included only if collection location and year was known. Locations were grouped into the following six regions: Bear Island, Iceland, Faroe Islands, Shetland, Orkney, and West Scotland. Where I had measurements from different colonies within a region from the same year, I tested within-region differences.

The egg size data for the three species in the Faroes had periodic gaps in the records, and therefore to analyse temporal variation in egg size two analytical approaches were taken. Firstly, a linear mixed effect model was fitted with egg size as the response variable and year as random effect with splines df=2 in a general linear mixed model. The second approach was to divide the data into 3 periods: 1840-1909, 1910-1979 and 1980-2014. The data was split into these first two periods in equal length (69 years), and the third and most recent period is 34 years to attempt and follow the data structure with large temporal gaps, so that there was a sufficient number of data in each period.

Where possible measurements from museum and field measurements taken in the same period and region were compared. To make this possible the great skua data were clustered into one group of eggs from Shetland (1971-1978) and another from Faroes (1940-1960). Within each of these two groups I compared museum and field measurements. With the fulmar and guillemot data there were no years or periods where there existed field and museum measurements from overlapping periods. So interpretation of the guillemot and fulmar data must consider the possibility of this confounding factor.

Geographic differences

To investigate spatial variation in egg size I compared egg size between the six regions across the range of great skuas in the northeastern Atlantic for the period 1980-2014. At a smaller spatial scale (<70 km) I also examined variation in egg size of great skuas between 3 different colonies in the Faroes within a single year (2014), and large spatial scale comparison within the same year (2014). There was also sufficient data from museum eggs in the period 1945-1959 from three regions to make a geographic comparison during that period between Iceland, Faroes and Shetland.

Statistical analyses

Statistical analyses were carried out in programme R 3.1.2 (R Core Development Team 2014) using regression and ANOVA analyses. Generalized linear model with random effect and splines was done using packs “lme4”(Bates *et al.* 2014) and ”splines”(R Core Development Team 2014).

Statistical tests where $p < 0.05$ were considered statistically significant. Means are presented with standard deviations.

Results

A total of 7611 (6916 field, 695 museum) clutch measurements were acquired. These measurements include great skua egg measurements from Bear Island, Iceland, Faroes, Shetland, Orkney and Western Scotland. In addition, egg measurements from Faroese guillemot (1650 – 1531:119 field:museum) and fulmar (711 – 635:76 field: museum) eggs were available. The field measurements of great skua eggs were taken from 1961 until 2014, and the guillemot measurements from 1977 until 2013, and fulmar field measurements from 1986 until 2013 (Table 3.1), and museum egg measurements were mostly from 1840 to 1950. Measurements of extreme outliers such as runt eggs, (fulmar n=6, guillemot n=4, great skua n=3) and one extremely large outlier (fulmar n=1) have been omitted from the analysis.

Firstly I tested if great skua egg size differed between three separate colonies in the Faroes within the same year (2014). The colonies, Saksun, Svínoy, and Skúvoy (fig 1.2) were of a similar size (100-200 pairs) and separated by a distance of less than 70 km. The average egg size showed no significant difference ($F_{2,242} = 2.24$, $p = 0.108$). Measurements from eggs measured in the same time period and from the same region did not differ between field and museum measurements (1) for Faroes between 1960-1969: ($F_{1,280} = 0.27$, $p = 0.605$), and (2) for Shetland between 1971-1978: ($F_{1,558} = 0.25$, $p = 0.617$). I therefore combined museum and field measurements for all subsequent analyses unless stated otherwise.

Spatial trends

Great skua eggs measured in 2014 show a significant spatial variation in egg ($F_{2,391}$ = 13.21, $p < 0.001$; Fig. 3.1). Eggs from Bear Island and Faroes were both significantly larger than eggs from West Scotland (both $p < 0.001$).

Comparing spatial variation of great skua eggs within the same period (1980-2014) show significant difference between six regions ($F_{5,3957}$ = 61.68, $p < 0.001$; Fig. 3.2). The general spatial trend showed eggs from the northernmost region (Bear Island) to be significantly larger than the eggs from the southernmost region (West Scotland) and they were also larger than eggs from Shetland (both $p < 0.001$). The eggs in West Scotland were significantly smaller than eggs from all other regions (all $p < 0.001$). The eggs on Bear Island were not significantly larger than eggs from the Faroes ($p = 0.99$) or Orkney ($p = 0.27$). The eggs in the Faroes are significantly larger than the eggs from Shetland ($p < 0.001$), West Scotland ($p < 0.001$), but are not significantly larger than the eggs in Orkney ($p = 0.56$). Icelandic eggs are significantly smaller than Faroese ($p = 0.020$) but not different to Shetland eggs ($p = 0.444$).

The spatial difference in great skua egg sizes in museum egg measurements from 1945-1959 between three regions was not significant ($F_{2,170}$ = 0.726, $p=0.48$; fig. 3.3). But an analysis of variance showed regional differences in great skua egg sizes during period 1 (1840-1909) ($F_{2,227}$ = 5.27, $p = 0.006$), a Tukey HSD test showed that Icelandic eggs were significantly larger than the eggs in Shetland ($p = 0.004$), but not signifcantly different to Faroese eggs ($p = 0.154$). During period 2 which includes both museum and field data (1910-1979) ($F_{2,1047}$ = 20.65, $p < 0.001$) the post hoc tests suggests that both Icelandic and Shetland eggs were significantly smaller than Faroese ($p < 0.001$) but not significantly different to each other ($p = 0.235$) eggs.

Temporal trends

I also tested for temporal trend in egg sizes and found that the model with a spline with two degrees of freedom (quadratic) had a better fit and lower AIC compared to the model with a spline with one degree of freedom (linear) (χ^2 = 8.12, df=1, p = 0.004) for Faroese eggs, but not for Shetland (χ^2 = 1.17, df=1, p = 0.280) or Iceland (χ^2 = 0.39, df=1, p = 0.535). Figures 3.4a-c shows temporal variation in great skua egg size in three regions (Faroes, Shetland and Iceland) with 95% confidence interval, where there was sufficient temporal data.

Separating the egg measurements into periods an analysis of variance with egg volume as response variable, period and region as explanatory factors, showed a statistically significant interaction between period and region ($F_{4,3170}$ = 5.17, $p < 0.001$). There was a significant temporal trend in egg size within the Faroes, the post hoc test showed that eggs from period 1 were significantly smaller than eggs from period 2 ($p < 0.001$) and eggs from period 2 were significantly larger than eggs from period 3 ($p < 0.001$). The great skua eggs in Shetland were also significantly smaller in period 1 than they were in period 2 ($p < 0.001$), and eggs in period 2 were larger than period 3 ($p < 0.001$). There were no differences in egg volume between the three periods in Iceland (all $p > 0.05$).

Comparison of temportal trends across the three Faroese seabirds

An analysis of variance of the Faroese seabirds with EVI as response variable and period and species as explantory variables showed that the interaction between period and species was not statistically significant ($F_{2,3054}$ = 2.21, p = 0.110; Fig. 3.2) implying that the predicted temporal trends did not differ between species. The fulmar egg sizes did not vary significantly between periods ($F_{2,705}$ = 0.47, p = 0.627) but guillemot eggs, did vary in size between periods ($F_{2,1647}$ = 3.14, p = 0.044). The post hoc test showed that guillemot eggs are significantly larger in period 3 than period 2 (p = 0.033), which is opposite the temporal change found in great skua eggs which are significantly smaller in period 3 than period 2 ($p < 0.001$) and are significantly larger in period 2 than period 1 (p = 0.005).

To test for a relationship between population size and egg sizes, egg size measurements of great skuas on Foula were used from 1969-2011. During this period, the population has been declining. A linear regression was calculated of the size of the Foula population on year (r^2=0.93) based on data from Furness (2015). There was a strong correlation between the population size and year ($p < 0.001$), so only population size was included in the generalized linear model with EVI as response. There was a strong relationship of population size on EVI (GLM t = -6.75, $p < 0.001$).

Discussion

With the limitations of a compilation of historical data in mind, the aim in this study was to explore the spatial and temporal variation in egg sizes of great skuas across the northeastern Atlantic.

There was significant temporal variation in great skua eggs in Faroes and Shetland over the last 150 years, but not for Iceland. The great skua eggs in Shetland and Faroes are both significantly smaller in period 3 than period 2. In contrast, in another Faroes seabird, the guillemot, eggs were actually significantly larger in period 3 than in period 2. This goes against the prediction that a bottom up control of demographic traits by changes in the food base which would result in smaller eggs in all species exploiting the marine environment. However the great skua and guillemot occupy different trophic levels, so it could be expected that different seabirds are affected differently by environmental changes, but it is unlikely to be simply by changes in the food base, but some other environmental factors are also likely to have changed that affect one species more than another. I thus will attempt to discuss the results in relation to possible environmental and intrinsic factors which may have played a role in the observed spatial and temporal difference in seabird egg sizes.

This study also found support for spatial variation in egg sizes of great skuas. Other studies have shown similar latitudinal gradients in egg sizes (Martin 2008, Bownds *et al.* 2010). The overall spatial trend in egg sizes follows the predictions of Bergmann's rule, that larger body masses are found at higher latitudes. Whether the spatial difference in egg sizes is potentially a secondary consequence of difference in female size can not be explored under the scope of this study. However, there are interesting discrepancies in this latitudinal trend. Great skua eggs from Iceland have on average been smaller than eggs of Faroese great skuas since 1900 despite Iceland being more northerly than the Faroes. The reason for this discrepancy is not known.

There also might be alternative explanations why the regions differ in egg size. One possibility could be differences in diet. Generally it is thought that the southern populations of great skuas in Shetland, Orkney and West Scotland have fed mainly on fish such as sandeel and fishery discards (Votier *et al.* 2004), while the northern populations on Bear Island and Faroes are more seabird predatory, feeding mainly on kittiwakes, puffins, guillemots and fulmars (Chapter 2, Knutsen 2010). There is a lack of detailed contemporary studies on the diet of great skuas in Iceland, however, historically there are indications that the population in Iceland fed to a lesser extent on other seabirds, than compared to their conspecifics in the Faroes (Furness 1987). A significantly lower pollutant load and nitrogen isotope ratio in Shetland and Iceland great skuas blood samples compared to Bear Island also suggests that they feed at lower trophic level (Bourgeon *et al.* 2012). This could lead to a general indication that higher trophic diets result in larger eggs for the great skuas.

The population trend on Foula (1969-2011) showed a significant relationship with egg size, but the population trend in the Faroes over the same period has been positive, yet the eggs have gotten significantly smaller. This study is not able to further disentangle the potential intrinsic vs extrinsic variables that explain this temporal trend of egg sizes. The sustained growth of the great skua population around Scotland over the past century is believed to be mainly due to high abundance of sandeel, and fishing discards (Phillips *et al.* 1997), but simultaneously other populations such as on Hirta, St. Kilda have also shown population growth in the absence of sandeel. So the answer may not lie in the quality but rather the availability of food, that drives great skua breeding performance and population trends. With the decline of coastal fisheries and discarding around Shetland since 2000, a reduction in breeding performance, and decline in the population of great skuas is expected. At the same time the Faroese population has increased markedly between 2001 and 2010, but this growth appears to have plateaued off (Olsen 2011a; Own study). Although food availability may be an important driver in these two populations, the history and rate of persecution differs greatly between these populations, so population trends and food availability should be interpreted with this in mind.

This study represents an attempt to incorporate the use of museum egg and field measurements of eggs over a temporal scale that would otherwise not be viable to test. The study found strong support for a spatial variation which also fit well with the predictions that birds in higher latititudes or colder environments lay larger eggs. The temporal trend of great skua eggs from Faroes and Shetland showed that eggs are significantly smaller now than in the period 1910-1979. There are numerous potential factors influencing this trend, however the lack of similar trends in other seabird species in the Faroes, would suggest that it is not a simple ecological variable that causes this, or that different species may be influenced differently by these parameters.

Table 3.1. Sample sizes (clutches) of great skua, guillemot and fulmar egg measurements in the field. *excluding eggs from 1992,1993 (Ratcliffe, 1993) and 2013 due to supplementary feeding experiment.

	Year(s)	Bear Island	Iceland	Faroe Islands	Shetland	Orkney	West Scotland
Great skua							
G. R. Potts	1961			278			
Bob Furness	1975, 1976				549		
Keith Hamer	1988-1990				500		
Norman Ratcliffe*	1991-1994				368	214	
Hallvard Strøm	1995-2014	735					
Paolo Catry	1994-1995				356		
Stephen Votier	1998-1999				106		
Henrik Dahlgren	2004		14				
Claire Smith (RSPB)	2004-2007, 2009-2011, 2013-2014						505
Will Miles	2007-2009						444
Eliza Leat	2009,2010		105		84		
Helen Wade	2011, 2012					48	
Sjúrður Hammer	2011, 2012, 2014			340			
Halldór Walter Stefánsson	2014		7				
Rob Dunn	2014						99
Total		**735**	**126**	**618**	**1963**	**262**	**1048**
Guillemot							
Bergur Olsen	1977, 1978, 1979, 1986, 1987, 1991, 1996, 2003			1530			
Sjúrður Hammer	2013			1			
Total				**1531**			
Fulmar							
Bergur Olsen	1986, 1991			239			
Jens-Kjeld Jensen	1990, 1991			274			
Sjúrður Hammer	2013			122			
Total				**635**			

Table 3.2. Sample sizes (clutches) of great skua, guillemot and fulmar egg measurements in museum collections.

	Great skua					**Guillemot**	**Fulmar**
	Faroe Islands	Iceland	Orkney	Shetland	West Scotland	Faroe Islands	Faroe Islands
Booth Museum of Natural History, Brighton	1	1		1			1
Zoology Museum Copenhagen	4	2				52	9
Denver Museum of Nature and Science		2		1			
Finnish Museum of Natural History		12		1	1	2	3
Glasgow Museum Resource Center				21			
Hancock Museum, Newcastle			1	12			
Hunterian Collection, Glasgow				3			
Icelandic Institute of Natural History		58					
Leibniz Institute, Berlin	1						
Manchester museum	6						
Martin Luther Universitat Halle Wittenberg		3					
Museums Sheffield			1	6			
National Museum Scotland	8	4	18	50		3	4
Natural History Museum of Geneva	3						
Naturhistorisk museum Århus	14	2				35	23
Oxford University Museum	1						
Natural History Museum, Faroe Islands	1					1	4
The Field Museum of Natural History		5		1			
Natural History Museum, Tring	42	26	5	76	2	15	31
University Museum of Bergen	2	1					1
Western Foundation of Vertebrate Zoology	2	36	1	39			
Zoologisches Forschungsmuseum Alexander Koenig		21		2		11	
Total	85	173	26	213	3	119	76

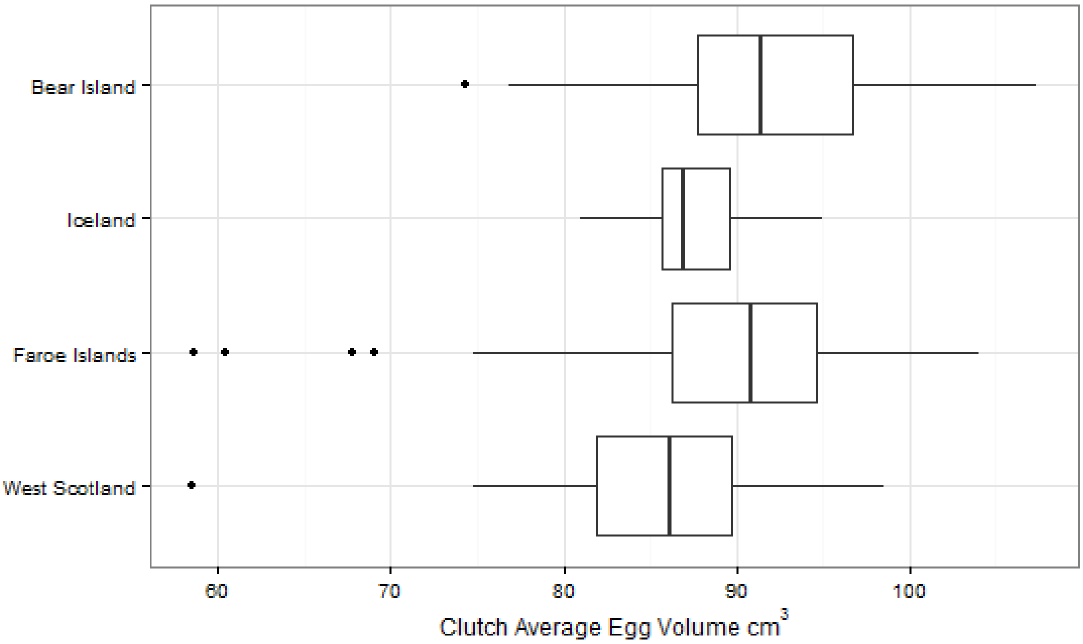

Figure 3.1: Spatial variation in the egg volume of great skua eggs in a single season (2014) between four regions with regions in order of lattitude (most northerly region at the top and the most southerly at the bottom of the vertical axis). Only field measurements included.

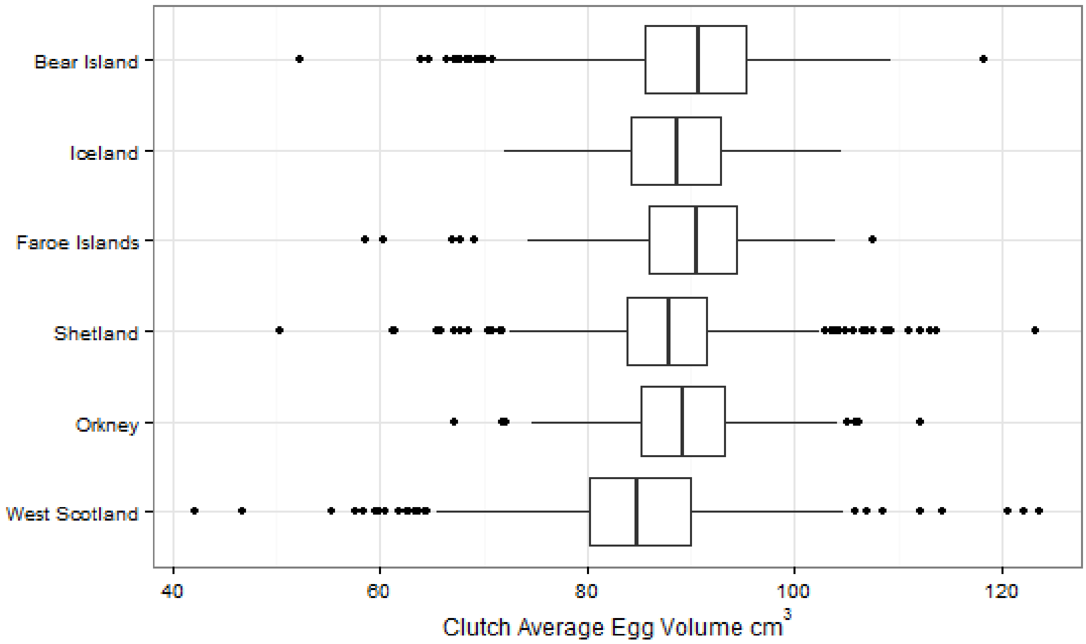

Figure 3.2: Spatial variation in great skua egg volume (1980-2014) with regions in order of lattitude (most northerly region at the top and the most southerly at the bottom of the vertical axis). Both museum and field measurements were included.

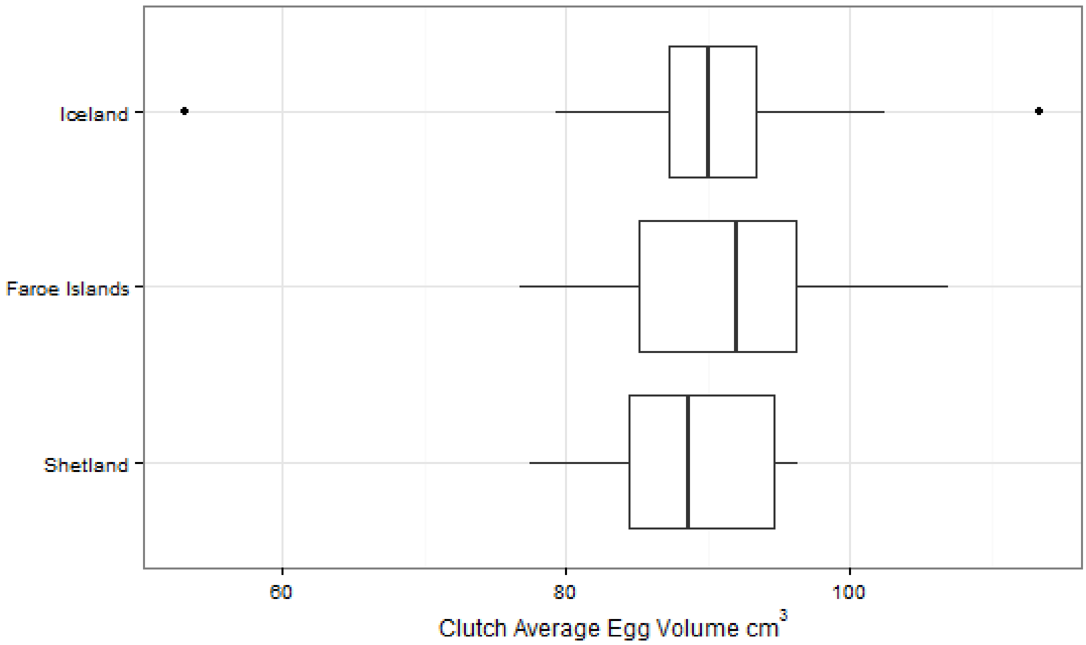

Figure 3.3: Spatial variation in the size of great skua eggs from 1945-1959 measured from museum eggs. Iceland (n=90), Faroe Islands (n=30), Shetland (n=50)

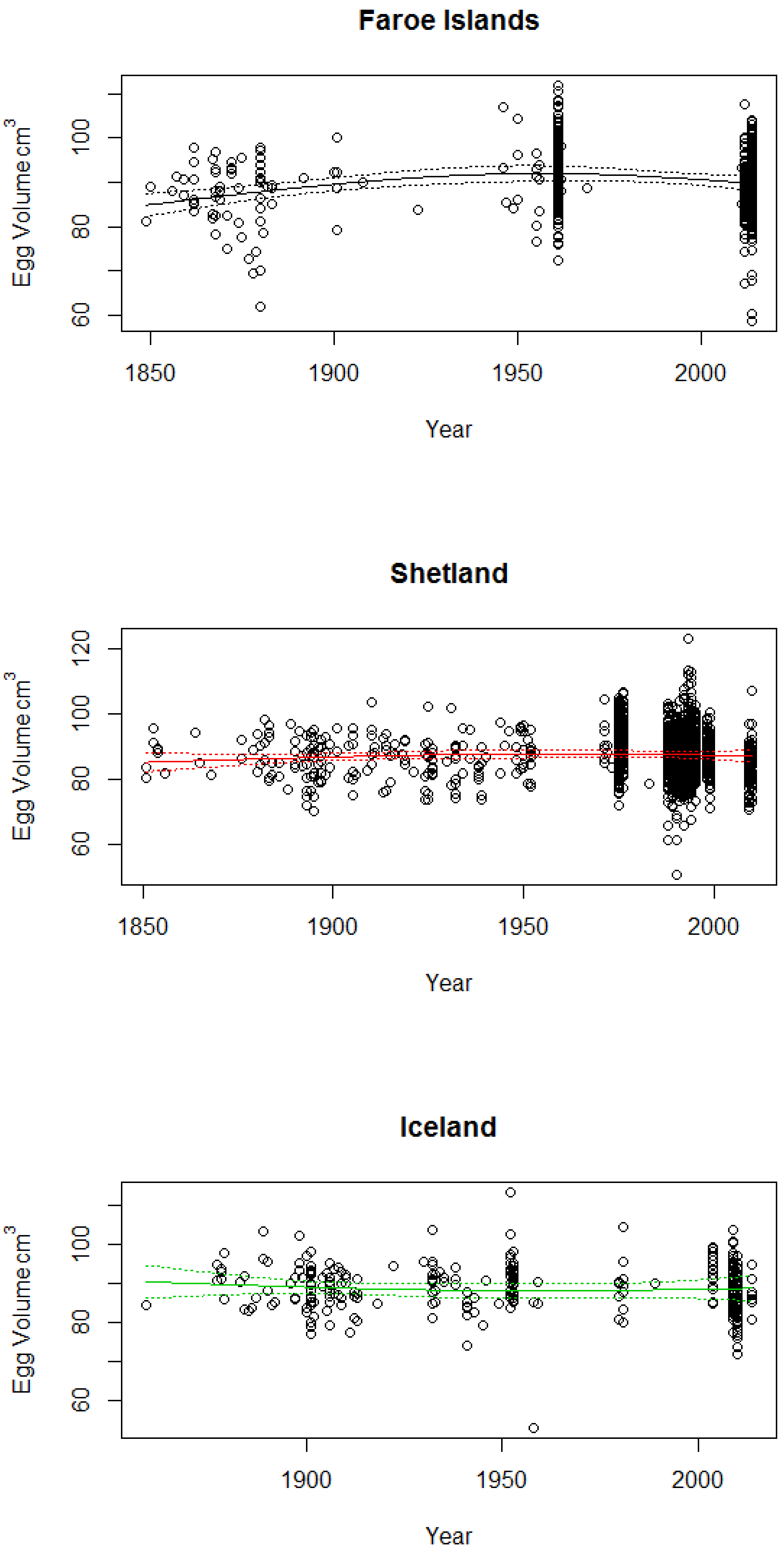

Figure 3.4 a-c: Egg volume data and modelled mean great skua egg sizes (solid lines) in (a) Faroes, (b) Shetland and (c) Iceland with year as random effect, shown with 95% confidence interval (dotted lines).

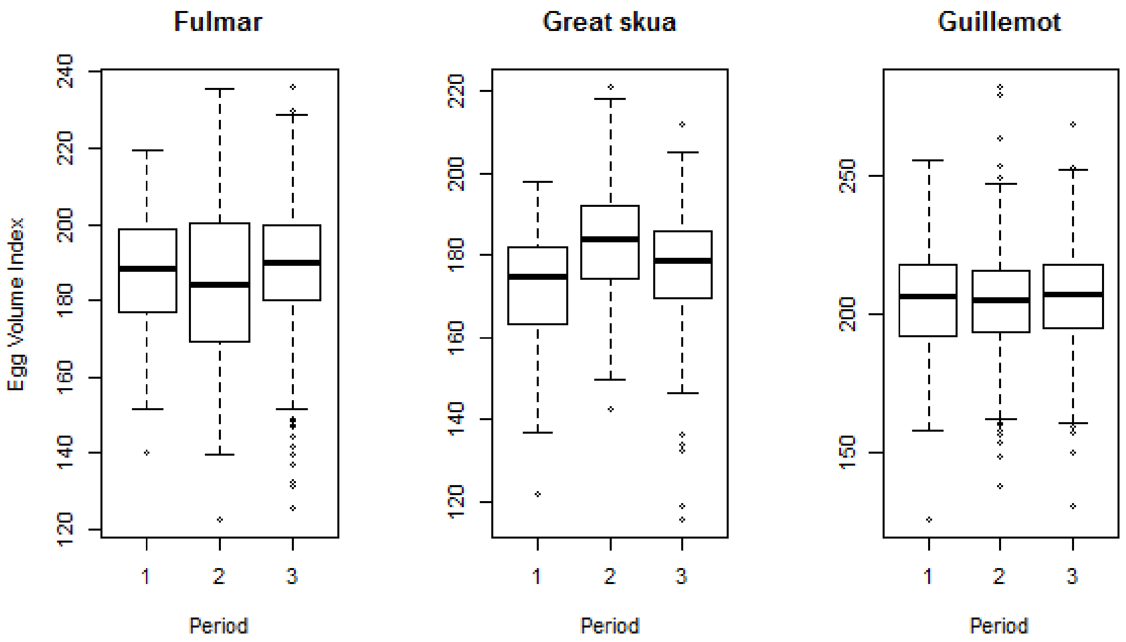

Figure 3.5: Temporal differences in egg volume index of fulmar, great skua and guillemot eggs from the Faroes. Egg volume index was used to compare egg size between species. Period 1 is from 1840 – 1909, period 2 from 1910 – 1979, and period 3 from 1980-2014.

4. Legacy Pollutants are Declining in Great Skuas (*Stercorarius skua*) but Remain Higher in Faroe Islands than in Scotland

Abstract

To monitor environmental pollutants in Faroese biota, samples from a top predator were analysed and put into a spatial and temporal context. Analysis of 20 great skua eggs sampled in 2012 from the Faroe Islands showed >70% lower concentrations of legacy persistent organic pollutants (POPs) than in samples analysed in 1977. The 2012 Faroese eggs showed higher concentrations than for eggs in Shetland from about the same period (2008). Eggshells were analysed for sub-lethal effects but there were no detectable effects of legacy POP levels on eggshell colour or thickness. A temporal decline in legacy POPs would indicate a reduction in the general pollutant levels present in the environment as has been shown in other areas of the North Atlantic, but there are significant geographic differences in POPs levels likely due to differences in diet resulting in significantly different exposures on a relatively limited spatial scale.

Introduction

Top predators are particularly exposed to environmental pollutants which magnify in the food-chain (Newman 2010), and as such are often used as monitors of pollution levels in the environment (Furness & Camphuysen 1997). Due to the high trophic position of seabirds, they have been found to accumulate lipid-soluble persistent organic pollutants (POPs). There may, however, be strong geographic differences in pollutant concentrations found in top predators due to various factors such as proximity to pollutant sources, latitudinal variation in atmospheric deposition, and spatial differences in diet (Bourgeon *et al.* 2013).

Eggs from great skuas (*Stercorarius skua*) a top predator in the Faroese marine ecosystem were sampled in 1977 showed exceptionally high concentrations in total PCB, DDT and DDE and four and five orders of magnitude higher concentrations of PCB and DDE respectively, compared to eggs of fulmars (*Fulmarus glacialis*) (Bloch *et al.* 1987). With the implementation of regulations restricting the use of PCBs in the 1970s and the ban agreed by the Stockholm convention of 2004, several POPs have been phased out of use (Hagen & Walls 2001). However, they may still persist in the environment, despite production having been halted or reduced, and are referred to as *legacy POPs*. Moreover, large volumes of PCBs applied prior to the restrictions are today part of buildings and the technosphere in general and leak into the environment (Breivik *et al.* 2002). Considering the historic high levels in Faroese great skua eggs, an evaluation of the pollutant status of great skuas in the Faroe Islands (Faroes hereafter) is timely and important. A recent study from Shetland comparing great skua eggs from 1980 and 2008 showed a significant decline in most legacy POPs (Leat *et al.* 2011). The decline was greatest for the least persistent pollutants such as DDT and some PCB congeners, suggesting a reduced presence in the wider marine ecosystem of some of the legacy POPs (Leat *et al.* 2011). The aim of the present analysis of eggs collected in the Faroes in 2012 is to determine if there is also a significant decline in legacy POPs in the Faroese environment, similar to Shetland.

Some pollutants, such as DDT and DDE influence calcium metabolism of birds, and have been shown to cause eggshell thinning (Ratcliffe 1970). A thinning of eggshells is widely associated with reduced hatching success (Beyer *et al.* 1996). The concentrations in Faroese great skua eggs in the 1970s was at a level that caused eggshell thinning in other seabird species such as ivory gull (*Pagophila eburnea*) (Miljeteig *et al.* 2012). The potential of DDT and DDE to interfere with the organisms’ calcium metabolism has also been proposed to have a measurable effect on eggshell colour (Jagannath *et al.* 2008), and a recent study on herring gulls (*Larus* argentatus) detected a relationship between eggshell colour and POPs levels in the eggs (Hanley & Doucet 2012). Therefore, as a part of our analysis of pollutant concentrations in great skua eggs, we also measured eggshell thickness and colour and tested if there was a relationship the egg’s pollutant load.

There was a significant geographic difference in POPs levels between great skua eggs from Shetland and Faroes in the 1970s (Bloch *et al.* 1987, Leat *et al.* 2011). Here we will also investigate the geographical variation in contemporaneous POP levels between Faroes and Shetland using published data for Shetland from Leat et al. (2011) and freshly collected eggs from the Faroes. Among the factors that could contribute to the geographic differences in POPs concentrations is difference in diet between breeding areas. We expect populations that forage on a higher trophic level (measured as $\delta^{15}N$ stable isotope ratio of the egg material) accumulate higher POP levels due to bio-accumulation of contaminants through the food web.

Method

In 2012, 20 eggs from 20 different nests were collected from the great skua colony at Skúvoy, Faroe Islands (61°46'N 6°49'W). Nesting territories were located and selected randomly throughout the colony, by observing presence and aggressive behaviour of at least one parent. Within approximately 1 week after laying, single eggs were collected from two-egg clutches only, and were refrigerated overnight. The next day, eggs were opened along the long axis and the egg content emptied, homogenized and frozen at -20˚C until analysis. Eggshells were dried at air temperature and then stored in a dry and dark condition.

The POPs analysis on egg content was performed by the Centre de Toxicologie du Québec (Québec, Canada) which is accredited under ISO17025 and participates in the Arctic Monitoring Assessment Programme (AMAP). The samples were enriched with internal standards, mixed with dichloromethane and chemically dried using sodium sulphate. The compounds were then extracted in an ultrasonic bath followed by a filtration. A subset of the sample was used to determine lipid percentage by gravimetry. The sample for analyses was concentrated by evaporation and purified using gel permeation chromatography (GPC) and cleaned-up on Florisil column. The extracts were analysed using an Agilent 5973 gas chromatograph equipped with a PTV injector and an AutoSpec Ultima High Resolution Mass Spectrometer (HRMS) from Waters/Micromass. The HRMS was operated at Resolution 10,000 at 10%. All chromatography was performed on a 60m, 0.25mm DB5 MS capillary column. The analysis was done for the following compounds: PCB congeners 28, 52, 99, 101, 105, 118, 128, 138, 153, 156, 163, 170, 180, 183, 187, PCB arochlor 1260, o,p'-DDE, α-chlordane, γ-chlordane, cis-nonachlor, trans-nonachlor, hexachlorobenzene, Mirex, oxychlordane, p,p'-DDE, o,p'-DDT, p,p'-DDT, β-HCH, Toxaphene parlar 26, 32, 50, 62. In order to control for variation in lipid content each sample was divided by lipid percentage and is reported as wet weight (ww), and all concentrations are reported as µg/kg. 100% Gamma chlordane and 90% of PCB congener 52 were below their detection limits of 0.004 µg/kg ww and 13.6 µg/kg ww, respectively,and these compounds were excluded from further analysis. The sum of PCB congeners is referred to as PCB14.

To assess trophic level of Faroese great skuas during egg formation, stable isotope analysis of the egg content was undertaken at the NERC Life Sciences Mass Spectrometry Facility. The egg material was oven-dried at 40°C for >24 hours. Stable nitrogen isotope analyses can be used as a proxy for the trophic level of ingested prey (Hobson & Welch 1992), and were performed by continuous flow isotope ratio mass spectrometry (CF-IRMS) on an average of 0.8 ± 0.1 mg of sub-sampled material loaded into tin cups and combusted in a Costech ECS 4010 elemental analyser coupled to a Thermo Finnigan Delta Plus XP mass spectrometer. Lab standards (gelatin, alanine and glycine) were run between every 10 samples to correct for instrument drift. Isotope ratios are expressed as parts per thousand (‰) according to the equation $\delta X = [(R_{sample}/R_{standard})-1]$ x1000, where X is ^{15}N, R is the $^{15}N/^{14}N$, and $R_{standard}$ is the ratio of the international references AIR for nitrogen. Lab standards were calibrated with international reference standards and the measurement precision is calculated as the standard deviation of multiple measurements of internal lab standard material (tryptophan) which was ±0.209 ‰.

Eggshell thickness, included the inner and outer membrane, was measured using a micrometer with a ballpoint tip, to the nearest 0.01 mm at three different points along the long axis of the egg (pointed, equator and blunt). Measurements at each location along the long axis were repeated three times and the repeatability of the measurements at each location of the egg was tested using Intraclass Correlation Coefficient (ICC package, Wolak et al 2012; in R version 3.1.2, R Core Team 2014). Measurement repeatabilities were high at each of the locations - between 0.90 and 0.92. In order to compare with previously reported thickness values (measured without membranes) we also measured eggshell thickness without membranes where possible on a subset of samples.

The eggshell background colour was determined using photographs in RAW format taken by a digital SLR camera (Nikon D7000). The photographs were taken on the intact egg outside in ambient light during the middle of the day, with the eggs placed on a flat platform with colour reference material (X-rite ColorChecker Passport, Michigan, US) on each photograph. Care was taken to shelter each photograph from direct sunlight. From the image we recorded red (R), green (G) and blue (B) values using the Pixel Inspector Tool plugin in ImageJ (Rasband 2014) from six different pixels of the standardised grey colours on the ColorCheckerPassport and from six different pixels at the blunt end of the egg avoiding maculation and dirt. To control for the effect of variation in light condition on colour (linearization) we used the standardised greyscale colour from the colour reference material where RGB values are known. Known and observed RGB values of the standardised grey colours were regressed against each other and the resulting correction equation applied to the RGB values of the eggshell. It has been suggested that colour data are better interpreted as ratios as opposed to absolute values (Bergman & Beehner 2008), so we analysed R:G as a ratio.

Comparison with published data was done by t-test where appropriate, and Mann-Whitney U test where the data did not fulfill the normality criteria. Bonferroni correction was applied where multiple t-tests were carried out on the different POP compounds from the same eggs. For testing differences in thickness between locations on the eggshell, a linear mixed effect model was created using lme4 package in R (Bates *et al.* 2015b). A paired t-test was used to compare eggshell thickness measurements with and without membranes. To test for associations between POPs concentration and eggshell thickness and color the Spearman ranked correlations were used. We tested correlations between POP compounds and trophic level ($\delta^{15}N$). If there is no association between POP and trophic level then positive and negative correlations are equally likely to occur. To test this we compared the proportion of observed positive correlations against 50% using a binomial test. All statistical tests were done in R version 3.1.2 (R Core Team 2016). Means ± 1 standard deviation are reported and two-tailed $p < 0.05$ was taken as statistically significant.

Results and Discussion

In the Faroese eggs collected in 2012 had lower DDT, DDE and sum of PCB levels than eggs in 1977 (table 4.1). The concentrations of other compounds in Faroese eggs from 2012, but not measured in 1977 such as ß-HCH, HCB, Mirex,Cis-Nonachlor, Oxychlordane, Toxaphene parlar 26, 50, 62, were also significantly higher than in contemporary eggs from Shetland and none of the compounds were significantly lower in Faroes compared with Shetland (table 4.1). The reduction in concentrations of legacy POPs from 1977 to 2012 is so large that we can be confident that this reflects a real and considerable decline and is not attributed to differences in analytic approach. A similar temporal decline in legacy POPs concentrations has also been seen in other marine animals such as black guillemot (*Cepphus grylle*) eggs, juvenile pilot whale (*Globicephala melas*) blubber and cod (*Gadus morhua*) from the Faroes (Nielsen *et al.* 2014). A decline in legacy POPs in the marine environment over the last few decades has also been found in other regions in the North Atlantic and Arctic (Helgason *et al.* 2008, Muir & de Wit 2010). The relatively greater decline of DDT (99.5%) in relation to DDE (70.2%, table 4.1) could be explained by the restriction of DDT use as pesticide, while its metabolite – DDE – persists in the environment for longer than the parent compound (Peakall 2007). PCBs also declined by 63.6%. However caution is needed when comparing PCB data between 1977 and 2012 because different quantification methods were used. The egg samples collected by Bloch et al (1987) were not available to re-analyse alongside contemporary samples. Nevertheless, we assume the sum PCB as quantified with Clophen A60 in 1977 is broadly comparable to single congener quantification Aroclor 1260. The sum of 14 PCB congeners analysed in the 2012 samples is reported in table 4.1, however for comparison with Leat et al (2011) which did not include congener 163 in its sumPCB this congener was excluded.

The linear mixed effect model showed the mean eggshell thickness to vary along the longitudinal axis ($t = 4.30$) . A Tukey posthoc test showed the pointed end 0.32 mm (±0.028) was signficantly thicker than than the blunt end 0.31 mm (±0.023) ($p < 0.001$), but the difference was not significant between pointed end and the equator 0.31 mm (±0.026) ($p= 0.58$). Other studies have shown similar variation in eggshell thickness along the length axis with thinner shells at the blunt end than at the equator and pointed end (e.g. Maurer et al. 2012). Since the difference was small between the locations we used the mean of the eggshell thickness across all three positions for further analysis and the mean eggshell thickness of Faroese great skua eggs in 2012 was 0.32 mm (±0.022). Bloch et al (1987) reported eggshell thickness of 0.28 mm (±0.016) for 19 great skua eggs sampled in the Faroes in 1977, although location of thickness measure was not specified. However these measurements were taken without membranes. In our sample we found a difference between shell thickness with and without the membranes of on average 0.06 mm (± 0.028, $n = 17$ eggs; paired- $t = 11.84$, $df = 16$, $p < 0.001$), which means that the membranes included in the shell thickness measurement could potentially account for the apparent difference in eggshell thickness between 1977 and 2012.

There was no significant correlation of eggshell thickness with DDE (Spearman $r_s = 0.17$, $n = 20$, $p = 0.477$) or with DDT (Spearman $r_s = 0.09$, $n = 20$, $p = 0.696$). There was also no significant correlation between DDE, DDT or PCB14 and eggshell colour (R:G ratio) (DDT: Spearman $r_s = 0.24$, $p = 0.311$, DDE: $r_s = -0.16$, $p = 0.504$, PCB14: $r_s = -0.30$, $p = 0.197$). Current DDT concentrations in Faroese great skua eggs are now below the limit where we would expect to find an effect on eggshell thickness (Beyer & Meador 2011). The mean DDE concentration of 1823 ±1213 µg/kg ww, is however within the range of concentrations where eggshell thinning would occur in some birds of prey (>100 µg/kg ww for golden eagles *Aquila chrysaetos*) (Newton & Galbraith 1991). However it is well established that bird species differ in their tolerance of DDE (Beyer & Meador 2011), and the marine diet is generally richer in calcium than in terrestrial ecosystem (Reynolds & Perrins 2010), so calcium may not become a limiting factor, despite the detrimental effects from DDE and DDT on calcium metabolism.

In addition to a decline in POP levels in great skua over a period of 35 years, our data also showed that Faroese eggs in 2012 had statistically higher POP levels than Shetland great skua eggs in 2008 (table 4.1, fig.4.1). There might be at least three reasons why Faroese great skuas have a higher pollutant load than Shetland great skuas: Difference in wintering areas with different pollutant loads, differences in atmospheric deposition of pollutants in their breeding area, and differences in diet. Recent studies have shown that wintering area can significantly influence the pollutant load of several seabird species in the breeding season (Bourgeon *et al.* 2013, Leat *et al.* 2013, Fort *et al.* 2014, Carravieri *et al.* 2014). However ringing data suggest that Faroese great skuas have similar wintering areas to the great skuas breeding in Shetland (Hammer et al. 2014). Between-population differences in POP levels may also be due to differences in atmospheric deposition of POPs in the birds' breeding area. POPs vary in volatility which means that some compounds may travel far in gaseous form, and then precipitate in colder areas far from their source (Jones & de Voogt 1999). This is particularly exemplified by the accumulation of POPs in Arctic biota (de Wit *et al.* 2002). While it is not known whether the deposition rate of POPs differs between the Faroes and Shetland, the relatively close proximity and similarity in climate between these two sites could suggest there is another important factor to consider in relation to the difference of POPs concentrations between Faroes and Shetland great skuas rather than differences in deposition rate.

All POPs accumulate through the food chain, and organisms will potentially accumulate POPs to different extents, depending on their trophic level (Peakall 2007). Since the great skua occupies some of the highest trophic levels in the Faroese marine ecosystem (feeding on fish, birds and mammals Furness 1987) it is therefore not surprising that it should accumulate high concentrations of pollutants as was found by Bloch et al (1987) and in this study (fig. 4.1). Studies of regurgitated pellets suggest that in Iceland, Shetland and further south, great skuas feed mainly on sandeels and fishery discards, while in the Faroes, great skuas feed mainly on other seabirds (Bayes *et al.* 1964, Leat 2012). Faroese great skua eggs had significantly higher δ^{15}N values (12.54 ± 0.50) than Shetland eggs (Leat, unpublished): $t = 6.77$, $df = 48$, $p < 0.001$), suggesting Faroese skuas forage at a higher trophic level than Shetland skuas. Differences in stable isotope ration in predators in different geographic regions may not only be due to differences in prey but due to geographic variation in baseline stable isotope values (Cherel & Hobson 2007). However, across Shetland, Iceland and Bear Island populations, differences in stable isotope values from blood samples were corroborated by between-population differences in diet interfered from analysis of pellet composition (Bourgeon *et al.* 2012).

We also investigated whether the trophic level measured in the eggs would correlate with POP levels within the Faroese population in 2012. As in Leat et al (2011) we found no individual POP compound to correlate significantly with δ^{15}N ratio in the eggs (table 4.2), but assuming the null hypothesis half of the correlations would result in positive and half in negative correlation coefficients. The distribution of correlation coefficients, however, deviated significantly from this prediction as all correlation coefficients are positive (binomial test: 50% $p < 0.001$), which suggests that Faroese great skuas that feed on a higher trophic level might have higher levels of POPs in their eggs. Differences in diet between the Faroese and Shetland great skuas may also therefore help us to understand the marked difference in pollutant concentrations between Faroes and Shetland.

This study presents evidence that concentrations of some legacy POPs found in the Faroese environment have declined over the last 35 years. There were no detectable sub-lethal effects from these pollutants on the eggs of contemporary samples. However, the difference in POPs concentrations between the Faroes and Shetland lends support to the idea that the diet at the breeding area influences POPs exposure more than other factors such as atmospheric deposition and wintering area.

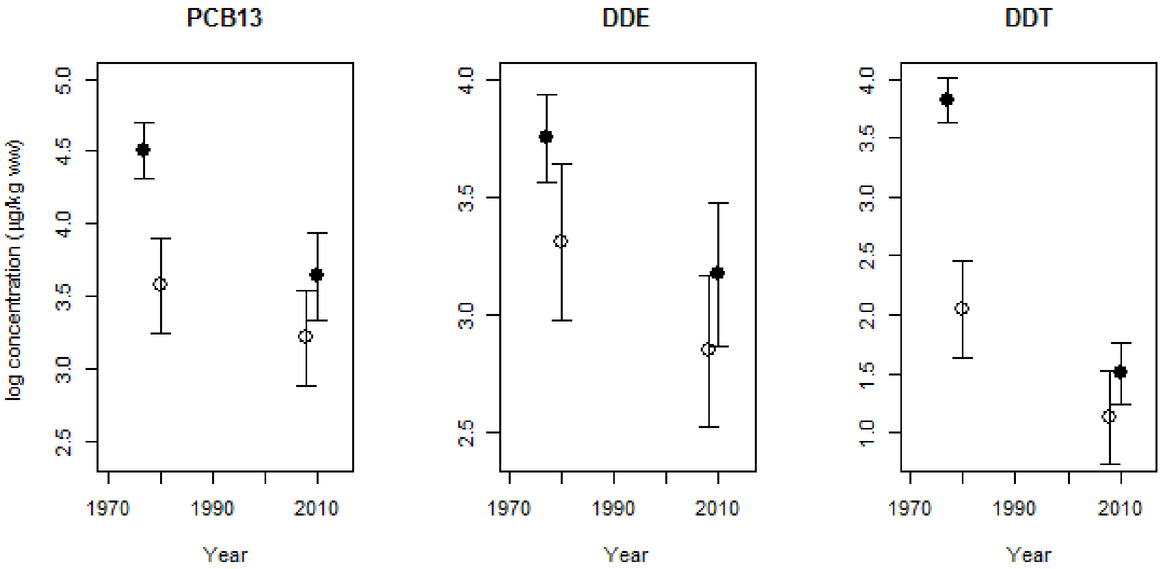

Figure 4.1. Showing historic and contemporary (Bloch et al. 1987; Leat et al. 2011; this study) concentrations of three compounds from great skua eggs as log transformed means. Open circles are Shetland and filled circles are Faroes.

Table 4.1. Mean (stdev) and median (range) concentrations (µg/kg wet weight) of organochlorines assayed in great skua eggs from the Faroes in 1977 (Bloch et al., 1987), from the Faroes in 2012 (this study) and from Shetland 2008 (Leat et al 2011). For the t-test and Welch test the data were log transformed. Comparisons between 1977 & 2012 of Faroese eggs and between Faroese eggs in 2012 and Shetland eggs in 2008 are shown with significant differences after Bonferroni correction (corrected p = 0.0038) in bold. [a] n=18, [b] n=10.

	Faroes								Shetland	
	1977 (n=19)				2012 (n=20)				2008 (n=29)	
	Mean (SD)	Median (min-max)	t-value	p-value	Mean (SD)	Median (min-max)	t-value	p-value	Mean (SD)	Median (min-max)
sumPCB14			**10.78**	<0.001	5419 (3604)	4530 (1205-12307)	**4.58**	<0.001	2405 (1829)	1614 (620-7492)
PCB, Aroclor 1260	35800 (17614)	32000 (13300-96500)			13100 (9100)	10660 (2592-31950)				
p,p'-DDE	6121 (2829)	5500 (1900-16000)	**7.24**	<0.001	1823 (1212)	1543 (394-4691)	**3.62**	<0.001	924 (908)	598 (254-4588)
p,p'-DDT	7226 (3371)	7000 (2300-18700)	**31.92**	<0.001	37.8 (24.9)	30.2 (7.2-120.7)	**4.06**	<0.001	18 (15)	15.8 (2.5-63)
ß-HCH					5.5 (5.1)	4.5 (1.2-20.6)	***w* = 477**	<0.001	1.8 (1.5)	1.4 (ND-8.6)
HCB					84 (56)	64 (29-223)	**5.11**	<0.001	23 (18)	20 (ND-88)
Mirex					160 (119)	134 (34-459)	**8.46**	<0.001	24 (20)	20 (3.3-110)
Cis-nonachlor					31.6 (18.8)	23.4 (10.8-81.9)	2.09	0.043	22 (11)	20 (7.6-53)
Trans-nonachlor					71 (37)	58 (29-149)	1.14	0.258	103 (83)	77 (6.5-358)
Oxychlordane					176 (148)	126 (34-564)	**7.00**	<0.001	28 (42)	15 (ND-207)
Toxaphene, Parlar no. 26					61 (35)	52 (26-170)	**4.90**	<0.001	32 (15)^{b}	26 (17-56)^{b}
Toxaphene, Parlar no. 50					144 (76)	116 (65-355)	**5.59**	<0.001	72 (31)^{b}	67 (39-125)^{b}
Toxaphene, Parlar no. 62					33 (23)^{a}	27 (11-105)^{a}	**2.76**	<0.001	20 (13)^{b}	16 (5.4-47)^{b}
Toxaphene, Parlar no. 32					1.7 (0.7)	1.8 (0.8-3.2)				
Alpha-chlordane					4.9 (2.4)	4.8 (1.1-9.2)				
Gamma-chlordane					ND	ND				
PCB, IUPAC # 28					5.5 (3.3)	4.8 (1.5-14.9)				
PCB, IUPAC # 52					ND	ND (ND-12.07)				
PCB, IUPAC # 99					123 (90)	96 (23-321)				
PCB, IUPAC # 101					42 (37)	31 (12-156)				
PCB, IUPAC # 105					63 (42)	48 (14-156)				
PCB, IUPAC # 118					306 (208)	255 (59-710)				
PCB, IUPAC # 128					82 (54)	61 (19-189)				
PCB, IUPAC # 138					656 (422)	536 (135-1420)				
PCB, IUPAC # 153					1868 (1330)	1504 (362-4686)				
PCB, IUPAC # 156					80 (54)	70 (18-185)				
PCB, IUPAC # 163					102 (84)	84 (23-336)				
PCB, IUPAC # 170					354 (261)	267 (81-910)				
PCB, IUPAC # 180					1214 (833)	940 (319-2911)				
PCB, IUPAC # 183					217 (142)	180 (50-497)				
PCB, IUPAC # 187					305 (234)	269 (77-1050)				

Table 4.2. Spearman rank correlations between POPs and $\delta^{15}N$ ratio in great skua eggshells. *Tied values.

	Spearman's Rho	p - value
sumPCB	0.18	0.437
p,p'-DDE	0.05	0.831
p,p'-DDT	0.20	0.831
ß-HCH	0.41	0.075
HCB	0.09	*0.702
Mirex	0.28	0.226
Cis-nonachlor	0.37	0.112
Trans-nonachlor	0.37	0.112
Oxychlordane	0.13	0.577
Toxaphene, Parlar no.	0.27	0.247
Toxaphene, Parlar no.	0.23	0.331
Toxaphene, Parlar no.	0.22	*0.342
Alpha-chlordane	0.29	0.214
PCB, Aroclor 1260	0.17	0.484

5. Plastic debris in great skua (Stercorarius skua) pellets corresponds to seabird prey species

Abstract

Plastic is a common item in marine environments. Studies assessing seabird ingestion of plastics have focused on species that ingest plastics mistaken for prey items. Few studies have examined scavenger and predatory species that are likely to ingest plastics indirectly through their prey items, such as the great skua (*Stercorarius skua*). We examined 1,034 regurgitated pellets from a great skua colony in the Faroe Islands for plastics and found approximately 6% contained plastics. Pellets containing remains of Northern fulmars (*Fulmarus glacialis*) had the highest prevalence of plastic. Our findings support previous work showing that Northern fulmars have higher loads of plastics than other sympatric species. This study demonstrates that marine plastic debris is transferred from surface feeding seabird species to predatory great skuas. Examination of plastic ingestion in species that do not ingest plastics directly can provide insights into how plastic particles transfer vertically within the food web.

Introduction

Plastic pollution has been recognized as an emerging global environmental issue (UNEP, 2014). Plastic debris is ubiquitous in the marine environment, and has been found in both highly populated regions, and remote areas of the world such as the Arctic (Obbard et al., 2014; Vegter et al., 2014). Plastic particles have been regularly found to be ingested by marine animals, and dozens of seabirds species have now been reported to have ingested plastic pollution (Gregory, 2009; Laist, 1997). Seabirds have been shown to ingest both macro- (pieces greater than 5 mm) and micro-plastics (pieces less than 5 mm), making this group particularly susceptible to marine debris (Provencher et al., 2015; UNEP, 2011, 2014).

Marine plastic debris includes both industrial plastics and user plastics (Moore, 2007). Industrial plastics are commonly found in the marine environment in the form of hard plastic pellets (van Franeker et al., 2011). These pellets are formed as precursors to the formation of consumer products. User plastics come from consumer products, including all hard plastics (polyethylene) and styrofoam (polystyrene). Once in the environment plastic pieces are broken down over time due to chemical and physical degradation.

Seabirds have been shown to be important for monitoring plastic pollution in the environment (van Franeker et al., 2011). For example, Northern fulmars (*Fulmarus glacialis*) (hereafter fulmar) are part of the North Sea ecological monitoring program designed to track marine pollution (van Franeker et al., 2011). Ingestion of plastics by most seabirds is thought to occur because they mistake plastic items for prey in the water column (Cadee, 2002). There are differences in plastic ingestion between seabirds with different foraging strategies which has been shown in several studies comparing ingestion across seabird foraging guilds (Avery-Gomm et al., 2013; Provencher et al., 2014). To date, much of the work on seabird ingestion of plastics has focused on species that are thought to directly ingest plastics from the environment when mistaking plastics for prey items (Avery-Gomm et al., 2013; Cadee, 2002; Donnelly-Greenan et al., 2014; van Franeker et al., 2011). Less attention has been given to species that risk ingesting plastic indirectly through their prey items (Furness, 1985; Ryan and Fraser, 1988). Species that ingest plastics indirectly can play a role in expanding our understanding of marine plastics pollution in the environment, specifically in tracking how plastics move through the environment, and what species are affected by plastic pollution, both identified as priorities for marine debris research (Vegter et al., 2014).

The great skua (*Stercorarius skua*), is a top predator seabird in the North Atlantic region. It scavenges, kleptoparasitises or predates on other marine bird species (Furness, 1987; Phillips et al., 1997), which potentially makes it a suitable model monitor of prevalence of plastics quantitatively and qualitatively in different components of the food web. Seabirds that forage at the surface of the water column, where plastic debris often floats, tend to have higher burdens of ingested plastics than those that forage deeper in the water column (Avery-Gomm et al., 2013; Bond et al., 2014; Provencher et al., 2014). Some species are also more prone to accumulating ingested plastic depending on their capability to regurgitate indigestible stomach content (Furness, 1985). Since plastic ingestion has been found in several species of seabirds from the Faroe Islands (Faroes hereafter) (van Franeker et al., 2011, Jensen, 2012; Provencher et al., 2014), we expected great skuas in the region to show evidence of plastic ingestion, but we expect the prevalence and number of plastics pieces to vary in respect of the type of prey species the great skuas have consumed. The diet of Faroese great skuas includes fish, seabirds, and sometimes also terrestrial birds and mammals (Hammer, unpub. data). The main seabird species they feed on are black-legged kittiwakes (*Rissa tridactyla*) (hereafter kittiwake), Atlantic puffins (*Fratercula arctica*) (hereafter puffin), and fulmars. In addition to these seabird prey species, great skuas scavenge fish from behind fishing vessels or steal fish from other birds near the colony (Bayes et al., 1964; Hammer unpub. data). More rarely Faroese great skuas also feed on common guillemots (*Uria aalge*), mountain hares (*Lepus timidus*), Manx shearwater (*Puffinus puffinus*), and eggs from various birds (Bayes et al., 1964; Hammer unpub. data).

The aim of this study is to assess prevalence of plastic ingestion in Faroese great skuas based on sampling pellets, a common method of assessing great skua diet. Pellets contain indigestible material such as feathers, bones, hair and plastic (Furness, 1987). Due to the described foraging strategies of great skuas, it is likely that most ingested plastics from these birds come from the marine environment (Ryan and Fraser, 1988). First, we examine the prevalence of plastic debris in the population and whether it depends on the number of pellets sampled per territory. Second, we compare plastic debris between pellets containing different prey types, and discuss how our estimates of prevalence in seabird species that skuas prey on compares to other reported values for those same species collected through direct sampling of the birds. This allows assessing if sampling through this indirect method yields similar quantitative results to direct dissection methods.

Method

1,034 regurgitated pellets from 165 great skua territories were collected during the breeding season April-August 2013, at Skúvoy in the Faroes (61°46'N 6°49'W). Pellets were collected during territory visits, which occurred 2-3 times a week after first apparent sign of territory attendance. The median number of pellets found in each territory per visit was 1 and the highest number of pellets found in a territory during one visit was 36. Considering how ardently great skuas defend their breeding territories (Furness, 1987), it is reasonable to assume that the regurgitated pellets found within a great skua colony are produced only by the great skua pairs within each territory. All pellets were collected and examined in the field to determine prey type. The prey type was recorded for all pellets and if plastic material was found, the pellets were individually bagged to prevent mixing of contents between pellets. If there was no plastic found in the pellet they were collected in a separate bag. While the content of some pellets were distinguishable to species level by size and colour of feathers and odour (e.g. fulmar and kittiwake), other pellets could not readily be identified to species level such as puffin, common guillemot, black guillemot (*Cepphus grylle*), and razorbill (*Alca torda*), but could still be distinguished from other seabirds as auks. These species were thus grouped as “auks” in this study. Other pellets which contained fish or mountain hare were also identified. 46 pellets contained more than one type of prey, and 27 (3.3%) of these contained a mixture of bird and fish and were excluded from all analyses. The remaining mixed pellets (n=12) contained a mixture of different bird prey (with 6 containing plastic). The mixed bird pellets were included in the general comparison between (bird, fish and other) types of pellets only, but were excluded from the comparison between different bird types.

All plastic particles from the pellets were collected, dried, sorted, and processed. Plastic particles were sorted using the 'Save the North Sea' protocol (van Franeker et al., 2011) into fragments, threadlike, sheetlike, foamed, industrial and other and weighed. Mean values of plastic weight are reported for the entire sample of pellets including pellets with no plastic (mass abundance) and only for the pellets which contained plastic (mass intensity). The colour of each piece was also noted and recorded by a single observer. The prevalence (presence or absence) and abundance (number of pieces per pellet) of plastics in each pellet collected is presented, along with the prevalence and abundance of plastics in each pair's territory.

Statistical analyses were carried out in program R (R Core Development Team, 2014). First we looked whether the prevalence of plastics in a territory was related to search effort (measured in number of pellets collected per territory) to determine if number of collected pellets influenced the detection of plastic pollution using a generalised linear model (GLM) with a binomial distribution. The number of plastic pieces in the pellets was compared between pellets with different prey types using a Generalized Linear Mixed Effects Model (lme4 Bates et al. 2014) with a binomial distribution, logit link function and territory as random effect to account for the non-independence of pellets collected from the same individual birds. Number of plastic pieces per pellet were compared across pellets containing different bird prey species only (fulmars, kittiwakes and auks). The data contain a low number of non-zero values. The general mixed model assuming zero-inflation (glmmADMB Skaug et al. 2013), and a negative binomial distribution, showed no evidence for zero-inflation (estimated zero-inflation proportion = 0.00002), thus zero-inflation was no longer considered for further analyses as it is unnecessary and difficult given the size of the dataset. Among error distributions that could be suitable to fit the observed distribution of our data (negative binomial and Poisson lognormal), the negative binomial error distribution had the better fit to our data structure, because the negative binomial distribution better justified the assumption of homoscedasticity of the Pearson residuals. However, currently available models that allow the use of a negative binomial distribution don't support the inclusion of a random effect. To examine the importance of territory as random effect, which, if not important, could potentially lead to an overfitted model, we fitted a mixed model with an alternative error distribution (poisson log distribution) with territory as a random effect. The variance estimate for the random effect was zero (glmmADMB). It would be therefore justified for our data to exclude territory as a random effect without compromising the conclusion from a model without random effect. Hence we used the mixed model with negative binomial (glmmADMB) to compare number of plastic items per pellet between pellets containing remains of the three seabird prey remains (fulmar, kittiwake, auk).Statistical tests where $p < 0.05$ were considered statistically significant. Means are presented with standard deviations.

Results

On the 165 study territories, between 1 and 63 pellets were collected per territory (median = 4) over the breeding season and the number of pellets found during a single visit ranged from 0-32 pellets per territory. Pellets containing at least one piece of plastic (Fig 5.1) were found on 48 territories (30%). The prevalence of plastics in a territory did not significantly vary with the number of collected pellets per territory (GLM, Z = 0.97; $p = 0.33$). From the total of 1,034 pellets, 59 individual pellets (6 %) contained plastic debris with a total of 179 plastic pieces ranging from 1-15 pieces (median of 2 pieces) per pellet. The plastic pieces found in the pellets were both from consumer and industrial sources. The most common plastic type found was hard fragments of user plastics (Table 5.2, Fig 5.1a). Although many colours of plastics were found, the most common colour of plastic found in the pellets was white/yellow (68%). Red plastic was the next most common colour found in the pellets (10%), followed by pink (5%), orange (4%), black (3%), green (2%) and blue (2%). The final 6% of the plastics were made up of other colours.

The proportion of pellets containing plastic pieces (prevalence) varied between pellets containing the remains of different prey species (GLMM with binomial error and territory as random factor (lme4, Bates *et al. 2014*): $F^{837} = 3.78$, df = 6; $p < 0.001$) (Table 5.1). 86% of the pellets containing plastics were from bird prey, 7% from fish, 5% from mixed bird and fish and 2% from mountain hare. Where identification of bird prey type was possible we found that pellets containing the remains of fulmars had significantly higher prevalence of plastics (GLMM with binomial error and territory as random factor: Z = 2.79 $p = 0.005$), than pellets containing auks (GLMM Z = 7.57 $p < 0.001$).

The number of plastic items found per pellet also differed between seabird prey species. Pellets with fulmar remains contained the highest numbers of plastics (range 1-15), kittiwake pellets had 1-9 and auk pellets had 1-3. The pellets with fulmar remains contained 0.37 (95% CI = 0.17-0.62) plastic pieces which was significantly higher than for pellets with auks (mean of 0.08 pieces (95% CI = 0.04-0.16) for auks, GLM with negative binomial error $Z = 3.59$, $p < 0.001$).

The total plastic pieces per pellet weighed on average 6.6 (SD=5.97) mg (n=1,034 pellets including pellets with no plastic, mass abundance). The mean mass of the plastic in great skua pellets which contained plastic (mass intensity) was 116.5 (SD=225.0) mg per pellet (n=59). On average mass abundance, fulmar pellets contained 15.9 (SD=54.6) mg of plastic debris (n = 173), kittiwake pellets contained 2.2 (SD=15.9) mg of plastics (n = 293) and pellets containing auks remains had on average 5.2 (SD=28.9) mg of plastics (n = 151). Pellets containing fulmar remains did not have a significantly higher mass intensity of plastics as compared with other types of pellets (GLMM with territory as random effect Z = 0.916; $p = 0.916$), but pellets containing auk prey remains had significantly lower mass intensity compared to other types of pellets (GLMM Z = 2.29 $p = 0.022$).

Discussion

Less than a third (29%) of the great skua territories showed evidence of plastic ingestion, suggesting that a minority of great skuas at the Skúvoy breeding colony are exposed to plastics during the breeding season. This was not simply due to small number of pellets picked up in some territories as prevalence of plastic in a pair's diet was independent of the number of pellets collected. Only a small proportion of regurgitated pellets examined contained plastics (6%). Both user and industrial plastics were found in skua pellets. Among user plastics we found hard, threadlike, foamed and sheetlike plastics illustrating that great skuas are susceptible to multiple types of plastic pollution. Our findings suggest that plastic ingestion does occur among great skuas in the Faroes, but prevalence and number of plastic pieces ingested is low compared to other species in the North Atlantic and the North Sea (Provencher et al., 2014; van Franeker et al., 2011).

We found that the most common colour of plastic pieces in great skua pellets was white/yellow. Without knowledge of the background availability of plastics in the environment it cannot be determined if this shows a preference for debris colour among certain seabird species which the great skua preys on, or simply a sampling of the plastics available to the seabirds in the area. Future plastics work around the Faroes should combine at sea surveys of plastics (e.g. Desforges et al., 2014); with seabird assessments to determine if different seabirds selectively ingest different types and colours of plastics from the environment.

The number and weight of plastic particles found in pellets of great skuas from the Faroes was also relatively low. It should, however, be noted that individual dietary specialisation, which is commonly seen among great skuas (Votier et al., 2004), could potentially result in a low number of pairs taking up a disproportionally high amount of plastic-rich prey. For example, out of the 48 territories where pellets with plastic were found in this study, 12 territories had pellets with plastic on consecutive territory visits. Unlike petrels which accumulate plastic in the gizzard, due to their gizzard being separated from the proventriculus by a sphincter, skuas have an anatomy that allows them to regurgitate both gizzard and proventriculus contents (Furness, 1985). Although this would suggest that plastic does not likely accumulate in great skua stomachs (Furness, 1985), we should consider the implications for great skuas specialising as seabird specialists which may carry high loads of plastics could result in a chronic exposure to marine debris. Perhaps more importantly such chronic plastic ingestion could lead to increased exposure to persistent organic pollutants which are found in and on marine plastics (Hirari et al., 2011). More work is needed to assess the relationship between the high levels of persistent organic pollutants and plastics in Faroese great skuas (Teuten et al., 2009).

Plastic debris burden was found to be associated with prey species that are known to ingest plastics (e.g. fulmars; Jensen, 2012). Similarly, plastic debris was less in pellets that contained seabird species known to ingest low levels of plastics, for example puffins where stomach examination of these birds around the Faroes showed only 1-5% to contain plastic (Bergur Olsen, pers. comm.). Similarly, a recent examination of 14 adult kittiwake stomachs found 1 plastic thread, in each of two stomachs (Jens-Kjeld Jensen, pers. comm.). This difference in plastic debris load between species has also been found on a wider spatial scale (e.g. auks; Bergur Olsen, pers. comm.; Provencher et al., 2014). The association between plastics and prey type indicates that great skuas are taking in plastics with their seabird prey meals. Although great skuas may also ingest debris directly when scavenging, these results suggest that most of the plastic ingestion by great skuas is related to their seabird prey. Alternatively, if great skuas were ingesting plastics from other sources frequently, little difference would be expected in the plastics associated with the prey type; note that we found low levels of ingested plastic in pellets containing fish remains.

Our findings suggest that marine plastic pollution is being transferred up the food chain to top level predators in the North Atlantic that are likely ingesting most plastics indirectly through their prey items. Importantly, we show that plastic pollution is transferred to great skuas mainly through fulmars, although these seabirds are not the main proportion of the skua diet (Table 5.1). This suggests that plastic pollution may be transferred up the food chain disproportionately when prey species differ in propensity to accumulate marine debris. Additionally, these plastic particles are regurgitated on land and the fate and further implications for the terrestrial ecosystem remains unclear.

In the Faroes 91% of fulmar stomachs examined (n = 699) contained ingested plastics (Jan van Franker pers. comm.). While it is recognised that each fulmar ingested by a great skua produces approximately 4-5 pellets (Votier et al., 2001), and several great skuas may share a fulmar carcass as food at sea, the prevalence of plastic assessed directly in fulmar stomachs is much higher than we demonstrate for fulmar pellets in this study (13.4%). This suggests that great skua pellets may not be a reliable tool for quantitative assessment of plastic of their various prey species. Ryan and Fraser (1988) showed similar findings for the south polar skua (*Stercorarius maccormicki*), and suggested that smaller plastic pieces are not likely incorporated into pellets but pass through to the faeces, or are small enough to be lost from the pellets before collection. Votier et al. (2001) showed that proportion of auks consumed are underrepresented in great skua pellet production than larger gulls and fulmars. Considering this difference in turn-over rate between prey species it could perhaps suggest that there is more plastic in auks than we would expect, but this contradicts stomach analysis of Faroese puffins, which suggest that only 1-5% of puffins have plastic (Bergur Olsen, pers. comm.). Although overall trends of plastics ingestion in marine birds is found by examining skua pellets, the absolute amount of plastic ingestion is not quantitatively reflected in pellets.

One pellet containing mountain hare remains also contained plastics. As hares are herbivores that graze on low lying vegetation, the plastics associated with hare pellets are therefore unlikely to have come from hares. Thus, ingested plastics in great skuas may not be completely regurgitated with each meal, and may actually be retained over some period and regurgitated with future meals. It has been suggested that for instance fulmarine petrels excrete ca. 75% of plastic particles within a month ingestion (van Franeker and Law, 2015; but see Ryan, 2015). This may suggest that although great skuas may regurgitate plastics associated with their meals, plastic debris may remain within the digestive tract of great skuas beyond the meal and regurgitation, and the difference in plastic prevalence between prey species may be even bigger than suggested by our results. Therefore, even though skuas are not likely to accumulate plastics to the same degree as other birds that do not regurgitate (i.e. the fulmar), they may still be susceptible to accumulating debris and thus susceptible to the potential negative effects of ingesting plastics (Teuten et al., 2009; Yamashita et al., 2011).

While it must be recognised that quantitative assessment of plastic through regurgitated pellets may be confounded by various factors, we believe that the study of these plastic particles reveals relevant aspects of how plastic pollution moves in the food web. We show that bird species that are primarily ingesting plastic debris indirectly are still being exposed to plastic debris from the marine environment. This illustrates how plastic debris is being transferred up the food web in the marine environment, and that the potential impacts of ingested plastics may affect upper trophic level wildlife that prey upon species that directly ingest plastic pollution.

Table 5.1. Types of pellets and which contained plastic, and a modelled prevalence of plastic assuming a binomial distribution with 95% confidence interval and territory as random effect. [a] Other types of pellets included eggs, insects, sheep and terrestrial birds. [b] Computation of 95% CI for this category was not possible.

Prey type	Total number of pellets	Number of pellets containing plastics	Modelled plastic prevalence % (CI)
Fulmar	174	26	13 % (6,26)
Kittiwake	308	9	2 % (1,6)
Auk	181	10	5 % (2,10)
Mixed seabird	46	6	11 % (4,28)
Fish	98	4	3 % (1,11)
Mixed fish and bird	27	3	8% (2,27)
Mountain hare	11	1	8% (1,48)
Other[a]	189	0	0[b]
Total	1034	59	

Table 5.2. Mean number and mass abundance and standard deviation of different plastic types found in different pellet types. Prevalence is percentage of occurrence in pellets of that prey type.

	Prevalence	Number of plastics		Mass (g) of plastics		
	(%)	mean	sd	mean	sd	max
FULMAR (n=26)						
All plastics	15.0	0.532	2.101	0.0146	0.0297	0.2042
Industrial plastic	2.3	0.043	0.444	0.0008	0.0064	0.0329
User plastic	13.9	0.489	2.130	0.0013	0.0303	0.2042
Fragments	13.9	0.457	2.195	0.0020	0.0261	0.1723
Foamed	0.6	0.005	0.115	0.0022	0.0003	0.0022
Threadlike	2.9	0.027	0.245	0.0023	0.0253	0.2042
KITTIWAKE (n=9)						
All plastics	3.4	0.116	0.773	0.0024	0.0088	0.0868
Industrial plastic	0.3	0.003	0.062	0.0001	0.0011	0.0174
User plastic	3.4	0.113	0.772	0.0023	0.0087	0.0868
Fragments	3.1	0.102	0.771	0.0020	0.0080	0.0868
Foamed	0.3	0.003	0.062	0.0000	0.0001	0.0015
Sheet	0.3	0.003	0.062	0.0001	0.0025	0.0410
Other	0.3	0.003	0.062	0.0002	0.0030	0.0478
AUK (n=10)						
All plastics	4.6	0.106	0.408	0.0062	0.0236	0.1472
Industrial plastic	0.7	0.007	0.086	0.0002	0.0024	0.0277
User plastic	4.6	0.099	0.402	0.0060	0.0236	0.1472
Fragments	4.6	0.079	0.384	0.0046	0.0203	0.1472
Foamed	0.7	0.007	0.086	0.0005	0.0067	0.0784
Thread	0.7	0.007	0.086	0.0000	0.0005	0.0053
Other	0.7	0.007	0.086	0.0009	0.0117	0.1366
MIXED SEABIRD (n=6)						
All plastics	19.4	0.645	1.556	0.279	0.3022	0.0543
Industrial plastic	9.7	0.097	0.426	0.076	0.0131	0.0023
User plastic	16.1	0.548	1.696	0.305	0.3182	0.0572
Fragments	16.1	0.387	1.443	0.250	0.0057	0.0630
Foamed	3.2	0.161	1.390	0.259	0.3509	0.0010
FISH (n=4)						
All plastics	4.1	0.041	0.199	0.0014	0.0097	0.0909
Industrial plastic	1.0	0.010	0.103	0.0002	0.0020	0.0195
User plastic	3.1	0.031	0.174	0.0012	0.0095	0.0909
Fragments	3.1	0.031	0.174	0.0012	0.0097	0.0909
MIXED BIRD AND FISH (n=3)						
All plastics	11.1	0.148	0.362	0.0045	0.0167	0.0853
User plastic	11.1	0.148	0.362	0.0045	0.0167	0.0853
Fragments	3.7	0.037	0.204	0.0006	0.0035	0.0170
Thread	7.4	0.074	0.277	0.0034	0.0171	0.0853
Other	3.7	0.037	0.204	0.0005	0.0025	0.0122
MOUNTAIN HARE (n=1)						
All plastics	9.1	0.091	0.316	0.0042	0.0104	0.0332
Industrial plastic	9.1	0.091	0.316	0.0030	0.0105	0.0332
User plastic	9.1	0.091	0.316	0.0012	0.0042	0.0132
Fragments	9.1	0.091	0.316	0.0012	0.0042	0.0132

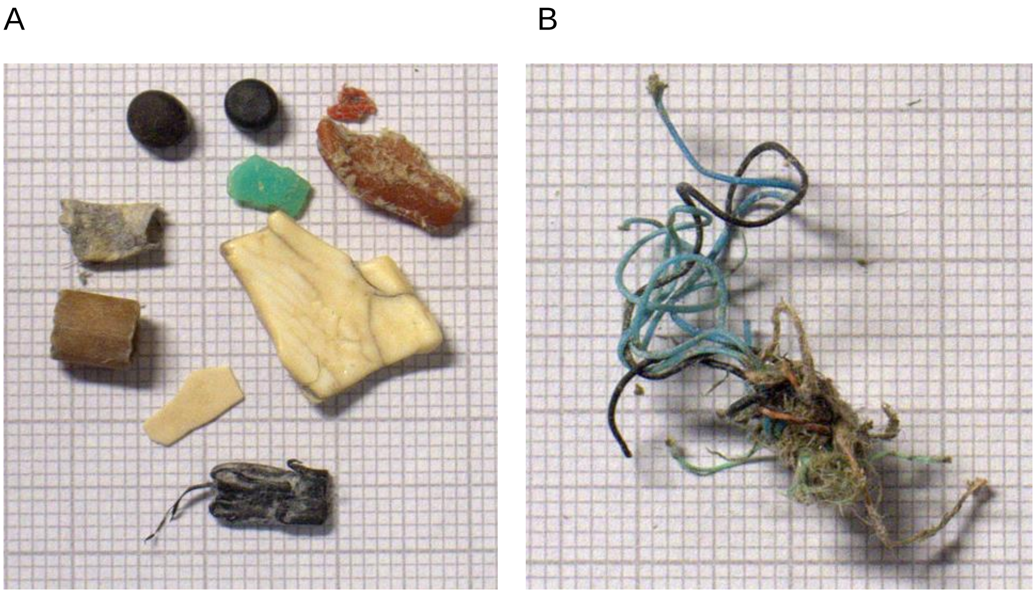

Figure 5.1. Sample of plastic debris pieces recovered from great skua regurgitated pellets. A – shows industrial plastics (two small black pellets at the top left), and hard fragment plastics. B – threadlike plastic pieces. Minor grid paper shows 1 mm by 1 mm dimensions.

6. General discussion

No detailed analysis has been undertaken of great skua breeding biology and diet in the Faroes for over 50 years. This study has in that regard provided some long overdue ecological information of a population which counts approximately 3.5-5% of the global population of great skuas. There are several new questions that can be tackled due to this gained insight, because despite the Faroes being relatively close to Shetland, the ecology of the great skuas of these two regions evidently differ quite markedly. The study of regurgitated pellets on Skúvoy found that a great majority of pellets were of seabirds or their eggs (84%). This makes this population ecologically quite distinct compared to the Shetland population, and allows us to test certain predictions in relation to bioaccumulative POPs (chapter 4). In comparison to Shetland, the Faroese great skuas feed on higher trophic scale, and this results in higher rates of bioaccumulation.

Individual dietary specialisation has been described in many seabirds including great skuas in Shetland (Votier *et al.* 2004), and this specialisation could be foreseen to explain a difference in pollutant exposure (both POPs and plastics) and in breeding performance (egg sizes, laying date etc). However, the diet of Faroese we did not find a significant relationship between occurrence of bird pellets (bird specialisation) and egg size, but we did find that bird specialist pairs had significantly earlier laying dates. Considering historical work, if food availability or diet can be the cause of this decline in great skua egg sizes, we would expect to find a relationship between individual (pair) diets and their egg sizes. The study of the diet of great skuas on Skúvoy over two consecutive seasons in the Faroes has shown that although many pairs can be described as bird specialists, they did not lay significantly larger eggs. Other studies have however shown this (Votier *et al.* 2004). The feeding experiment was undertaken with this in mind, and my prediction was that a supplementary food prior to egg laying would result in larger eggs. This was not observed, but I found that supplementary feeding significantly decreased the egg size dimorphism. This would suggest that either the second laid egg which usually is slightly smaller, benefits from the supplementary feeding, or the feeding stimulates a response in the females egg investment. This would certainly warrant further study. If it is the case that the second laid egg is smaller due to energetic depletion, then this would suggest that the second laid egg was a better measure of female quality, and would also possibly have implications on the use of eggs for biomonitoring of pollutants.

In chapter 3 I investigated the spatial and temporal variation in great skua eggs. While the spatial variation generally adheres to Bergmann’s rule, there are Reproductive investment can be understood as a compromise between fixed and flexible factors. The fundamental premise of monitoring breeding ecology is that some factors are flexible and may be influenced by a combination of intrinsic and extrinsic factors. The main focus of this study has been to expand our understanding of ecological variables which may or may not influence the egg production of great skuas. Great skua eggs vary highly in size 84 cm^3 – 151 cm^3 (1.82 ratio smallest:largest). This variability is large also in comparison to other birds (Christians 2002), which should provide a promising prospect in understanding the mechanisms which underlie egg sizes and shapes. This allows for study of some of the potential causes of these individual variations. Food availability have been hypothesised to cause an overall decline in egg sizes of puffins and glaucous gulls. Great skua eggs have also been found to be smaller now than a few decades previously, and I have found this trend to be consistent both in the Faroes and Shetland.

Both these populations may be under some dietary constraint – in Shetland due to decline in fisheries and reduction of bycatch discarding, and in the Faroes through the decline of their typical prey species, kittiwake, puffin, guillemot and perhaps also fulmar. We did also supplementary feed some pairs, but were not able to detect significant difference in any breeding parameter. Stable isotope analysis of chick down feathers did however successfully detect a distinct carbon profile of the pairs which had successfully fed on the supplementary food. With a relatively low protein content, it is possible that the food was simply not of a high enough quality to influence the egg sizes.

Stable isotope analysis did also provide an opportunity to investigate post-moult wintering areas. Considering the importance of trophic level pollutant exposure of great skuas, it should become a particular priority to disentangle the relationships between wintering area and breeding the following season. Stable isotopes which have been analysed for this study, have indicated that great skuas from the Faroes winter in 2 or 3 different areas. Investigating the impact of these on pollutant uptake, fitness and carryover effects upon breeding would be an avenue worth pursuing.

The relatively higher trophic level of Faroese great skuas is also the most likely explanation of the difference found in POPs concentrations between these two regions (Chapter 5). But this study also found a significant temporal reduction in POPs concentrations compared to samples from the 1970s. The comparison of nitrogen isotope values of this study with published values in another study can be contentious, as the lack of a baseline value makes the data uncomparable. However the POPs concentrations are also significantly higher, which is also consistent with the Faroese great skuas feeding on a higher trophic level.

Their high trophic level, yet opportunistic lifestyle means that great skuas predate on a variety of seabirds in the Faroes, and wider region. This would also provide a future testable hypothesis that great skuas in the Faroes are likely to consume more plastic than great skuas in Shetland for example, even though the occurrence of plastic is higher around the North Sea than around the Faroes (van Franeker *et al.* 2011). It can at least be inferred that the rate of plastic consumption is lower in Shetland great skuas since plastic in pellets has so far not been observed to the extent that it has been noted, despite extensive fieldwork done in Shetland over the past 3 decades. This suggests that diet can potentially result in differences in pollutant uptake and will get deposited into their eggs. With an estimated number of plastic in the world's oceans numbering between 15 and 51 trillion particles (van Sebille *et al.* 2015), and especially with a projected "plastic gyre" in the Barents sea (Cózar *et al.* 2017), great skuas will be uniquely well suited species to monitor – assuming that they prey on other seabirds. Chapter 5 lays the foundation for great skuas to be a top predator monitoring species for seabird ingested plastic in the Northeast Atlantic, and this area of research could benefit greatly with a more extensive geographic comparison of regurgitated pellets from across the breeding range of the great skuas.

As top predators in the Faroese ecosystem, great skuas continue to be relevant for biomonitoring. Future work should emphasise the influence of wintering areas upon pollutant exposure, and the rise of emergent pollutants such as Bisphenol, pharmaceuticals, perfluorinated compounds. To understand emission and transport of marine plastic among seabirds, great skuas pellets from throughout their breeding distribution will be investigated in the future. Although no indications of acute toxicity such as eggshell thinning were detected in our study, other studies have shown that a combined effect of high pollutant load and low food availability can have a negative influence on reproductive success.

While low reproductive success at some of the largest great skua colonies in Shetland is the most likely cause of population declines of great skuas, persecution is currently the most likely driver of population change in the Faroes. The Faroese great skua population is historically high, and this has over the past years also resulted in an increase in great skua culling. The perception of the great skua as a threat to sheep and seabirds persists. Future research focus on the positive aspects of great skuas such as soil enrichment could potentially alleviate some of the negative sentiment towards them. A growing interest in the Faroes as a tourist destination, could potentially also be beneficial to public perception of them. Public awareness of the ecological importance of predators and scavengers in general would probably benefit the conservation of great skuas, arctic skuas, corvids and gulls in the Faroes.

In conclusion, although this thesis has advanced our understanding of the great skua diet and how the diet influences their pollutant load, there remains great uncertainty with regards to explanatory factors behind the temporal variation in great skua egg sizes. The supplementary feeding experiment did not significantly influence the egg sizes, however it did reduce the egg dimorphism. I am in this study unable to disentangle if this reduction in egg size dimorphism was due to the nutritional quality of the supplementary food, or the act of feeding the female may have manipulated its egg investment. This, in my view is the most compelling indication that there remain unexplained variables determining egg sizes, and that this question should be tackled with future experiments or field studies. While the use of great skuas and their eggs as biomonitors of marine pollution is well established, this study illustrates the importance of considering potential dietary variation on a relatively limited spatially scale. Gaining further understanding of the type of plastic which is consumed by great skua prey, could be developed into a very cost:effective way of monitoring multiple species in the Northeast Atlantic, and is certainly an avenue worth pursuing.

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