Using the thick-billed murre (*Uria lomvia*) as an indicator species of Arctic marine ecosystems

Émile Brisson-Curadeau

Natural Resource Sciences
Agricultural and Environmental Sciences
McGill University, Montréal

Submitted April 2018

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Science in Renewable Resources

Preface

This Master's project was supervised by Dr. Kyle Elliott, from Macdonald campus of McGill University. The thesis' purpose was to explore how the thick-billed murre (*Uria lomvia*) could be used as an indicator species of the Arctic by developing methods to facilitate the monitoring of murres, and by describing its foraging behaviour, a crucial component for the use of an indicator species.

This article-based thesis is divided in three chapters. First, the use of drones to survey murres is examined to provide tools to quickly and efficiently monitor the at-colony behaviour of this indicator species. This chapter was published in *Scientific Reports* in 2017. The second chapter links the social aspect of murres with their foraging behaviour, as the distributional pattern of an indicator species is often used to infer ecosystem health. This chapter was submitted to Marine Biology in 2018. The third chapter looks for direct applications of how the thick-billed murre's foraging behaviour could be used to obtain the distribution patterns of lower trophic level organisms occurring in Arctic oceanic ecosystem. This chapter is to be submitted to the journal The Auk in 2018. The introduction is based on a paper published in Frontiers in Marine Science in 2017.

Contribution of coauthors

I designed, conducted and analyzed all experiments of this thesis with the help of Dr. Kyle Elliott, with the minor exception of the few common murre (*Uria aalge*) observations from chapter 1, which were reported by the coauthors of the publication (David Bird, Paul Pace, Richard Sherley, Dave Fifield and Chantelle Burke). Coauthors of chapter 2 (Akinori Takahashi and Grant Gilchrist) provided crucial help with the complicated logistics of wildlife studies in the Arctic and commented early versions of the manuscript. Pierre Dutilleul helped with the statistic of chapter 2. Coauthors of the paper used for the introduction helped with the writing. I am the first author of all papers presented in this thesis. Along with all coauthors of the papers, the thesis was only possible with the help of many people, which are mentioned in the acknowledgment section.

Abstract

Climate change will have many effects on the Arctic marine ecosystem, including the disturbance of the aquatic species composition and fish population dynamics. Seabirds could be used as indicator species to help us assess the changes occurring in the ocean. The thick-billed murre (*Uria lomvia*), a deep-diving seabird that breeds in colonies, is a potential candidate indicator species of the Arctic marine ecosystem. For example, at-colony information (breeding success and colony attendance) could be correlated with prey availability, therefore providing crucial information on the ecosystem's health. Furthermore, at-sea foraging behaviour of murres could be used to monitor the marine environment by using aggregations of foraging individuals to detect fish hotspots or by combining diet and distribution of murres at sea to obtain distribution maps for the different fish species. However, much needs to be done before these applications become possible. For at-colony measures, better sampling techniques are needed, such as drone surveys. However, the impact of drones on murre behaviour as well as their accuracy for surveys is still unknown. For at-sea measures, the mechanisms that underlie foraging aggregations and prey selection need to be better understood to be associated correctly with prey abundance. I studied these poorly known aspects in three ways, separated into three chapters. In the first chapter, I assessed the impact of drones on the behaviour and breeding success of thick-billed murres. I found that the impact of drones on the breeding success of murres is negligible, while its accuracy for colony counts is better than observations from the ground. In the second chapter, I determined what factors cause foraging aggregations of murres. At a small scale, foraging aggregations were most likely formed by groups of murres actively foraging together to increase searching efficiency, while at the large scale foraging aggregations were driven by individuals converging at foraging hotspots. In the third chapter, I examined the factors contributing to prey selection by individual murres. Prey selection was driven by the spatial distribution of prey, where some locations were more conducive to the capture of certain prey types than others. In summary, my results facilitate the use of thick-billed murres as indicators for the Arctic marine ecosystem by proposing guidelines for the use of drones in colony monitoring, as well as clarifying the mechanisms underlying foraging aggregations and prey selection at-sea, which is crucial if murres are to be used as indicator species.

Résumé

L'écosystème marin de l'Arctique risque grandement d'être affecté par les changements climatiques, notamment en ce qui attrait la dynamique des populations animales aquatiques. Les oiseaux marins pourraient servir d'indicateur de ces changements, puisqu'ils sont intiment liés à la faune aquatiques. Le guillemot de Brünnich (*Uria lomvia*), un oiseau plongeur nichant en colonie, est un bon candidat d'espèce indicatrice des milieux marins de l'Arctique. Par exemple, des informations récoltées à la colonie même (succès reproducteur, présence à la colonie) pourraient être corrélées avec l'abondance des proies, nous fournissant ainsi des indices sur l'état de santé de l'écosystème marin. Il en va de même les agrégations de guillemots en mer, qui pourraient servir à localiser les bancs de poissons. Ou encore, en combinant la diète des guillemots avec leur utilisation de l'espace d'alimentation, nous pourrions obtenir indirectement des cartes de distributions des proies. Cependant, un manque de connaissance à plusieurs niveaux empêche l'utilisation à son plein potentiel des guillemots comme espèce indicatrice. Par exemple, la récolte de données à la colonie reste laborieuse, et une meilleure méthodologie telle que l'usage de drones doit être implémentées pour faciliter l'échantillonnage. Cependant, l'effet des drones sur le comportement des guillemots, ainsi que l'exactitude des informations qu'ils récoltent restent à déterminer. Pour les informations récoltées en mer, les mécanismes d'agrégation et de sélection des proies doivent être mieux compris pour qu'une association adéquate des comportements des guillemots avec les populations de poisson soit possible. J'ai tenté d'éclaircir ces aspects peu étudiés en trois façon, divisé en trois chapitres. Dans le premier chapitre, j'ai tenté de déterminer l'impact des drones sur les guillemots ainsi que leur

précision pour le dénombrement d'individus. J'ai découvert que l'impact des drones sur les guillemots est minime, alors que leur précision et efficacité pour le dénombrement d'individus sont nettement supérieures à celles des techniques traditionnelles basées sur l'observation au sol. Dans le deuxième chapitre, j'ai définit les facteurs qui causent l'agrégations des guillemots s'alimentant en mer. La formation d'agrégations des guillemots en mer était dictée à l'échelle locale par la formation active de groupes favorisant la recherche de nourriture, alors qu'à l'échelle globale, elle était formée par la convergence des guillemots vers les « hotspots » d'alimentation. Dans le troisième chapitre, J'ai étudié les facteurs responsables de la sélection des différents types de proies. Cette sélection des type de proies par les guillemots s'opérait spatialement, puisque certains endroits étaient plus propices à la captures de certaines proies que d'autres. Mes résultats facilitent l'utilisation des guillemots de Brünnich comme espèce indicatrice des milieux marins de l'Arctique en proposant des recommandations et clarifications quant à l'usage des drones pour la collecte de donnée en colonie, et également en mettant en lumière le comportement des guillemots lors de l'alimentation en mer, une étape cruciale à réaliser pour que cet oiseau marin puisse être utilisé comme sentinelle des mers.

TABLE OF CONTENTS

Acknowledgment

I thank all the people who have help me in the field: Tianna Burke, Will Black, Bruen Black, Graham Sorenson, Sara Poole, François St-Aubin, JH Martin, Scott Flemming, as well as my labmates, especially Thomas Lazarus, Allison Patterson, Esteban Gongora and Shannon Whelan (pronounced as “Whale”-an). I thank J. Nakoolak for saving my skin from polar bears in the field (and making good panik bread).

Tony Gaston, Pierre Dutilleul, Allison Patterson, committee members Grant Gilchrist and Murray Humphries, Guillaume Larocque from QCBS, GIS team Kristen Lalla, Filip Rakic, Eric Ste Marie and Francis Van Oordt as well as all members of the weekly “lab meetings” have all helped me with the analysis and development of ideas.

I thank the Northern Scientific Training Program, Canada Research Chair in Arctic Ecology, Polar Continental Shelf Project, Pacific Seabird Group, Canadian Society of Ornithologists and the Arctic Institute of North American for funding. R. Amstrong at the Nunavut Research Institute and M. Janssen at Environment Canada who helped with field logistics. I also thank Akinori Takahashi for giving us a camera logger

I thank all my family and friends for supporting me throughout those two years. Especially my mom, dad, as well as my mother-in-law Sylvie De Blois for guiding me through the McGill system. A special thanks to my girlfriend Lisa Galantini for encouraging me constantly.

Finally, a big thanks to my supervisor Kyle Elliott, who encouraged me throughout my master whenever I came up with an idea (the good and the bad ones!). He also gave me tons of opportunities: thanks to him, I have travelled the America and learned so much about birds!

List of tables

List of figures

Introduction and literature review

Note on the introduction

The introduction corresponds partly to the paper titled "Tracking Cairns: Biologging Improves the Use of Seabirds as Sentinels of the Sea", published in Frontiers in Marine Science (Brisson-Curadeau et al., 2017a), which was made in collaboration with Allison Patterson, Shannon Whelan and Thomas Lazarus, all from McGill University. It was adapted to be more specific to the topic of the thesis.

Climate change and the Arctic

Climate change is disproportionately affecting the Arctic (NOAA, 2017). The warming of the water in this region is occurring faster than almost everywhere else in the planet, with some parts of the Arctic warming at a rate of 0.5°C per decade (Timmermans, 2015). Sea-ice, critical to many aquatic animals (Lønne and Gulliksen, 1989; Meier et al., 2004), is disappearing at a fast pace, and sea-ice in September will likely vanish before the end of the 21st century (Boé et al., 2009). Still, the Arctic environment remains difficult to sample and the consequences of those changes are difficult to forecast. Some fish species may decline due to changes in the environment and habitat, while others may increase (Poff et al., 2002). The vanishing of summer sea-ice will also affect unevenly primary and secondary production (Slagstad et al., 2011), as well as bringing consequences to the distribution of higher trophic level animals (Wyllie-Echerrieva and Wooster, 1998). Furthermore, global warming will upset trophic interactions (Häder et al., 2007), and some marine animal species will be found at higher latitudes (Daufresne et al., 2009).

Traditional sampling

To monitor and mitigate these changes, traditional methods using fishing vessels or scientific boat surveys are possible. However, these methods are costly and time consuming, often requiring days of active sampling only to obtain a single snapshot of the fish distribution and abundance of a region (Marchand et al., 1999; Simard et al., 2002). These methods also introduce bias caused by the method of capture and the scale of the fisheries (Kleiber and Maunder, 2008; Richards and Schnute, 1986; Rose and Kulka, 1999). For instance, the most widely used metric derived from fisheries data to obtain fish abundance estimate, Catch Per Unit Effort (CPUE), is only representative of a small proportion of the fish population and may miss life-stages that are important for predictive models (Salthaug and Godø, 2000). Finally, boat surveys create risks for biologists and crew members, as two large ships sink every week worldwide (Casey, 2010).

Indicator species

An alternative to traditional sampling methods is the use of an indicator species. An indicator species is defined as a species that provides indirect information about an ecosystem (Rolstad et al., 2002). Indicator species are useful in ecosystem-based management, as they reduce sampling effort while still providing valuable information on the health of the environment. There are various applications of indicator species to ecosystem monitoring. For example, the presence of certain plant species can indicate the quality of a habitat (Peterken, 1974). Similarly, bird species composition can reveal the level of grazing in an environment (Bock and Webb, 1984). As a final example, the diet diversity of top predators such as otters can give clue on the habitat complexity of rivers (Ruiz-Olmo and Jiménez, 2009). Consequently, indicator species provide an array of possible indices useful for monitoring the environment, including ecosystem health, habitat composition and contaminant levels. The Arctic is critically in need of an indicator species that could provide, at low cost, accurate information about the changes in distribution and abundance of aquatic animals living in the Arctic Ocean (Meehan and Divoky, 1998; Montevecchi, 1993).

Seabirds as indicator species

The idea to use seabirds as indicator species has been around for a long time, and is still highly discussed (Brisson-Curadeau et al., 2017a; Cairns, 1988; Piatt et al., 2007). There are multiple ways that seabird species can be used to gain insights about changes in aquatic fauna. First, at-colony measures, such as breeding success, chick growth and colony attendance, can be used to approximate prey abundance and distribution. For example, breeding success (number of chicks fledged per pair) of some species of seabirds, like kittiwakes and penguins, is sensitive to low levels of prey availability, with reduced breeding success recorded in poor years (Crawford et al., 2006; Cury et al., 2011; Oro and Furness, 2002). Similarly, chick growth can be lower in very poor years, as has been demonstrated with common murres (*Uria aalge*; Österblom et al., 2006). Finally, colony attendance can also correlate with prey availability, as shown in the common murre, with individuals spending more time away from the colony when prey are scarce (Harding et al., 2007; Piatt et al., 2007). In the Arctic, those at-colony variables might be used to assess food supply. However, better observation and sampling techniques are needed to monitor the at-colony parameters previously mentioned. Colony attendance for example, is mostly measured by ground observers, which is time-consuming, especially in the context of long-term monitoring. Drones have been proposed as alternatives to ground observers. Advances in technologies have made drones cheaper and more accessible, with off-the-shelf models readily available for science. They can quickly survey colonies and obtain information on the colony attendance (Goebel et al., 2015; Grenzdörffer, 2013; Ratcliffe et al., 2015; Zmarz et al., 2015) and breeding success (Ratcliffe et al., 2015) of seabirds. Additionally, drones may reduce the risk of injuries, which can be high for biologists working on cliffs. However, two problems arise when using drones to monitor seabirds: (1) their impact on the behaviour and breeding success of seabirds is unknown, so that scientists are reluctant to use such technologies; and (2) the accuracy of drones when counting seabirds is still debated. Thus, drones are seldom used in seabird studies, and this potentially useful tool for the monitoring of indicator species is not employed to its full potential. Research on these concerns would facilitate the use of at-colony measures to infer on prey availability by potentially providing evidence on the efficacy of drones.

Another way to obtain information on prey availability using seabirds is by recording their at-sea foraging behaviour. For example, at-sea aggregations of seabirds, like petrels or penguins, are often easier to monitor than the prey with which they spatially associate (Fauchald and Tveraa, 2006; Pichegru et al., 2010), and therefore can be used to provide information on the distribution of fish and invertebrates. Those at-sea aggregations of seabirds can be monitored by boat (e.g. Fauchald et al., 2000; Ainley et al., 2005; Scott et al., 2010; Zamon et al., 2014), but the same problems described earlier associated with such techniques still remain (i.e. cost, efficiency, etc.). With the development of logging technologies, however, the distribution and spatial use of seabirds can be obtained quickly and efficiently. Table i.1 summarises the literature where biologgers were used to associate foraging behaviour of seabirds with food supply. The applications of biologging to the monitoring of the marine ecosystem are plentiful: GPS-equipped birds have, for example, provided insights about where fish schools were located, and how these fish schools are changing spatially and temporally (Croll et al., 2006; Weimerskirch et al., 2005). Biologgers are also useful tools for demonstrating how seabirds adjust their foraging behavior to fish stocks and distributions, sometimes showing strong correlations (Bertrand et al., 2012; Boyd et al., 2015; Cohen et al., 2014; Litzow and Piatt, 2003). Three of those studies found a linear correlation between fish stocks and foraging parameters (Bertrand et al., 2012; Cohen et al., 2014; Litzow and Piatt, 2003), which suggests that foraging distance from the colony, diving depth, and diving activity may be good candidate parameters for detection of changes in food supply. The fourth study (Boyd et al., 2015) found a relationship between foraging and prey vertical distribution (rather than fish stocks). While the behaviour of birds likely reflects prey availability, the exact shape of the relation (linear, non-linear) is often difficult to determine due to the short temporal scale of studies, with very few studies having access to long-term datasets of fisheries data for validation (Angel et al., 2015; Monaghan et al., 2008; Pichegru et al., 2010; Suryan et al., 2002).

The link between fish stocks and seabird distribution likely varies among species (Cairns, 1988). For instance, studies examining two species of albatrosses and one species of petrel found correlations between the distribution of birds and prey (Catry et al., 2004; Fauchald and Tveraa, 2006; Weimerskirch et al., 2005), while one study on penguins found no relationship between foraging effort and fish stocks (Croll et al., 2006). Another study of Cape gannets (*Morus capensis*) found a relationship only with primary productivity, rather than fish stocks (Grémillet et al., 2008). Thus, species may vary in their responses to food supply in both colony-based reproductive parameters and biologger-derived foraging parameters. Other factors may also add variation to the observed patterns, which would also be true for at-colony measures. For example, differences among colonies likely play a role in the variation in responses observed. More research is needed on more species and colonies to better understand what factors influence such variation. The shape of the relationship between biologger-derived parameters and fish stock also varies depending on the parameter considered. While this relation seems to be linear for some parameters (Bertrand et al., 2012; Cohen et al., 2014; Litzow and Piatt, 2003), other parameters are non-linear. For example, seabird energy expenditure is often thought to be at a ceiling over a large range of food supply (Elliott et al., 2014a). Years with low food supply may prevent birds from expending high energy while birds may not need to expend high energy expenditure during years of high food supply.

Seabirds can finally be used as indicator species in a third way. As some seabirds are generalist predators, they could not only provide general information about the location of prey hotspots, but also help us understand the distribution of the different fish species. Therefore, by combining diet information with the foraging behaviour and feeding locations of seabirds, we could obtain more detailed information about the habitat selection for each species of fish that are preyed upon by seabirds. As an example, the spatial distribution of different prey species in northern Hudson Bay near a colony of seabirds was exposed using solely the combination of diet information and foraging behaviour of those seabirds (Elliott et al., 2009a).

Table i.1: Studies that used biologgers to link seabird foraging parameters to food supply (from Brisson-Curadeau et al., 2017a)

Metric of food supply estimated	**Behavioral parameter**	**Species of seabird**	**Relationship between metric of food supply and behavioral parameter**	**Citation**
Temporal abundance of fish	Time budget	*Uria aalge*	Foraging trip duration and dive frequency increased in years of low prey abundance	Monaghan et al., 1994
Temporal abundance of fish	Time budget	*Cepphus columba*	Time spent diving increased in years of low prey abundance	Litzow and Piatt, 2003
Spatial distribution of fish	Spatio-temporal distribution	*Thalassarche chrysostoma*	Individuals spatially associated with areas of predictable prey concentrations	Catry et al., 2004
Spatio-temporal distribution of fish	Spatio-temporal distribution	*Diomedea exulans*	Individuals spatially and temporally associated with specific prey types	Weimerskirch et al., 2005
Temporal abundance of fish	Time budget; foraging effort	*Pygoscelis antarctica*	Foraging effort (i.e., length and number of foraging trips per day; dive depth, rate and duration) did not vary among years with varying prey abundance	Croll et al., 2006,
Spatio-temporal distribution of fish	Spatio-temporal distribution	*Thalassoica antarctica*	Large-scale prey hotspots had a turn-over within weeks, while small-scale hotspots had a turn-over within days	Fauchald and Tveraa, 2006
Temporal abundance of fish	Time budget	*Rissa tridactyla*	Foraging trip duration and distance increased in years of low prey abundance	Suryan et al., 2006
Spatial distribution of area with high primary productivity and fish abundance	Spatial distribution	*Morus capensis*	Individuals spatially associated with areas of high primary productivity, but not with areas of high fish abundance	Grémillet et al., 2008
Spatial-temporal abundance of fish	Time budget	*Spheniscus demersus*	Foraging trips duration and distance decreased after closure of purse-seine industrial fishing, relative to the year before the closure and other colonies where fisheries continued; dive metrics did not change across colonies or years	Pichegru et al., 2010
Temporal abundance of fish	Time budget	*Sula variegata*	Foraging distance and dive depth increased on days of high fishery activity	Bertrand et al., 2012
Temporal abundance of fish	Time budget	*Morus capensis*	Foraging distance increased in years of low prey abundance	Cohen et al., 2014
Temporal abundance of fish	Energetic expenditure; time budget	*Morus serrator*	Energetic expenditure per foraging trip increased in years of low primary productivity; foraging trip duration and distance did not vary in response to prey abundance	Angel et al., 2015
Abundance and spatial distribution of fish	Probability of diving at a given location	*Phalacrocorax bougainvilliorum*	Individuals dove more often when prey were located at shallow depth, but not necessarily when the relative abundance of prey was higher	Boyd et al., 2015

Study species

The well-studied thick-billed murre (*Uria lomvia*), an Arctic seabird of the family Alcidae, is a potential candidate for being an indicator species. First, it is one the most abundant seabird in the Arctic, with up to 20 million individuals distributed across the Arctic (Gaston, 1998). As warming occurs across the Arctic, the thick-billed murre could provide crucial information about changes in the environment at a large and extensive scale. Second, murres are cliff-nesting seabirds breeding in populous colonies of up to 1.5 million individuals (Brown et al., 1975). These aggregations provide large sample sizes readily accessible for scientists to study, and therefore facilitate the application of this species as an indicator. Third, thick-billed murres are generalist diving predators that forage up to 150 m deep (Elliott et al., 2008a), and so are in immediate contact with several species of the Arctic aquatic fauna. The versatility of their diet can provide potential information about the health and species composition of the environment.

The recent advances in biologging technologies have permitted to unveil many aspects of this seabird. For example, its foraging ecology was previously poorly known, as this bird feeds itself far at sea and in deep waters, where it is hard to observe. Temperature- and depth-recorders (TDR) have permitted to better understand the underwater behaviour of the thick-billed murre when feeding. Searching strategies are now known, with individuals increasing the chances of capturing a bigger, benthic prey when increasing underwater search time (Elliott et al., 2008b, 2009b). TDR have also revealed how different the strategies can be within individuals, for example when an individual changes its dive depth depending on the water type, mixed or stratified (Takahashi et al., 2008), or across individuals, with different foraging behaviour driving diet specialization (Elliott et al., 2008a; Woo et al., 2008). Devices that measure the second and third dimensions of space, such as GPS loggers, have led to the detection of even larger foraging specialisation, where the location of a whole colony could lead to not only different foraging behaviour, but also different morphological traits optimizing a given foraging specialization (Harding et al., 2013; Paredes et al., 2015). Another aspect of the thick-billed murre that was previously unknown prior to the biologger revolution is energetic balance and behavioural optimisation. Again, TDR-GPS loggers played an important role (Linnebjerg et al., 2014), making possible discoveries, such as direct evidence for Ashmole's halo, whereby individuals foraging further from the colony dive shallower than those diving in the vicinity of the colony (Elliott et al., 2009a). However, fine-scale movements and energetic costs could only be exposed with the emergence of accelerometers. Accelerometers, for example, demonstrated that the level of activity is greater during pelagic dives than during bottom dives, as individuals tend to chase more during pelagic dives (Elliott et al., 2009c), and that head-winds affected the energy costs of prey delivery to the chicks, therefore also affecting the prey type delivered (Elliott et al., 2014b).

Biologgers have also permitted the study of an important aspect of this species: ecological partitioning. While GPS loggers have revealed that the thick-billed murre uses yearlong different habitat than the closely related common murre (Linnebjerg et al., 2015; McFarlane Tranquilla et al., 2015), TDRs have shown that the segregation is also vertical, with thick-billed murres using shallower layers of the water column (Kokubun et al., 2015). Ecological segregation also exists between sexes, with male thick-billed murres feeding on more predictable food sources, and having reduced chick-provisioning effort near the time of fledging in anticipation of the post-fledging parental care given exclusively by the male (Elliott and Gaston, 2014; Elliott et al., 2010). Finally, loggers have helped with the conservation of seabirds. GPS have indeed identified zones of wintering and breeding foraging hotspots for the application of protection zones (Gaston et al., 2011, 2013; Montevecchi et al., 2012).

Still, much needs to be learned about the foraging behaviour of thick-billed murres before its entire potential as an indicator species can be realized. While this species could provide critical information on the ecosystem through the sampling of at-colony parameters, like breeding success and colony attendance, there is no methodology yet to collect efficiently this information. The use of drones to collect efficiently these measures is highly relevant for this species, as ground counts of colonies numbering in the hundreds of thousands is time-consuming. However, studies looking at the effect of drones on murres are lacking. Furthermore, no previous studies have looked at the accuracy of drone counts on cliff-nesting birds, where the breeding environment is much more complex in terms the spatial organization than the few flat-ground nesting seabirds for which the accuracy has been studied (Goebel et al., 2015; Grenzdörffer, 2013; Ratcliffe et al., 2015; Zmarz et al., 2015).

Thick-billed murres, like most seabirds, are known to associate tightly with their prey (Fauchald et al., 2000). Therefore, murres could be used as indicators of the Arctic Ocean by providing information on the spatio-temporal distribution of prey, although the intrinsic social nature of murres is rarely taken into account when associating groups of foraging murres with prey abundance. For example, are at-sea groups always formed through the aggregations of prey, or do birds actively form groups, independently of prey distribution? While the use of murres to understand prey distribution is promising, there needs to be better understanding of how at-sea aggregations of thick-billed murres are formed and maintained to better interpret at-sea behaviour and its association with the food supply.

Combining diet information with the foraging behaviour of thick-billed murres to obtain information on the different fish species is also a possible avenue. Indeed, diet information on individual thick-billed murre prey can easily be obtained at the colony via direct observations of adults coming back with prey items to feed their chicks (Elliott et al., 2008a; Hipfner et al., 2006), stable isotopes of tissues (Hobson, 1993) or via analyses of the stomach content (Provencher et al., 2013). By coupling the diet extrapolated from these techniques with the foraging distribution of murres, we could potentially obtain information on how each prey type is distributed at-sea. Furthermore, by attaching depth-loggers to birds, which collect information on a third dimension – below the surface – we could understand better the habitat use of the different prey species (Elliott et al., 2008a). Still, much needs to be learned before these methods are implemented. For example, it is unknown whether murres truly associate spatially with the different prey types, or how they select the different prey types for their diet. Moreover, the foraging behaviour of murres during incubation is different from the foraging behaviour during the chick-rearing period, with individuals increasing their foraging effort during the chick rearing period to compensate for the rise in energy demand (Benvenuti et al.; Davoren and Burger, 1999; Elliott et al., 2008c; Ito et al., 2010). Thus, the breeding period has to be taken into account when using foraging behaviour to obtain information on prey species distribution. More research is needed to understand why changes in behaviour within the breeding period occur.

Objectives

The objective of the project is to develop methods and acquire information that would facilitate the use of thick-billed murres as indicators of environmental changes in the Arctic Ocean, as well as adding to the general knowledge of the seabird foraging ecology. The first chapter aims to facilitate the monitoring of indicator species using drones by measuring their impact on the behaviour and breeding success of thick-billed murres, and by assessing the accuracy of drones to survey cliff-nesting birds. I also seek to provide recommendations and guidelines on how to use such technologies with seabirds. My research sheds light on the role that UAVs have in the monitoring of indicator species. Potentially, my research will promote a new and efficient way to collect information on colony attendance and breeding success, which can be related to prey abundance. I hypothesise that taking off and flying the drone farther from the nests will greatly reduce their impact on thick-billed murres' behavior and breeding success. I also hypothesise that drones are more accurate to survey plots of breeding murres, especially the denser ones, due to their ability to obtain the best angle for bird counts.

The second chapter examines how and why at-sea aggregations of foraging murres are formed at multiple scales, and relates the aggregations with the different foraging strategies used by this seabird. The study will help the interpretation of thick-billed murre clusters, which is currently used to infer prey distribution without considering social behaviour and foraging strategies. Our hypothesis is that murres actively travel and forage together to increase foraging success, so that areas containing small-scale aggregations of murres cannot be interpreted as dense prey hotspots. At a larger scale, we hypothesise that groups of murres converge on foraging hotspots, therefore providing a good proxy of fish abundance.

Finally, the third chapter examines how individual murres select different prey types through different foraging behaviours. Understanding of murre prey selection will allow fish species maps to be extrapolated from thick-billed murre behaviour, by coupling data-loggers with information on diet. Our hypothesis is that individuals actively select different prey types by choosing different foraging locations. Furthermore, we investigate the difference in foraging behaviour between the incubating and the chick-rearing period to facilitate the interpretation and association of murre foraging behaviour with the different prey types. We hypothesise that birds will dive deeper during the chick-rearing period to compensate for the energetic demand of the chicks.

Chapter 1: Seabird species vary in behavioural response to drone census

Note on this chapter

This chapter correspond exactly to the paper titled "Seabird species vary in behavioural response to drone census", published in Scientific Reports (Brisson-Curadeau et al., 2017b), which was made in collaboration with David Bird from McGill University, Chantelle Burke from Memorial University, Dave Fifield from Environment Canada, Paul Pace and Richard Sherley from University of Exeter. Although it focuses mainly on establishing methods and guidelines to survey thick-billed murres using drones, it also contains section on three other species: Iceland gull *Larus glaucoides*, glaucous gulls *Larus hyperboreus* and common murres *Uria aalge*. The data on common murres were collected by the coauthors. The sections on those three other species are minor and were kept in the chapter, as they still provide general guidelines for the use of drones to collect at-colony information on cliff-nesting seabirds.

Abstract

Unmanned aerial vehicles (UAVs) provide an opportunity to rapidly census wildlife in remote areas while removing some of the hazards. However, wildlife may respond negatively to the UAVs, thereby skewing counts. We surveyed four species of Arctic cliff-nesting seabirds (glaucous gull *Larus hyperboreus*, Iceland gull *Larus glaucoides*, common murre *Uria aalge* and thick-billed murre *Uria lomvia*) using a UAV and compared censusing techniques to ground photography. An average of 8.5% of thick-billed murres flew off in response to the UAV, but >99% of those birds were non-breeders. Counts of breeding pairs were more accurate with drones, especially on denser ledges. We were unable to detect any impact of the UAV on breeding success of murres, except at a site where aerial predators were abundant and several birds lost their eggs to predators following UAV flights. Furthermore, we found little evidence for habituation by murres to the UAV. As for gulls, most flew off in response to the UAV, but returned to the nest within five minutes. Counts of gull nests and adults were similar between UAV and ground photography, however the UAV detected up to 52.4% more chicks because chicks were camouflaged and invisible to ground observers. UAVs provide a less hazardous and potentially more accurate method for surveying wildlife. We provide some simple recommendations for their use.

Introduction

The number of individuals in a population has long been recognized as a key parameter in population ecology (Schnabel, 1938; White, 1996; Zippin, 1958). In most cases, it is not possible to completely census wild organisms and the estimated number of individuals is derived by correcting the counted population to account for animals not sampled (Cook et al., 1967; Yoccoz et al., 2001). Furthermore, in remote areas, such as the Arctic or deep ocean, it is logistically difficult, expensive and hazardous to conduct wildlife surveys. In fact, boat and air accidents are the main cause of job-related mortalities for wildlife workers in the United States (Sasse, 2001). Unmanned aerial vehicles (UAVs), commonly referred to as drones, provide an opportunity to quickly sample more individuals in inaccessible environment, increasing the proportion of individuals observed and therefore the accuracy and precision of the population estimates, while improving security of biologists (van Andel et al., 2015; Anderson and Gaston, 2013; Hodgson et al., 2013; Koh and Wich, 2012; Sardà-Palomera et al., 2012).

While the potential benefits of UAVs are widely recognized (Linchant et al., 2015; Marris, 2013; Mcclelland et al., 2016; Ratcliffe et al., 2015), the use of such vehicles also faces some potential drawbacks. First, early models required experienced operators, were prone to crashes and were often illegal even if widely used. The legality of unmanned aerial vehicle use has become clearer in many jurisdictions while technological advances have greatly simplified and improved operation (Junda et al., 2015). Second, UAV observations may influence the behavior of wildlife and potentially bias the number of individuals counted (Ditmer et al., 2015; Grenzdörffer, 2013); the effect of UAVs on wildlife behavior has meant that wildlife agencies are reluctant to grant permits and that population estimates may be inaccurate. However, some wildlife show minimal reaction to UAVs and/or habituate rapidly to their presence (Chabot and Bird, 2015; Vermeulen et al., 2013), potentially allowing for accurate population estimates (Hodgson et al., 2013). Given the growing use of UAVs by professional ecologists, amateur wildlife photographers and nature enthusiasts, guidelines for the ethical use of UAVs are increasingly needed (Vas et al., 2015).

Colonial birds are one group of organisms where UAVs may be particularly suited for population surveys. Because many nest on flat ground or on cliffs, seabirds can be easily photographed and counted by a UAV. In contrast, the limited perspective of ground observers, usually standing in blinds, makes it difficult to fully census cliff-nesting species. Aerial surveys with human observers are another alternative, but can be dangerous and expensive, especially on remote islands where seabirds often occur. Recent work on terns (*Sterna* spp.) showed that UAVs can provide less variable estimates of tern numbers (Hodgson et al., 2013), and that terns quickly habituate to vehicles (Chabot et al., 2015). Similarly, another study on waterbirds showed little behavioral response to UAVs (Vas et al., 2015).

To develop an effective method for counting cliff-nesting Arctic seabirds using UAVs, we examined its effect on breeding seabirds and compared counts made from the UAV with those made from observer-based photography. Environment and Climate Change Canada

(ECCC) has a well-researched protocol for assessing changes in populations of Larus gulls and murres (Uria spp.) (Gaston et al., 1986, 2012). Those protocols have been used for over 40 years, and are based on counting standardized plots within colonies. However, because of the difficulty of accessing some locations, estimates for many colonies have not been completed since the 1970s (Gaston et al., 2012). The ECCC protocol is based on correcting the number of birds present by accounting for the proportion of birds present likely to be reproducing (breeding pairs). That correction factor is referred to as the k-ratio, and is estimated to be ~0.7 for murres and ~1.0 for gulls (Gaston et al., 2012). In other words, 70% of murres and 100% of gulls on the cliff are breeding. Typically, the k-ratio varies with time of day because birds usually forage at the same time of day, and declines with date because young, non-breeding birds arrive later in the breeding season (Gaston et al., 2012). The k-ratio may also vary across the colony, as plots with many non-breeders ("loafing ledges") have especially low k-ratios (Gaston et al., 2012). Continuing the earlier research on k-ratios developed from observer-based counts, we addressed a series of questions: How do seabirds respond to UAVs? Do they habituate, and how quickly? Does the approach direction or distance matter? Are UAV counts comparable to those derived from traditional census techniques and are they more or less variable?

Methodology and Results

The study was conducted on thick-billed murres (Uria lomvia), a model-species for Arctic seabirds. In addition to the experiments on thick-billed murres, observations from three other surveys using UAVs as a secondary tool were added to this paper. These surveys were conducted on common murres (Uria aalge), on glaucous gulls (Larus hyperboreus), and on Iceland gulls (Larus glaucoides). As these differentiate from the main experiments on thick-billed murres for being opportunistic observations with low sample size, they should only be interpreted as additional considerations. To simplify the comprehension of these experiments, we separated the methodology and results for each species. All methods were approved through the Canadian Wildlife Service permit (permit number: NUN_SCI_16_03_Elliott) and the Wildlife Research permit emitted by the Department of

Environment of the Government of Nunavut (permit number: 2016-036). All methods were performed in accordance with the Canadian Council of Animal Care norms and the Transport Canada legislations.

Thick-billed murres

Methodology

Two arctic colonies were chosen for being the most accessible and studied colonies in Canada: Coats Island west murre colony (62°56′52.20″N, 82°01′03.70″W) and Digges Island colony (62°33′27.23″N, 77°43′18.20″W). We ran experiments between 18–23 July 2016 at Coats Island and 28 July to 10 August 2016 at Digges Island, using a drone Phantom IV (DJI, Shenzhen, China), equipped with an in-built 12 M pixel camera (20 mm lens). At Coats, we estimated the effect of the vehicle on nest failure rate by monitoring six plots (each with 60 to 200 pairs of murres) daily for five days before and two days after one to five days of flights. Plot monitoring consisted of watching the murres from a blind and recording which individuals had an egg on each day (Gaston and Nettleship, 1981). Thus, daily nest failure rate could be calculated. As a polar bear (*Ursus maritimus*) eliminated all eggs on two plots prior to the first UAV flights, we eliminated those two plots from statistical analyses of reproductive success. Those two plots were kept in the analysis of murre’s response to UAV, as they represented a good opportunity to study plots with low k-ratio. All plots were less than 20 m from a blind.

To examine the behavioral response of murres on these six plots to the UAV, we slowly flew the UAV toward the breeding plot until the horizontal distance from the plot was either 15 m or 30 m, let it hover long enough to take a picture, and then flew the UAV back (Fig. 1.1). The UAV started either on the edge of the cliff directly above the plot (~15–20 m above the plot) or 30 m further along the edge of the cliff. In the latter case, we also approached the plot either from above (flew the UAV up in the air, then brought it to 15 m or 30 m horizontal distance from the plot, then lower for the plot photo) or from below (lowered the UAV, brought it to 15 m or 30 m horizontal distance from the plot, then raised it for the plot photo). The sequence of flight patterns was randomly attributed. In all cases, the drone and the pilot were not visible for murres during the take-off. While the pilot was controlling the UAV, a second person recorded the number of birds flushing by videotaping (about 60 s) the plot from a blind and counting the number of birds leaving the colony using the recording. The ratio of birds flushing was then obtained by dividing with the total number of birds seen in the video. To examine habituation at small-scale, we repeated the previously described flights every five minutes for 4–6 flights on all six plots (and videotaped for one minute prior, during and one minute following each flight). We made the assumption that all flushed birds would come back to their nest within five minutes. On two plots, we repeated those same procedures for four and six consecutive days respectively, to examine habituation. Observers were invisible to birds at all times, either hidden behind the cliff face or in a blind. Assessment of the k-ratio prior to the flights were made by estimating the percentage of non-breeders in a plot. Birds without eggs or chicks were considered to be non-breeders.

We used the UAV to count 16 plots of ~30 to ~200 pairs. At Digges, we had the opportunity to repeat flights similar to Coats four times per day (09:00, 12:30, 16:00, 20:00) to evaluate the repeatability over time. In addition to the counts using the UAV, birds were counted by taking a photograph (Panasonic fz-1000) and by sight, using the same plot-counting technique in use for Arctic monitoring over the past 40 years (Bryant et al., 1999; Gaston, 2003). It took about two hours to count all plots once using both methods. This includes 15 minutes per plot for the UAV and 12 minutes for the ground method. It is important to note that the UAV method was not faster, only due to the fact that we walked the UAV between each plot (to synchronize with the ground counts) rather than scanning once all the plots with the UAV.

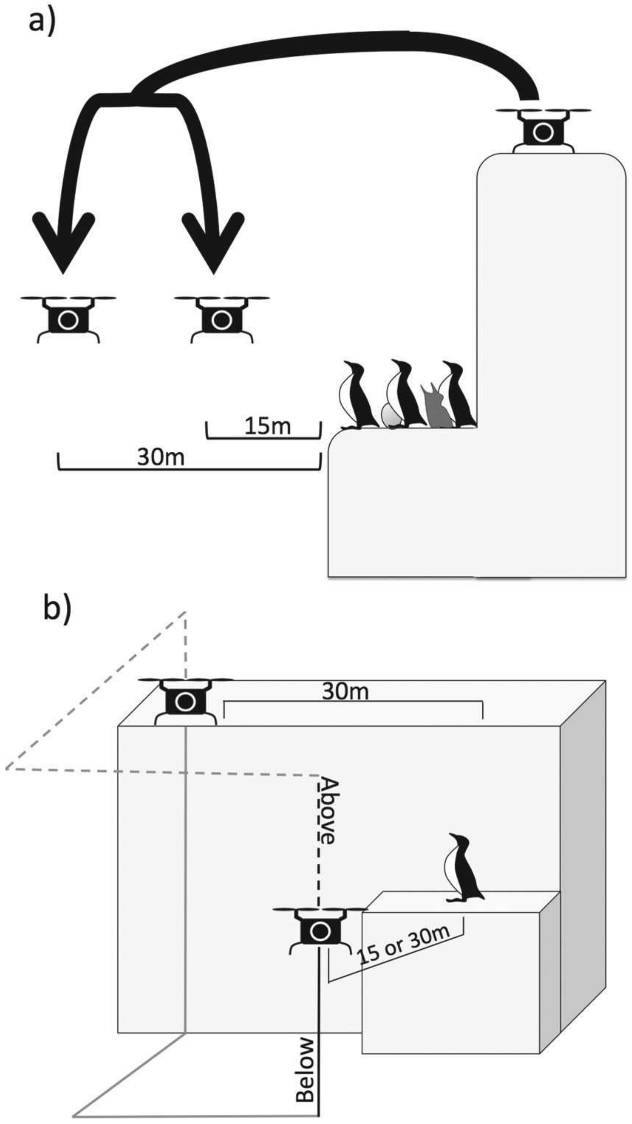


Fig 1.1 : Representation of every approach of the plots with the UAV. (a) Take-off directly above the plot, with in-flight distance of 15 or 30 m to the plot. Birds with chicks or eggs are noted as breeders, while others are noted as non-breeders. (b) Take-off 30 m away from the plot. Emphasize of the two approaches possible: from above (dashed line) and from below (full line). The final darker lines for both methods represent when the birds are most likely to see the UAV. As with a), the UAV can stop at either 15 or 30 m to take the picture, and the ratio of non-breeder is also noted.

All statistical analyses were done in R 3.1.2 (R Core Team, 2014). The packages nlme (Pinheiro, Bates, DebRoy, Sarkar and R Core Team, 2016) and AICcmodavg (AICc – Mazerolle, 2016) were also used. Thirty linear models using 5 explanatory variables were created to analyze flushing intensity of thick-billed murres in response to a flying UAV. Flushing intensity was quantified as the proportion of murres flushing from a plot from the moment of takeoff to the moment of landing. To achieve normality and account for the bounded nature of proportion values, we logit-transformed proportion data prior to analyses. The explanatory variables were: the number of previous flights on the same day of the on-going observation (i.e. short-term habituation), take-off distance from the plot, in-flight distance from the plot, the average ratio of non-breeding birds in the plot (which are bound to react differently to approaching danger), and the angle of approach (either from above or from below). We also included interactions, based on the possible biological explanations. Models were ranked using the Akaike Information Criterion corrected for small sample size (Burnham et al., 2011). Two variables were not included directly in the model, but rather in a separate analysis: 1- habituation over a long period (days) which was not included directly in the models, as high winds allowed us to only repeat the flights for three days or more at two plots 2- time of day, which could be consistently recorded at different time only in Digges Island, due to the conditions at Coats Island.

To examine the influence of UAVs on reproductive success, we used paired t-tests to compare site failure rates on days with UAV flights to days without UAV flights. The same test was also used to detect differences between ground counts and UAV counts relative to the time of the day. Prior to using parametric statistics, we tested for normality by inspecting the distribution of residuals from general linear models. We used an alpha level of 0.05. All averages are presented ± SD.

Results

Take off distance, in-flight distance and the ratio of non-breeders on a plot were retained in the best linear model to explain the flushing behavior of murres. Angle of approach and all interaction terms were not retained in the best-fit models. As for habituation over a short period, it was present in the third ranked model, which had a small delta-AIC of 1.76

compared to the best-ranked model. However, its relative importance (RI) compared to the other three retained variables was low (0.20), suggesting this variable was not important for our model. The ratio of breeders was positively correlated with flushing (slope = 0.033 ± 0.005, RI = 1.0), while Take off distance (slope = −0.056 ± 0.008, RI = 1.0) and in-flight distance (slope = −0.026 ± 0.015, RI = 0.65) on the other hand, were negatively correlated with flushing (Fig. 1.2). On average, 8.5% of birds flushed. Most of those birds (>99%) that flushed did not have eggs and were thus considered non-breeders. Observations using the UAV thus had higher k-ratios, as less non-breeders were counted. Five minutes after the series of flights, the majority of birds seemed to have returned to the plot, while all had returned after ten minutes. Flushing intensity stayed constant (SD = 0) within all plots monitored for several consecutive days and thus no habituation was detected. Nest failure rate averaged 0.11 ± 0.05% sites/d on days without vehicles compared with 0.09 ± 0.07% sites/d on days with UAV (t3 = 0.31; P = 0.78). We did not directly observe the loss of any egg within 1 hour following the vehicle flights.

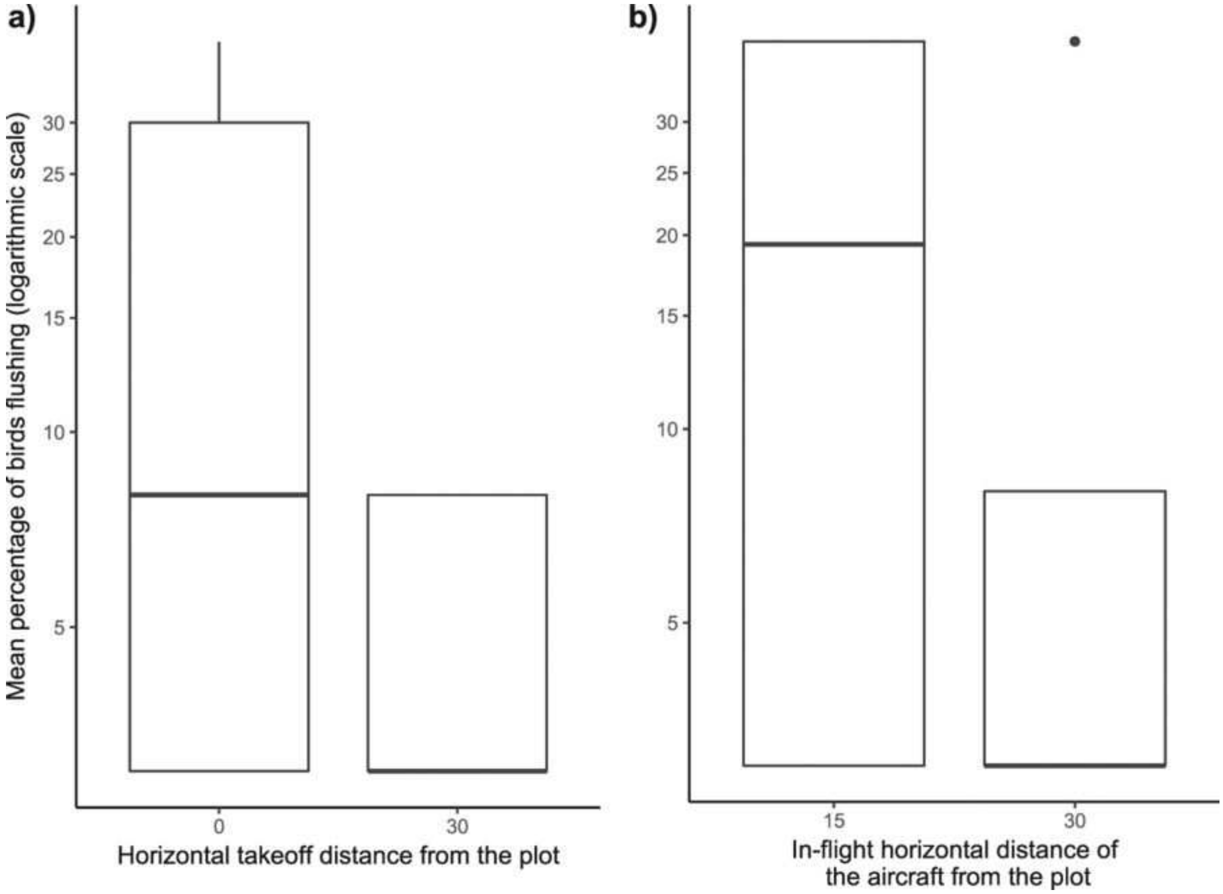


Fig 1.2: Boxplot of percentage of thick-billed murres flushing when (a) the UAV took off either 15–20 m directly above the plot at 0 m horizontal distance or 30 m away; (b) the UAV hovers at 15 m or 30 m from the plot surveyed. Y-axis was transformed with log10 to stretch the graph for visual purposes.

Counts were higher with the UAV than by sight, despite murres flushing from the plots when the UAV took off (t69 = 4.02; p < 0.01, see Fig. 1.3). The ratio of birds counted by UAV to those counted from the ground increased with density (t38 = 3.04, P < 0.01), and decreased with non-breeder density (t69 = −3.19, P < 0.01). In high-density plots (+100 birds), an aerial view with the UAV counted more birds, even if some murres flushed (Fig. 1.4a). In low density plots (−80 birds) with many non-breeders (+15%), counts were sometimes higher on the ground, especially at the end of the day, when proportionally more non-breeders were present at the colony. In these cases, few extra birds were counted with the better angle of the UAV and this could not account for the flushing birds (Fig. 1.4b). In low density plots with few non breeders (−10%), neither flushing nor aerial viewpoint were determinant factors, and counts on the ground (with camera or by sight) were similar to those using the UAV (Fig. 1.4c). Counts done on ground didn't show more variability throughout the day, as the coefficient of variation (CV = 12.5%) was similar to the counts done by the UAV (CV = 11.6%).

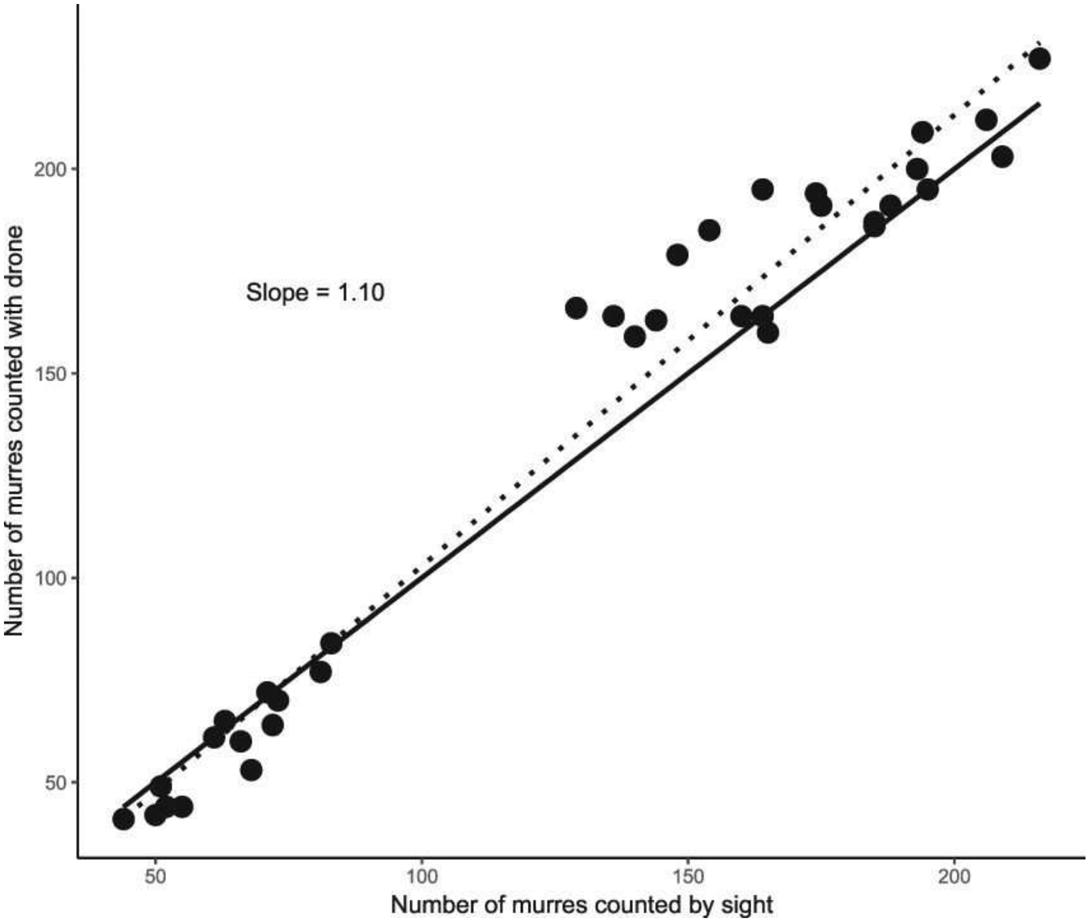


Fig 1.3: Comparing counts of thick-billed murres done by sight with counts done with the UAV. Dotted line represent the least squares regression while the filled line shows the line of 1:1 equality.

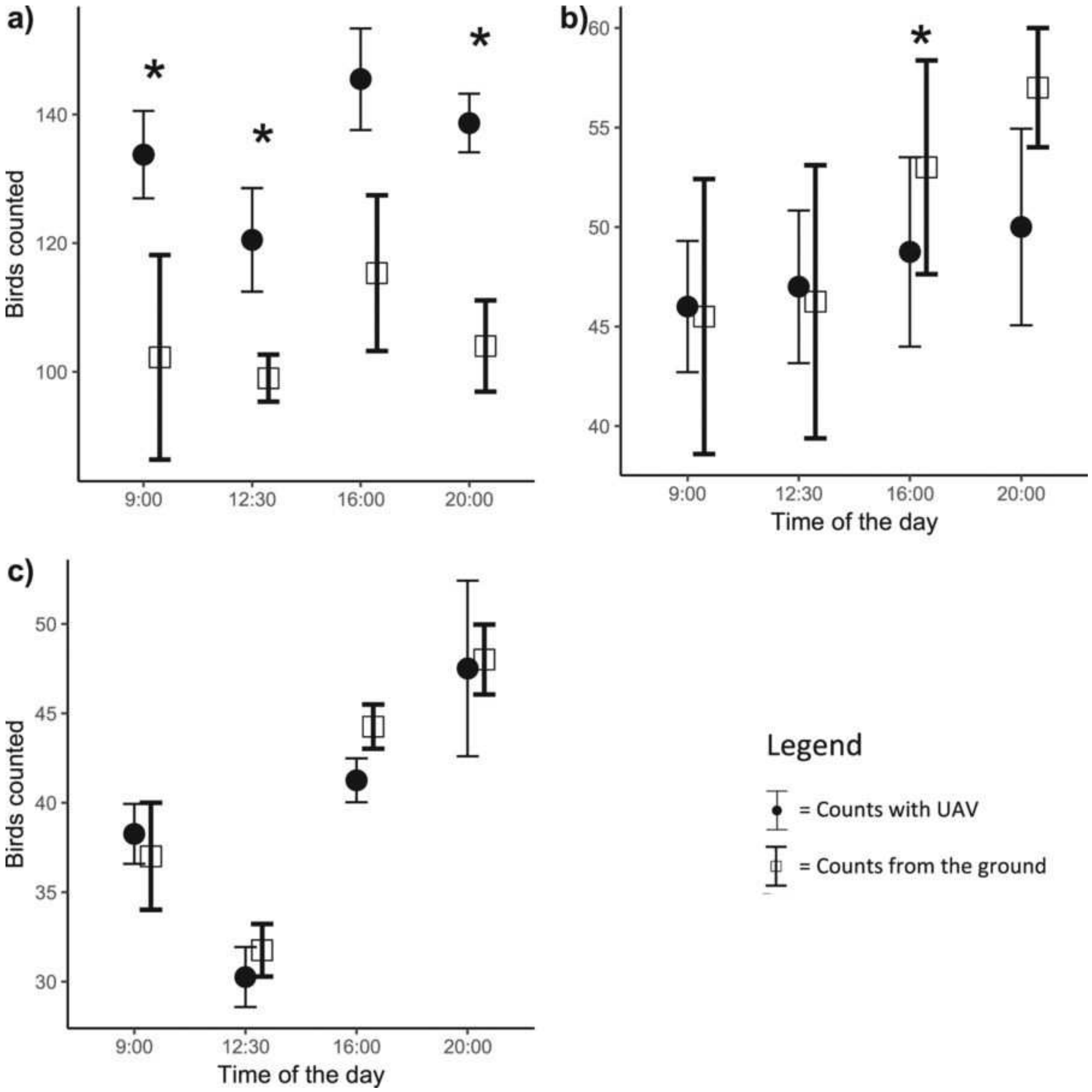


Fig 1.4: Thick-billed murres counted throughout the day from the ground and with the UAV, in (a) an example of very dense plot with few non-breeders (~0%), (b) an example of plot with low density, but with a considerable portion of non-breeders (~20%) (c) an example of plot with low density and few non-breeders (~0%). Stars indicate if a group is significantly different than its associated group for the same time of the day. Vertical bars represent 95% confidence intervals.

Glaucous gull

Methodology

Some scattered glaucous gull nests subsist within the thick-billed murre colony of Coats Island. Therefore, when flying the UAV for the thick-billed murre experiment, we also noted the behavior of glaucous gulls. Furthermore, as regular ground surveys of the glaucous gull population are conducted at Coats, we decided to use the drone to count all glaucous gull nests and chicks on 20 and 23 July 2016 for comparison with the ground surveys.

Results

We counted 16 nests and 20 chicks from the ground, compared with 16 nests (+0.0%) and 23 chicks (+15.0%) from the UAV. The adult glaucous gulls did not appear to respond to the UAV, whether it was during flights for the thick-billed murre experiment or for the glaucous gull survey. Thus, k-ratios were identical from site and UAV for gulls, but the number of chicks was underestimated by sight.

Common murres

Methodology

Experiments on common murres were conducted at the sub-Arctic Gull Island, Newfoundland (47°09′36″N, 52°27′36″W). A Spyder X8 (SkyHero, Brussels, Belgium) was flown four times for reconnaissance between 19h30 and 20h30 on 18 June 2015 and 5 July 2016 at an altitude of 25 m above the ocean and a flight speed of 5 m/s, each separated by five minutes, at 80, 50, 30 and 25 m horizontal distance from the colony. We thus videotaped the murres to record their reaction to the UAV. On each flight, we flew past two subcolonies on the southeast side of the island, and estimated the number of birds flushing from the cliffs. In 2016, we established a study plot on June 29th that included 40 breeding sites with incubating adults on the southwest side of the island. Over a four-hour observation period on June 30th, information relating to all observed flushing events were recorded including time of day, apparent cause of disturbance (gulls, observers, tour-boats, eagles), and total number of focal adults with eggs remaining on the study plot after each disturbance event.

Results

In 2015, 82% of murres remained after the first pass (80 m distant), followed by 81% (of the initial count) on the second pass (50 m), 83% on the third pass (25 m) and 78% on the fourth pass (20 m). We observed no birds with eggs leave the colony in response to the vehicle. In 2016, most birds frequently flushed when humans approached or made abrupt movements, even prior to UAV surveys. This year happened to be marked by the presence of four bald eagles (*Haliaeetus leucocephalus*) foraging near the colony. Therefore, many eggs were subsequently taken by herring (*L. argentatus*) and great black-backed (*L. maritimus*) gulls. Specifically, during baseline observations on 30 June, 12 large flushing events were observed over a 4-hour period (08:30–12:30), primarily attributed to gull disturbance (no eagles were seen). Disturbance involved widespread, synchronous flushing of non-breeding murres, but incubating murres did not abandon during any flushing event and no eggs were lost. During the single UAV flight, 93% of non-breeding birds within the established study plot flushed as the UAV approached the colony and 10% (4 of 40 active breeding sites) were lost. Adults were observed abandoning all four sites, resulting in egg displacement (n = 2) and subsequent egg predation (n = 2) by herring gulls. On 5 July 2016, the UAV was struck on the right front quarter with enough force to break the propellers by a single herring gull (*Larus argentatus*). This happened after passing the colony on the way back to land, about 75 m past the colony as it flew over gull nests with young chicks. The data telemetry logs indicate the UAV was working perfectly up to the point it was struck. The gull involved in the collision was seen flying away after impact, apparently unharmed. This incident ended the field experiment at Gull Island.

Iceland gull

Methodology

One ground survey is organized annually at the Coats Island gull colony (62°48′13.33″N, 82°03′53.99″W) to count the Iceland gulls that nest in the area. We seized the opportunity to use the phantom IV to surveyed adults and chicks on 17 July 2016 for comparison. We flew the UAV three times for five to ten minutes at one subcolony and a single time at two other subcolonies.

Results

Across all subcolonies, we counted 92 birds, 57 nests and 21 chicks from the ground compared with 94 birds (+2.2%), 57 nests (+0.0%) and 32 chicks (+52.4%) with the UAV. The gulls immediately alarmed upon the arrival of the UAV 32 ± 5 m from the cliffs. However, all birds had returned to the cliffs within 3.3 ± 1.2 mins

Discussion

Robots are increasingly being used in ecology (Grémillet et al., 2012; Guigueno and Sealy, 2011; Le Maho et al., 2014; Patricelli et al., 2002), and our study shows their promise for surveying wildlife. Using small, cheap (~$1600 US) rotary UAVs, we were able to accurately survey the number of breeding cliff-nesting birds at remote colonies, including one species of murre and two species of Larus gulls. Given that murres and gulls are well-known for their willingness to flush in response to human presence, we were surprised that breeding birds generally did not flush, and we could make accurate counts of the number of breeding birds on study plots. The only exception was in Newfoundland when the presence of eagles likely made the birds skittish, and a great number of breeding birds flushed in response to the UAV and lost their eggs. Thus, in contrast to an earlier study that found a similar response to UAVs among three species (Vas et al., 2015), we found substantially different behaviors for the four species studied. While we show that UAVs can be used to accurately survey several species of birds, we also show that they can lead to substantial behavioral disruption and inaccurate counts when aerial predators are common. Vas et al. (2015) found that angles of attacks similar to those used by aerial predators caused greater flushing. We recommend pilot studies that examine behavioral responses prior to actual surveys, especially under conditions where the UAV may be perceived as an aerial predator.

Iceland gulls, which typically scold nest predators, were the most reactive at first to the UAV with most individuals flying off their nests. However, because all birds returned to their nest after about three minutes and counts with the UAV were accurate, we believe using UAVs is a reliable way to survey those cliff-nesting birds. Moreover, we counted more offspring with the UAV than from the ground, presumably because the offspring tended to hide behind boulders and were well camouflaged with the background. From the ground, it was often hard to view the nests except through a telescope from a great distance. The UAV could approach the nest within a few meters with little apparent response from the chick, and we could consequently search for the offspring with a high resolution image that could be tilted or moved in search of offspring. Apart from the incident with the herring gull in Newfoundland, no bird approached the UAV close enough to create high risk of collision, including glaucous gulls and peregrine falcons (*Falco peregrinus*) nesting among murres, even when it was 5–10 m from their nest. We believe a UAV approach is thus safe for both parties, as long as the UAV pilot has reasonable experience.

For non-scolding birds (murres), the flushing behavioral response was greater for non-breeders than for breeders. Breeding birds are tightly programmed to stay on their site for potential nest defense (Gilchrist, 1999), while non-breeders are not attached to a specific breeding site, and will easily fly away when disturbed. We were able to efficiently mitigate flushing for these birds by starting the UAV far from the plot, while in-flight distance reduced flushing by less than 4% as birds flushed primarily in response to the starting noise of the drone. Flying the UAV farther away from the plot to mitigate flushing also reduced image quality and increased time spent counting. Counting from a greater distance would require a better camera, with a larger lens and consequently a larger UAV. The larger UAV may cause more disturbance; McEvoy et al. (2016) noted that a larger UAV caused waterfowl to move rapidly away when approached closer than 40–60 m. We recommend that a distance of 20–25 m for surveying cliff-nesting birds with a small (2 kg) UAV. Future research could examine the trade-off between a larger UAV (larger, higher resolution camera), murre flushing and distance from the colony needed for sufficient resolution.

Angle of approach did not appear in the best-fit model explaining thick-billed murre flushing ratio. In contrast, Vas et al. (2015) found that vertical approaches caused substantially more flushing than oblique angle approaches for waterbirds in a flat wetland. For cliff-nesting birds, where a vertical angle of attack may be less associated with predation, angle of attack is apparently less important. Larus gulls habituated after ~3 min, so we recommend taking survey photographs after at least 3 min for those species to allow for accurate censuses of the number of adults, nests and offspring. In contrast, we found no evidence for habituation over short (min) or long (days) scales in murres, and so we do not advocate for multiple flights to reduce flushing. We also suggest that researcher take into account the presence of predators in the area before using UAVs, as bird response could be excessive in that case and a high level of nest desertion might be observed.

Mitigation of flushing by birds may however not always be ideal for surveys. Because population censuses are usually considered to be counts of breeding pairs (Hatch and Hatch, 1989; Hipfner, 2005), the flushing of the 20% of non-breeders that occurred when we flew the UAV potentially reduces the coefficient of variation for the k-ratio, possibly leading to more accurate estimates. Similarly, counts of both temperate and tropical seabirds from UAVs averaged similar numbers to ground observers, but UAV counts were less variable due to reduced impact of geography and animal behavior on count numbers (Hodgson et al., 2013). Much of the past efforts to provide accurate population indices for Arctic seabirds have focused on reducing variability in k-ratios so that counts can be easily converted into numbers of breeding pairs (Gaston and Nettleship, 1982; Gaston et al., 2012). The proportion of non-breeders present is typically highest in the evening when pairs switch over their attendance duties, and when food availability is highest (late season in late-ice years, mid-season in early-ice years) and varies from year to year such that the proportion is high in years of high food availability (Gaston and Nettleship, 1982; Gaston et al., 2012). By flushing many non-breeders, that source of variability is reduced by the UAV. The ability of the UAV to reveal otherwise hidden breeding birds from a ground perspective also adds accuracy to the counts.

Another advantage of the UAV is to quickly survey parts of the colony that are inaccessible. In the field, counts from the UAV for all three species could be completed by an observer stationed at one site in a few minutes, whereas ground counts typically took 1–2 hours for each species and required travelling considerable distances. Scaled up to an entire colony (~1 million birds), the time-saving could be dramatic. For instance, we photographed half of the Coats colony (~7500 breeding pairs) at close range in about 4 h (EBC, unpubl. data). This operation can take days in inclement weather if the ice isn't secure for ground photos from the sea (Kampp, 1990). A UAV survey would then not only take less time, but may also be more accurate and less expensive. Moreover, of the 20 days we attempted to make censuses in 2016, we were only unable to fly on two days, although on several other days we could only survey sheltered areas of the colony. In Newfoundland, we were able to fly only a few hours out of the 10 days we had planned for surveys, mainly because of strong winds. Such issues could be overcome by using a fixed wing UAV that could fly in a larger range of wind conditions.

While we have focused on whether or not accurate surveys are possible, additional ethical concerns must be addressed for amateur photographers or enthusiasts. Repeated visits by humans are known to cause stress to wild animals, even if no obvious behavioral signs are observed. For example, bears showed strong physiological responses to UAVs even when there were seldom behavioral changes (Ditmer et al., 2015). Additional research on heart rate or other components of stress beyond flushing in birds could provide additional information to guide ethical guidelines for the use of UAVs.

We provide the following recommendations for the use of UAVs to survey cliff-nesting seabirds. Those recommendations are likely a strong starting point for surveying other wildlife:

(1) Given the species-specific responses, baseline tests are essential to determine whether wildlife disperse in response to UAVs, especially where avian predators are common.

(2) For gulls, a period of 5 min for habituation to small rotary UAVs is essential prior to counts.

(3) For murres, small rotary UAVs should be flown at a distance of at least 20 m and with a take-off outside of the hearing range of the colony. The UAVs are nonetheless likely to cause flushing in plots with high levels of non-breeders.

These recommendations apply mostly to small UAVs (<2 kg), similar to those used in the studies. We recommend that further research be conducted in the subject. More precisely, we suggest that future research focus on what exactly in the rotary-winged UAV (sound of wings, shape, etc.) causes bird to flush. We also recommend that further research compare the rotary-winged UAV with the fixed-wing UAV, as the latter might serve as an alternative in stronger winds.

Conclusion

Our study adds to the recent but growing body of literature that measure the reaction of wildlife to UAVs, and illustrate that, if used appropriately, UAVs can accurately survey wildlife without excessive disturbance (Gilchrist, 1999; Junda et al., 2015, 2016; Vas et al., 2015). Our results on cliff-nesting birds could be extrapolated outside the Arctic ecosystem. In difficult-to-access habitats, such as marshes, UAVs could be a better option for surveying populations than traditional methods. Although the camera resolution for small drones is only capable of detecting large birds and mammals from a distance, the rapid improvements in UAV technology promise to open new avenues for accurately surveying wildlife in remote habitats. Given the variation we observed among species, we recommend that preliminary work examining the level of disturbance to wildlife is undertaken before comprehensive surveys are launched, especially for species that experience substantial predation by other birds.

Connecting paragraph: Chapter 1 looked at the impact of drones on thick-billed murres, as well as their accuracy to monitor murres on their breeding sites. This will help obtaining at-colony information which can be related to prey availability. The next chapter, on the other hand, looks at the foraging behaviour of murres and the role of sociality in foraging. More precisely, it looks at the formation of aggregations, which needs to be understood in order to use clusters of murres to detect prey hotspots.

Chapter 2: The formation of murre aggregations

Note on this chapter

This chapter corresponds to the paper titled "The formation of foraging aggregations in a highly social seabird, the Thick-billed murre (*Uria lomvia*), at small and large scale", submitted in Marine Biology, which was made in collaboration with Grant Gilchrist from Environment and Climate Change Canada, Pierre Dutilleul from McGill University and Akinori Takahashi, from the National Institute of Polar Research.

Abstract

Analyzing how animals are distributed in space and time is important to understand the behavioural interactions that underlie population dynamics, especially for highly social species. Thick-billed murres (*Uria lomvia*) breed in some of the largest and densest colonies of any seabird. Although this bird is known to aggregate at sea, little is known about the "when", the "where" and the "why" of those clusters. We examined spatial and temporal patterns of foraging aggregations during the breeding season at various scale via (1) the synchrony of arrivals of adults feeding their chick at the colony, and (2) GPS and camera loggers to understand how birds are distributed at sea. Adult arrivals at the colony were synchronised when bringing capelin (*Mallotus villosus*), a gregarious pelagic fish, but not when bringing sculpin (primarily *Triglops* spp.), a solitary benthic fish. Camera loggers revealed very close encounters of foraging conspecific (<4m), much closer than what was predicted by chance, despite low prey densities. GPS loggers also showed diffuse at-sea aggregations with minimal distances typically between 500-1500m. However, those birds did not typically share foraging trajectories. We suggest that at smaller scale, tight groups are formed to increase searching efficiency. At larger scale, murres aggregations are most

likely a result of foraging individuals converging in the more prolific areas, either by independently encountering prey hotspots, or by cueing on other foraging birds.

Introduction

How animals are distributed in space and time when foraging can provide insights about the interactions between individuals and the environment, and between individuals and other conspecifics (Spiegel et al., 2017; Spieler, 2003; Waters, 1959). For example, a uniform distribution is often a sign of strong territoriality and interference competition (e.g. Wilschut et al., 2015). On the other hand, an aggregated distribution can reflect clumped resources (Grant, 1993; Halliwell et al., 2017; Schuttler et al., 2015), especially at large scale (Fauchald et al., 2000). At smaller scale, the interaction between individuals is unavoidable, and social foraging often drives the aggregation mechanism (Giraldeau and Caraco, 2000). While the comprehension of aggregation patterns – when, why and at what scale they are formed – can be difficult to achieve, the subject remains of high importance for conservation, especially for highly social species. The infamous case of the passenger pigeon, extremely abundant only decades before it disappeared, is just one of the few examples of how social species are vulnerable to changes in the demography. The importance of foraging aggregation for this species when foraging was key to understanding the rapid decline following its extinction (Halliday, 1980). Furthermore, foraging aggregation patterns must be identified and taken into account when establishing focus area for conservation. In this chapter, aggregations are going to be defined as any distribution pattern where individuals are closer to each other than what would be predicted by a random distribution, regardless of the scale.

The thick-billed murre (*Uria lomvia*; hereafter "murre"), a deep-diving Arctic seabird, displays among the most extreme cases of sociality in vertebrates, breeding in some of the largest and densest colonies in the world (Gaston and Nettleship, 1981). Some colonies count over 1.5 million breeding pairs (Brown et al., 1975), with most individuals nesting in physical contact with other breeders. Both parents raise the chick before fledging, with typically one of them foraging at night and the other foraging during the day, while the other partner is at colony (Elliott et al., 2010). At-sea foraging aggregations in this species during the breeding season are observed (Gaston and Nettleship, 1981), but the factors influencing the formation of these aggregations have not been described in enough depth to infer the underlying mechanism. In many seabird species, mixed species aggregations are formed at the surface to locate dense forage fish schools that are quickly depleted (Buckley, 1997a; Silverman et al., 2004; Thiebault et al., 2014). For example, in the closely related Common murre (*Uria aalge*), individuals which successfully located spawning capelin (*Mallotus villosus*) are used as cues by conspecific to locate the hotspot (local enhancement), resulting in the observed aggregation pattern (Bairos-Novak et al., 2015; Burger, 1997; Davoren et al., 2003). For the thick-billed murre however, which have a more generalist diet and which does not show the dense aggregations that are typical of many other seabirds (Cairns and Schneider, 1990) at-sea aggregation is likely more complex.

The development of miniature tracking technology, such as GPS and camera loggers, allows researchers to follow individuals at sea, potentially revealing more insights about foraging aggregations. We used such approaches to follow murres spatially and temporally during the breeding season through: (1) temporal aggregation via synchrony in the arrival of adults when feeding their chicks, (2) small-scale aggregation as revealed by camera tracking, and (3) foraging associations recorded by GPS. Synchrony of arrival occurring in a particularly short time window is often sign that individuals actively forage in groups (Bayer, 1981; Burger, 1997; Elliott et al., 2009b; Krebs, 1974). These groups can be formed via information exchange, with unsuccessful birds following successful ones, called information exchange (Brown, 1986; Buckley, 1997b; Campobello and Hare, 2007; Ward and Zahavi, 2008), through enhanced detection of prey when in groups (Mock et al., 1988; Wittenberger, 1985) or through synchronised attack on fish school (Bednarz, 2018; Berlincourt and Arnould, 2014). Therefore, we hypothesised that individuals feeding on schooling fish would come back to the colony to feed their chick more synchronised in time (i.e. displaying more temporal aggregation) than those feeding on solitary prey. As for camera loggers, they have the potential to detect smaller scale aggregations via the encounter rate of conspecific recorded. Moreover, camera loggers are also used to look for interactions among clustered foraging individuals (Berlincourt and Arnould, 2014; Watanuki et al., 2008). Finally, GPS loggers can reveal how aggregations were formed, especially at large scale, therefore giving insights on the cause of the foraging clusters. As previously mentioned, foraging groups formed when birds leave the colony often imply that individuals actively forage together to increase individual success. On the other hand, foraging aggregations formed at-sea more often indicate that birds independently accumulated in a productive habitat (prey-driven aggregation) or, similarly to common murres, used local enhancement to cue on other foraging individuals.

Methodology

Study Site

All data was collected at the Coats Island west murre colony (62°56'52.20"N, 82°01'03.70"W) in Hudson Bay, Nunavut, Canada between 1994 and 2017. The murre colony, situated on cliffs, hosts ~15,000 breeding pairs (Gaston, 2002). Murres forage within a semi-arc of 50km around the colony (Elliott et al., 2008a; Gaston et al., 2013). All analyses were conducted using R (R Development Core Team, 2014).

Chick Feeding Synchrony

We looked at the temporal pattern of adults returning to the colony to feed their offspring. We predicted that murres feeding on prey that form schools, such as capelin, would be more synchronised in their arrival time than those preying on solitary prey, such as sculpin (*Cottoidea*). Other rare fish items (<8%) were ignored for the analyses.

Data for this analysis were collected during “feeding watches” in 2006, 2008, 2009 and 2017. In 2008 and 2009, too few sculpin were recorded for the analysis, so only 2006 and 2017 were retained for this prey item. Feeding watches consisted of observing a plot containing around 19 breeding sites, for 12-20 hours a day over several days, during the chick-rearing period (Hipfner et al., 2006). Observations were made from a blind located 2 to 10m away from birds in the plot, and involved noting when an adult returned to its nest with a prey and what prey type was caught.

For the analysis, we separated the whole feeding watch period during a year into smaller periods of ten minutes. We decided to test for synchronisation of chick feeding at this scale, as murres sometimes circled several times around the colony with a prey in their beak before deliveries (pers. obs.). Two murres from the same foraging group could thus potentially return to their nest within approximately 10 minutes from each other. For every 10-minute period, we calculated the number of murres in the plot returning with capelin or sculpin. For each prey species and for each year, we then computed a variance-to-mean ratio from the counts made in the 10-minute periods. Using the Poisson distribution as reference to assess homogeneity of temporal point patterns (Dutilleul, 2011), a variance-to-mean ratio of 1.0, or close to, would imply that murres return at the colony in a completely random pattern, while a ratio above 1.0 would imply that their arrivals are grouped (aggregated pattern) and possibly synchronised. To test for significance, we computed 1000 simulations generated from a Poisson distribution, and took the fifth percentile variance-to-mean ratio as our threshold for significance. For every combination of prey species and year, we recomputed a significance threshold with simulation parameters set according to the observed data. We then redid the analysis previously described, but with periods of one hour rather ten minutes, to eliminate the possibility that synchronicity was due to a larger scale phenomenon, such as time-of-day effects.

To test the viability of the information center hypothesis through synchrony of departure from the cliff, we recorded the ratio in which two birds in the plot departed one minute within each others. We presumed that if information exchange happened on the cliff, birds would have to leave at the most one minute from each others, as otherwise the extreme density of flying murres around the colony would probably make it impossible for one murre to follow another.

At-sea distribution with GPS

In 2017, we deployed GPS-accelerometers (AxyDepth, 18 g, Technosmart, Rome, Italy, acceleration = 50 Hz; depth and temperature = 1 Hz; GPS point recorded every 5 min) on 93 birds for 2-4 days throughout the season. For the first analysis, only points where the recorded travelling speed was below 10km/h were retained, as we wanted to select only the points associated with foraging. We also removed all points within 2km of the colony (the splashdown), as these are associated with social behaviour rather than foraging (Burger, 1997; Elliott et al., 2009b). Finally, to create temporal snapshots, we retained only points at the time of the day when most equipped murres were actively foraging based on preliminary analysis. We chose a window of 30 minutes to accommodate the sampling rate of GPS while being short enough to be considered a temporal snapshot. We retained only days when >3 equipped murres were foraging during the snapshot window.

For every snapshot, we calculated the minimum distance observed between two murres. To test if these distances were smaller than what would be predicted by chance, we made 1000 simulations for all possible combinations of equipped murres present in the snapshot. Those simulations consisted of redistributing the points based on the observed murre density map. This density map was made using GPS data for the whole period of study so as to take into account any general habitat preference such as bathymetry or distance from the colony. We then calculated all minimum and mean distances for these simulations, and used the fifth percentile value as our significance threshold. Finally, when the minimum distance detected in a day was smaller than 2km, we plotted the individual GPS tracks of those murre pairs involved. We used time of departure from the colony and track shape to assess whether the murres were travelling together from the colony, or ended at the same foraging place while having two different initial paths.

At-sea distribution with camera loggers

In 2017, 20 birds were equipped with camera-loggers (DVL400M, Little Leonardo, Tokyo, Japan, 15 g), but four cameras were lost during the field season. The cameras recorded for ~1-2 hours, and all birds were recaptured within 24 hours. We analyzed every video to look for direct evidence of social foraging (coordinated attack, etc.), and we also noted every time a conspecific or prey item was encountered while diving. We tested if the encounter rate with a conspecific was higher than what would be predicted by chance by calculating the expected encounter rate using the adapted predator-prey encounter rate equation of Gerritsen and Strickler (1977):

$$Z_p = \frac{\pi R^2 N_b}{3} \left(\frac{u^2 + 3v^2}{v} \right) for\ v \geq u$$

Where Zp is the encounter rate, R the encounter radius, Nb the conspecific concentration, u the speed of the subject for which the encounter rate is being calculated and v the speed of the animals being encountered by the subject. This equation assumes that animals occur following a Poisson distribution in the environment, and an encounter rate much higher than the calculated output would suggest strong aggregation.

To calculate the expected encounter rate, we considered that half of the breeding population at Coats was at sea at any moment, for a total of 15 000 foraging individuals. The estimate is likely exaggerated the number of individuals at sea, as murres spend some time at the colony with their mates. Murres forage within a semi-arc of 50km around the colony (Elliott et al., 2008a; Gaston et al., 2013). However, areas near the colony are seven times denser than those near the 50km border, so we therefore multiplied the calculated concentration by seven so that the encounter rate would apply to most murres and be as conservative as possible. The average foraging dive is ~50m deep (Elliott et al., 2008a), making a concentration of 535 murres/km3. However, we considered for our analysis only birds encountered while diving. Assuming murres at sea spend ~30% of their time underwater (Elliott et al., 2014b), the actual concentration would be 160 underwater murres/km3. Considering an underwater speed of 7 km/h (Elliott et al., 2007; Lovvorn, 2004) and a camera detection range of 4m at 90 degrees, we expect an encounter rate of ~0.02 murres per hour. We used Fisher's exact test to determine if the observed encounter rate was significantly different from the expected rate.

Results

Chick Feeding Synchronisation

We observed 626 capelin feeds and 182 sculpin feeds. During all years, capelin were brought to the chicks at a rate that departed from the expected Poisson distribution at a 10-minute scale (Table 2.1). The distribution of feed counts in the 10-min periods consisted of more zeros and more high counts than the normal distribution, suggesting a clustered, or bimodal, distribution (Fig. 2.1-capelin). We detected no significant synchrony for sculpin at a 10-minute scale (Table 1, Fig. 1). No synchrony was detected at the 1-hour scale for either prey item, meaning the synchrony detected at the 10-min scale for capelin was not caused by a larger-scale phenomenon.

As for departure from the cliff, a negligible proportion of birds departed in synchrony (<1%). Furthermore, few birds faced incoming birds, and adults feeding their chick did not seem to draw the attention of other birds, a crucial condition to at-colony information exchange.

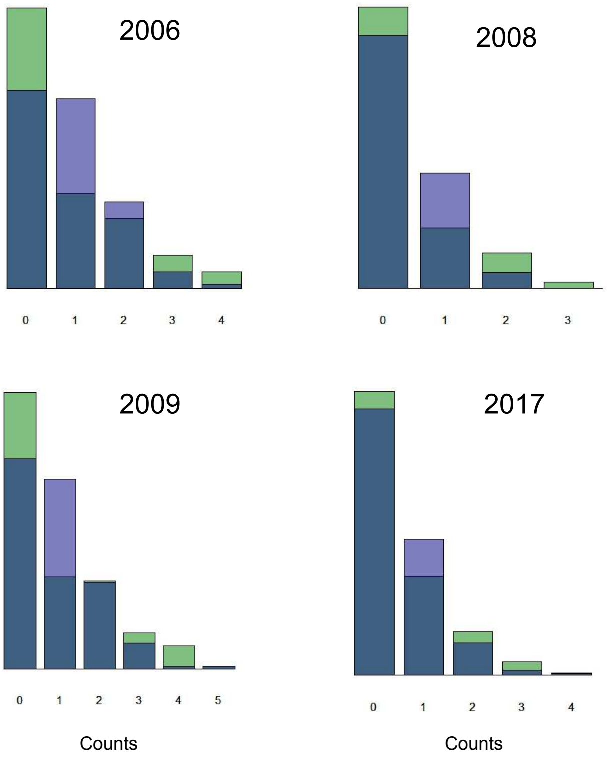
Table 2.1: Variance-to-mean ratios of prey delivery counts during 10-min periods and 1-hour periods

Capelin

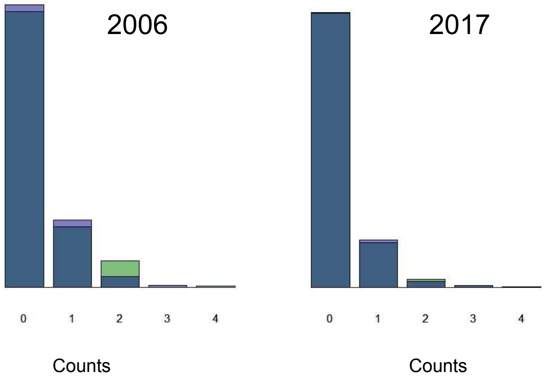
Year	*Observed variance-to-mean ratio at 10-min scale*	*Significance threshold at 10-min scale*	*Observed variance-to-mean ratio at 1-hour scale*	*Significance threshold at 1-hour scale*
2006	1.58*	1.13	1.17	1.45
2008	1.34*	1.21	0.90	1.85
2009	1.73*	1.22	0.84	1.83
2017	1.20*	1.10	0.97	1.30

Sculpin

Year	*Observed variance-to-mean ratio at 10-min scale*	*Significance threshold at 10-min scale*	*Observed variance-to-mean ratio at 1-hour scale*	*Significance threshold at 1-hour scale*
2006	1.23	1.24	1.12	1.41
2017	1.07	1.1	1.13	1.3



Capelin



Sculpin

Fig. 2.1 Observed distribution of the 10-min periods based on the number of feeds of a given prey (green). In purple is the Poisson distribution and in dark blue the overlap between the observed and Poisson distribution. A bimodal distribution typically has more counts than the Poisson distribution on low an high values, but less in the middle values (as in the four top figures).

At-sea distribution with GPS

Eight snapshots had four or more birds actively foraging (Table 2.2). Minimal distances observed were smaller than what was produced using simulations for all but two snapshots. Five snapshots recorded a minimum distance that was smaller than 2km. GPS tracks for those birds showed that, four out of five times, birds near to one another at sea departed from the colony at different times, and often had dissimilar trajectories (Fig. 2.2b-e). In one case, however, the two birds departed in synchrony, headed in the same direction, stopped at the same patch, and started foraging in the same direction (Fig. 2.2a). The two birds eventually separated, as one went back to the colony, while the other kept foraging.

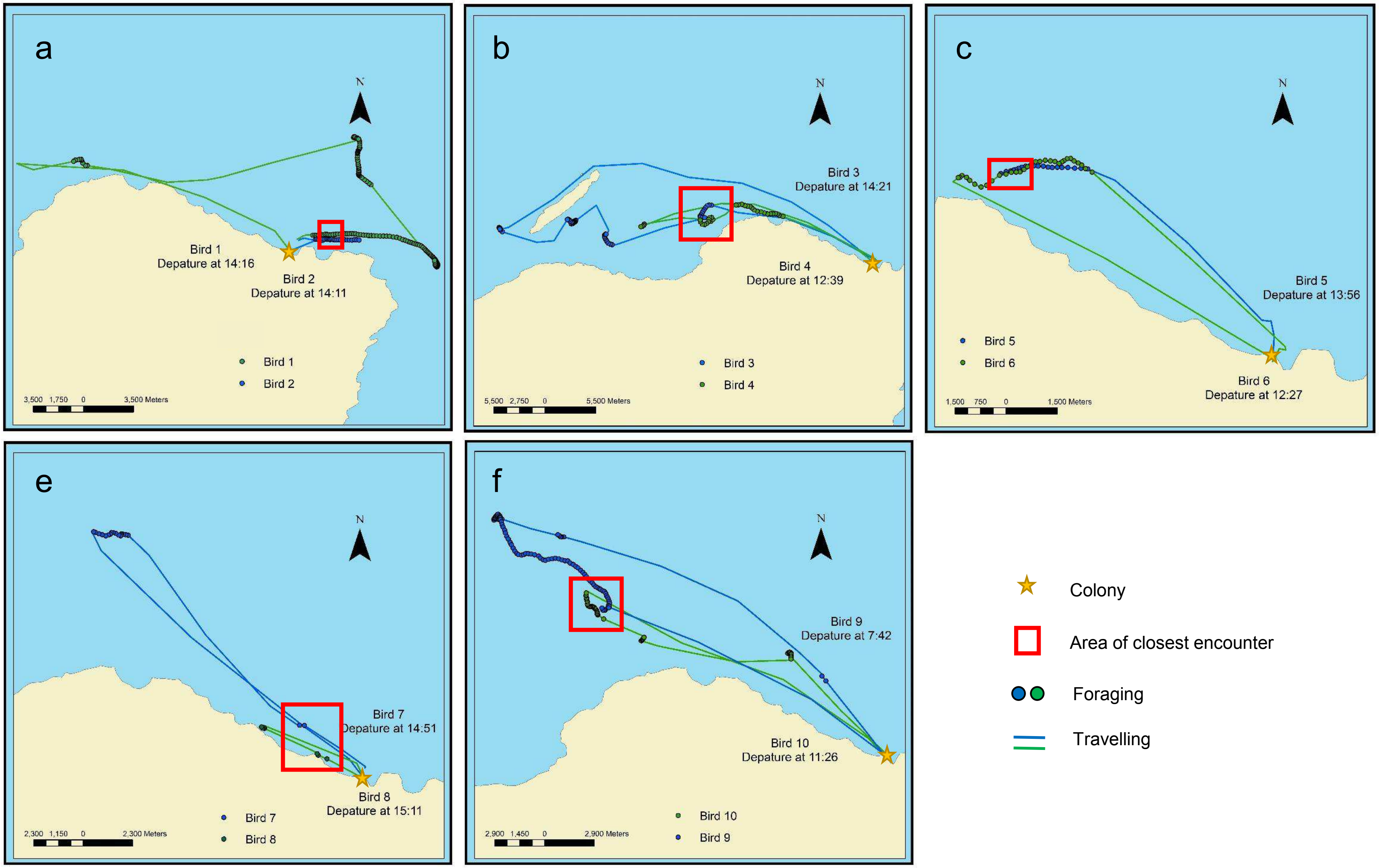
At-sea distribution with camera loggers

We recorded a total of 65 hours of video, 7.5 hours of which were filmed during dives. We did not detect any direct cooperation in the foraging behaviour of murres. We also rarely recorded more than one fish per screen, illustrating that fish did not occur in schools in our study site. Seven of the equipped murres (44%) recorded a conspecific on several occasions while diving, for a total of 19 encounters (Fig. 2.3). With a predicted 0.02 conspecifics encountered per hour, we did not expect a single murre to encounter a conspecific during the 7.5 hours of video recording. The observed proportion (seven out of sixteen) was therefore significantly different than what would be predicted by chance (Fisher's exact test $P = 0.006$).

Table 2.2: Observed minimal nearest-neighbour distance in the 8 snapshots compared with the significance threshold from simulation.

Day	Number of active GPS	Minimal nearest-neighboor distance (m)	Significance threshold	Track (fig 2.2)
20-07-17	4	3323*	3699	
22-07-17	4	418*	3699	a
23-07-17	5	277*	3465	b
24-07-17	4	1775*	3699	c
27-07-17	9	1864*	2370	d
28-07-17	7	4517	2934	
31-07-17	10	1498*	2172	e
01-08-17	8	3547	2295	

* < significant threshold (95% values from simulations)



Maps built under ArcGIS Desktop (ESRI)

Fig 2.2 : GPS track of the five closest encounters recorded during the snapshot analysis (see tab. 2.2)

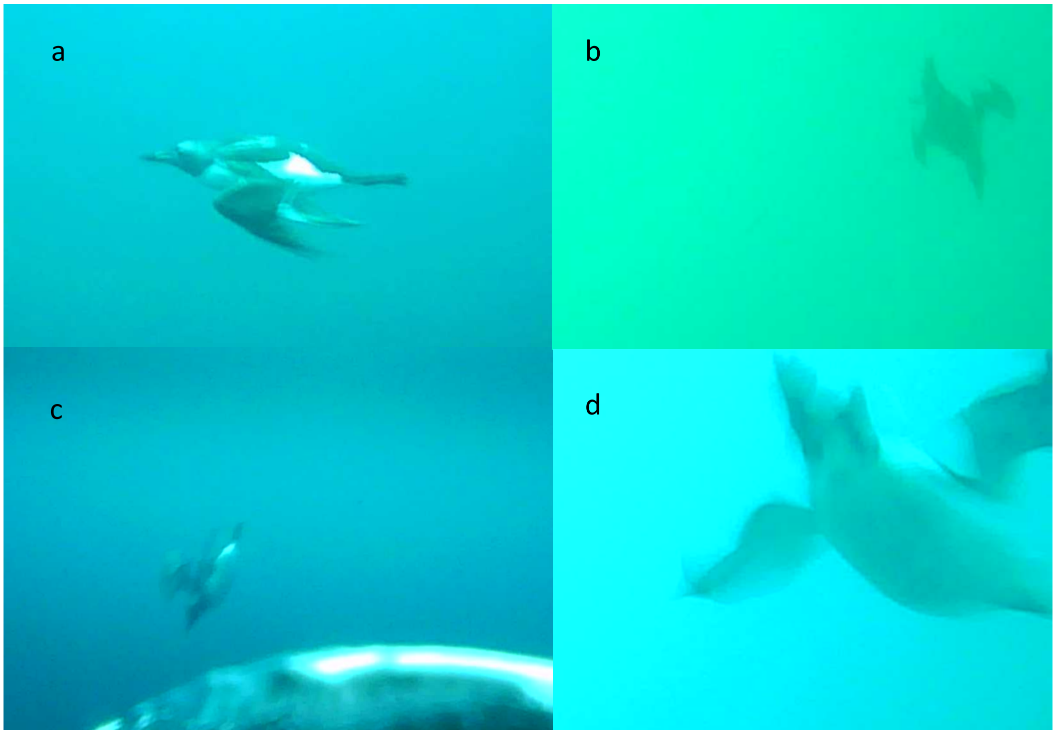


Fig 2.3 : Examples of conspecific encounters recorded by the camera loggers

Discussion

The aggregative nature of thick-billed murres while foraging is known mostly through boat or aerial surveys (Fauchald et al., 2000; Gaston and Nettleship, 1981; Mehlum et al., 1998), which limits the interpretation of the observed aggregations to the eye of the observer. On the other hand, our results using camera-loggers, GPS and at-colony observations revealed new insights about the temporal and spatial scale of those aggregations, and more importantly about how they are formed.

Small scale aggregations, temporal and spatial

Synchrony of returning adult to feed their chick can be an indication that murres actively forage in groups(Bayer, 1981; Burger, 1997; Elliott et al., 2009b; Krebs, 1974). While Elliott et al. (2009b) found little synchrony in the return rate of thick-billed murres feeding their chicks, they did not differentiate among taxa, clumping all benthic and pelagic items. In contrast, we found synchronisation of adults feeding their chick with capelin, not sculpin. The fact that this synchrony was discernable at a very small scale (<10min) but not at a larger one (>1h) suggests that the underlying mechanism is not simply a preference for individuals to forage at a given period in the day. The spatial clumping of resource in itself does not predict such strong temporal synchrony either. Rather, it is likely that the birds feeding on capelin were actively foraging in groups. Capelin is a pelagic fish forming aggregations, sometimes near the surface (Eschmeyer, and Herald, 1999). Feeding on this fish likely requires more aerial searching than for bottom solitary fish like sculpin. Individuals feeding on capelin would therefore reduce their searching time if foraging in groups. This strategy, called network foraging (Mock et al., 1988; Wittenberger, 1985), increases detection of prey, but also divides the resource among all group members. If fish aggregations are rare, but once they are found, are large enough to reward all individuals in a group, network foraging becomes a viable strategy. It could likely be the case for birds preying on capelin, while providing little to no benefits for those preying on sculpin. Another plausible explanation for the synchrony of arrival is the existence of information exchange among individuals, as proposed by Ward and Zahavi (2008), with naïve birds following those informed on the location of prey hotspot. This strategy also reduces search time per individual, and produces the same predictions about the synchrony of arrival of murres feeding on capelin compared to those feeding on sculpin. If this phenomenon exists in murres, however, the information exchange could not occur directly on the cliff, as initially suggested by Ward and Zahavi (1973). Murres were almost never observed following other murres directly from the colony's cliffs. On the other hand, murres often stop by the water adjacent to the colony, called the splashdown zone, before leaving to forage (Burger, 1997; Elliott et al., 2009b). Any information exchange or group formation – this is true as well for network foraging – will likely be formed in this area rather than on the cliff, as the conditions for information exchange on the cliff were not met.

At a small spatial scale, camera loggers detected several very close encounters of foraging conspecifics (<4m), more than what would be predicted by chance even in the context of spatial aggregation. However, in seven hours of active foraging over 16 birds, we did not observe cooperative hunting, which is displayed in species like the little penguin (*Eudyptula minor*), where several individuals circle around fish schools to prevent them from fleeing (Berlincourt and Arnould, 2014). Furthermore, capelin aggregations seemed to be quite dispersed, resembling more a hotspot than an actual dense school. It is unlikely that murres could have surrounded these aggregations efficiently. Following the results on temporal synchrony, those close encounters could have been individuals from a same foraging group formed initially to enhance searching efficiency. However, as the video recordings were not continuous, it is impossible to confirm that the birds arrived on the foraging spot at the same time.

Large scale aggregation

GPS loggers also recorded encounters that were closer than what would be predicted by chance, although these encounters were at the scale of hundreds or thousands of meters. Given that there are 30 000 breeding murres and that tight group formations might be small, recording individual encounters by GPS seems improbable (but see Cook et al., 2017). Among the closest encounter detected, only one consisted of two birds leaving the splashdown zone at the same time and heading in the same direction. All other tracks only converged briefly, and the two concerned individuals could not have been part of the same foraging group. This contrast with what was implied by the results on arrival synchrony suggests that more than one factors could dictate aggregation in the thick-billed murre, with some of them influencing different scale of aggregation. While those large scale encounters could have occurred through a prey-driven behaviour (each individual finding the prey hotspot independently), murres may also have cued on other feeding birds through local enhancement. Indeed, foraging murres are much easier to spot in the open sea than the prey themselves, especially considering that murres are visual predators. Gaston and Nettleship (1981) proposed a similar mechanism, with outgoing birds cuing on incoming birds to locate the direction of hotspots.

Conclusion

At smaller temporal and spatial scale, the close encounters and high synchrony of arrival suggest strong interactions among individuals, with murres likely foraging in active groups. Those groups are not form for cooperative hunting, and consequently an enhanced searching efficiently is more likely at cause (either via network foraging or information exchange). At larger scale, aggregations are not formed by groups actively travelling together. Convergence of murres occur at-sea, with individuals being independently attracted either by prey density, or cueing on other foraging conspecific to locate prey hotspot.

Connecting paragraph: Chapter 2 looked at the formation of seabird aggregations to facilitate the use of at-sea information for the assessment of prey availability. Chapter 3 continues with the same theme, but investigates further the association of murres with different prey types, so that the behaviour of murres could not only be used to obtain general information on prey availability, but also on the distribution and habitat use of different fish species.

Chapter 3: Prey type as revealed by foraging behavior

Note on this chapter

This chapter corresponds to the paper titled “Location, location, location: the geographic association of thick-billed murres with their prey promises a new economic way to map fish distribution in the Arctic”, soon to be submitted to The Auk.

Abstract

The marine environment is complex to sample. Often, the derived data from fishing vessels used to sample fish abundance, such as Catch Per Unit Effort, are costly to obtain and involve unavoidable bias. Seabirds have been proposed as indicator of food supply to complement boat surveys at low cost. Their mobility makes them great sampler of the sea, while their tendency to breed in colonies facilitates the accessibility for researcher. Thick-billed murres (*Uria lomvia*) are generalist predators that forage far at sea, and so have the potential to provide fish species map if diet information is coupled with GPS loggers. However, much needs to be learned on their foraging behaviour before this species can be used to assess food supply, including: (1) revealing the potentially different behaviours of foraging adults during the incubation as opposed to the chick-rearing period (2) exposing the mechanisms of prey type selection. We described the underwater behaviour of murres using camera-loggers and accelerometers, and we investigated how diving characteristics differed with breeding stage. We also identified how foraging behaviour influences the prey type caught during a dive by combining GPS-depth loggers with observations of adults feeding their chick at colony. Foraging adults were diving deeper during the chick-rearing period, probably as to compensate for the chick energy requirement. The location of a dive (distance from colony and distance to shore) were the best variables to predict which prey type was the most likely to get caught in a dive. Therefore, specialist individuals among this generalist species were likely formed by individuals having foraging location preferences. Our results suggest thick-billed murres could be a potential seabird used to map fish species, as they associate spatially with the different prey types.

Introduction

The marine ecosystem is one of the most challenging environments to sample. For example, studies often estimate fish abundance from commercial fisheries using catch per unit effort (CPUE), which introduces bias caused by the method of capture and the scale of the fisheries (Kleiber and Maunder, 2008; Richards and Schnute, 1986; Rose and Kulka, 1999). Fishing vessels are also intrusive to the aquatic fauna, with recurrent by-catches of endangered fish species and other vertebrates (Ambrose et al., 2005; Casale, 2011). Scientific boat surveys, on the other hand, are costly and time consuming. Furthermore, ocean navigation has its risk, with in average two large ships sinking every week worldwide (Casey, 2010).

Seabirds have long been proposed as alternatives to the traditional fish sampling techniques (Brisson-Curadeau et al., 2017a; Cairns, 1988; Piatt et al., 2007). One seabird can survey hundreds of kilometers in a day, potentially providing great insights about prey availability. Furthermore, with 96% of seabirds breeding in colonies (Coulson, 2001), the concentration of individuals facilitates the collect of information for biologists. Initially, information like breeding success or foraging trip duration was proposed as indicators of prey abundance (Cairns, 1988), with some studies successfully detecting dependences between these factors (Cury et al., 2011; Piatt et al., 2007). Yet, with the development of logging technologies, the idea to use seabirds as indicator of the marine fauna is more promising than ever before (Brisson-Curadeau et al., 2017a; Lescroël et al., 2016). One new avenue now possible with such technologies is the identification of prey hotspots. GPS-equipped birds have, for example, provided insights about where fish schools were located, and how these fish schools are changing spatially and temporally (Croll et al., 2006; Weimerskirch et al., 2005). Furthermore, the ability of birds to capture fish species that otherwise slip through the fishing vessels' net increases the potential to use seabird to map fish distributions. The applications for conservation are plentiful (Burger and Shaffer, 2008; Pichegru et al., 2010).

The thick-billed murre (*Uria lomvia*), the most abundant seabird of the Arctic, is one of the most promising indicators of the marine ecosystem. It breeds in colonies of up to a million and a half individuals (Brown et al., 1975), making this bird easy to study in the breeding season. Moreover, although some individuals are specialists, the species as a whole is generalist, so that its diet is representative of the fish species composition of the ocean (Vader et al., 1990; Woo et al., 2008). However, much needs to be learned about this species before information on the marine food supply can be extracted from its feeding behaviour. For example, little is know about how breeding stage (incubating vs chick-rearing) can affect its foraging behaviour. How the different foraging strategies among individuals influence the prey type captured in a dive is also poorly know. For instance, Elliott et al. (2008a) found that diving and flight behaviour (maximum depth, shape of the dive and flight duration) can be used to predict to a certain extent what fish species will be caught during a dive. However, they were unable to identify foraging locations as they lacked GPS loggers. Indeed, their methodology was not adapted to pelagic prey, which is the most abundant type, and only locations associated with benthic prey could be identified.

We aim to reduce the knowledge gap preventing the use of the thick-billed murre as an indicator species by examining in depth its foraging behaviour during the breeding period. We describe the diving behaviour of murres (maximum depth, prey-handling time, occurrence of capture events, etc.) using camera-loggers and accelerometers, and we investigate how underwater behaviour differs between incubating and chick-rearing birds. Thereafter, we identify how foraging behaviour influences the prey type caught during a dive by combining GPS-depth loggers with observations of adults feeding their chick at colony. Finally, we examine which foraging behaviour could explain the presence of specialization among individuals. Two hypothesis could explain the latter: (1) individuals specialize by adopting different underwater behaviour which will maximize the capture of a given prey type or (2) individuals specialize by choosing different foraging location, where the prey species composition is different, and therefore capture different prey types.

Methodology

All data was collected at the Coats Island west murre colony (62°56'52.20"N, 82°01'03.70"W) in Hudson Bay, Nunavut, Canada in July 2017. The murre colony, situated on cliffs, hosts ~15,000 breeding pairs (Gaston, 2002). All analyses were conducted using R (R Development Core Team, 2008) and ArcGIS for desktop (ESRI, 2011).

Biologger deployment and feeding watches

We equipped 16 birds with camera-loggers (DVL400M, Little Leonardo, Tokyo, Japan, 15g) attached on back feathers. Out of those birds, 7 were incubating, while 9 were chick-rearing. The cameras recorded for ~1-2 hours, starting 12h after the capture. As thick-billed murres typically have a 12h incubation shift with their partner, with one feeding at night and the other feeding during the day, a 12h delay would insure that the equipped bird would be at-sea when recording. All birds were recaptured within 24 hours. We also attached a Technosmart depth-logger (AXYdepth, 6.5g, Technosmart, Rome Italy, depth = 1 Hz) on the tail. The individuals equipped with cameras and accelerometers were not the same individuals as those used for feeding watches (see next section).

We deployed 28 Technosmart GPS (AxyDepth, 18g, Technosmart, Rome, Italy, depth and temperature = 1 Hz; GPS point recorded every 5 min) on 52 chick-rearing birds captured with a noose pole. All birds were banded to insure that he same bird was not equipped twice. Every GPS stayed for 2-8 days on the bird and was then retrieved via recapture of the individual. All birds captured originated from a plot containing around 30 breeding sites (‘Q Plot’). All deployments occurred within 9 days of each other.

While GPS were recording, we conducted feeding watches. Feeding watches consisted of observing the plot for 12-20 hours a day over several days, during the chick-rearing period (Hipfner et al., 2006). Murres typically deliver a single prey item to their chick that they hold in their beak, and so prey type can easily be observed at the colony. Observations were made from a blind located 2 to 10m away from focal birds, and involved noting when an adult returned to its nest with a prey and what prey type was caught. Prey length was also visually estimated relative to the length of the white stripe on the bill (Elliott and Gaston, 2008). We separated *Triglops* sp. from other sculpins, as *Triglops* are easily identifiable in the field and likely have a different life history than *Myoxocephalus scorpius* and *Gymnocanthus tricuspis*, which composes all the remaining sculpins (Elliott and Gaston, 2008).

Data analysis

Videos were watched using VLC. We recorded the behaviour of individuals during dives: prey catching events, prey handling time and dive type (bottom vs pelagic). We used the camera loggers as a training set to develop an algorithm that could tell apart bottom dives (or U-shape dives) from pelagic dives (V-shape, Elliott et al., 2008a) using solely depth profile, which was useful for analyzing the habitat use of birds only equipped with GPS-depth recorders. We recorded dive type from the camera logger based on whether the ocean bottom was observed on the video. We used a linear discriminant function analysis with (1) the ratio of the dive spent near maximum depth and (2) maximum depth, as input variables to discriminate between bottom (ocean bottom visible) and pelagic (ocean bottom not visible) dives.

We linked the prey type brought to the chick by a GPS-equipped bird with the information recorded during the previous dive bout. A bout is defined as a series of dives with a difference of less than 37.4 m or 63.4 s between sequential dives (Mori et al., 2002). Only dives deeper than 2m were considered. The variables used to predict prey type were: maximum depth, water temperature, distance from the colony, dive type and distance from shore. Distance from shore was calculated using a high resolution polygon of Coats Island

and Bencas Island, a small nearby island (Wessel and Smith, 1996). We used a principal component analysis to determine relationships among the variables and qualitatively assess the associations between foraging behaviour and prey type.

We compared the dive characteristic of camera-equipped birds that were incubating versus those that were rearing chicks using a Welch two-sample t-test (for depth) and Fisher's exact test (for dive type). We also compared the dive characteristics of camera-equipped birds versus GPS-equipped birds using the same two tests.

Finally, the diet specialization of an individual was determined in three steps: (1) if a prey type other than capelin constituted more than 25% of the diet of a bird, the individual was considered a specialist for this prey type, (2) if no prey type other capelin constituted more than 25% of the diet and if capelin consisted of more than 50% of the diet, the bird was considered a capelin specialist and (3) if no prey type other capelin constituted more than 25% of the diet, but capelin consisted of less than 50% of the diet, the bird was considered generalist. Only birds for which we observed five feeds or more could be classified as having a diet specialization. Feeds for a given bird were sometimes observed during the feeding watch when the individual was no longer equipped with a GPS, or had not been equipped with a GPS yet. These feeds were nonetheless used to establish the speciality of a bird.

Results

Diving behaviour

The camera loggers recorded a total of 278 dives from the 16 equipped birds. In total, 65 hours of video were recorded, of which 7.5 hours involved birds diving underwater. Most prey captures (>99%) were very small invertebrates, likely the amphipod *Parathemisto libellula*, averaging one capture per 3.75 seconds. Only 21 fish large enough to be distinguished were observed, and such captures occurred in 12 dives. The handling time

(time between capture and swallowing) for small prey was instantaneous, but was variable for larger prey (19±16s). More than half (57.1%) of the 21 large fish were brought back to the surface before being eaten, although some were swallowed almost instantly underwater. Capture events were most common in the ascending phase, occurring in 57.9% and 95.6% of the bottom and pelagic dives respectively. Prey captures also occurred in the descending phase for 26.3% of the bottom dives and 72.1% of the pelagic dives. All bottom dives contained captures at the ocean floor. Prey type at the bottom phase could not be identified due to camera position as the birds tilted their head downwards during such captures. The 21 large fish were all captured in the ascending phase, with five of them (four capelin *Mallotus villosus* and one *Triglops* sp.) being caught less than a meter below the surface. Only two prey captures intended to feed the chick were witnessed through the camera loggers. In one of them, the adult caught a capelin, and kept diving at shallow depth (<2m) with the fish in its beak, with some consecutive dives being separated by short flights. In the other, the bird directly flew back to the colony after capturing the fish.

The best algorithm to discern bottom dives from pelagic dives using depth profile did so with an accuracy of 95% (kappa index of 0.88). It used the percentage of the dive that occurred within 6% of the maximum depth, adjusted according to maximum depth as follow:

$$S = -0.01837d + 10.0249r$$

where S is the scaling value used to separate bottom dives from pelagic dives, d is the centered-reduced maximum depth and r is the centered-reduced ratio of the dive which occurred at 6% of the maximum depth.

Prey type as described by dive characteristics

We observed 199 feeds by GPS-equipped birds, with an average 2.4 feeds per bird per day. We randomly removed pseudo-replicates, which were defined as all feeds of a defined prey type from the same bird. With this, 84 feeds were randomly eliminated, the vast majority of them being capelin feeds. We also removed another 16 feeds which consisted of rare prey items (n < 5), leaving 89 feeds for the analysis. This included 9 feeds of invertebrates (shrimps and amphipods), 48 feeds of capelin, 11 feeds of Arctic Cod (*Boreogadus saida*), 7 feeds of daubed shanny (*Leptoclinus maculatus*), 9 feeds of *Triglops* sp. and 6 feeds of non-*Triglops* sculpin.

The two first axes of the PCA explained 67.0% of the variation (fig. 3.1). The first axis explained 38.7% of the variation and was almost exclusively composed of geographical variables (distance from the colony and distance from shore). The second axis (28.3%), while also influenced by the geographical variables, consisted mostly of underwater variables (depth and dive type). Geographic variables created a first dichotomy: colony-adjacent prey (invertebrate and sculpin) compared with remote prey (*Triglops*, arctic cod and daubed shanny, fig 3.2). Capelin was near the centroïd, being present both near and far from the colony. Among the remote prey, cod and shanny were found closer to coastal waters (but not as close as colony-adjacent prey), while triglops were found far off-shore. The second axis primarily discriminated sculpin from invertebrates, with sculpin being captured in shallower waters near the sea floor and invertebrates being caught in deeper water and in the middle of the water column. All species considered, distance from the colony had an asymptotic positive relation with prey size ($t_{84} = 5.96$ $P < 0.001$; Fig. 3.3). *Triglops* were also typically caught in the middle of the water column, while cod and daubed shanny were caught in a mixture of dive types (Table 3.1).

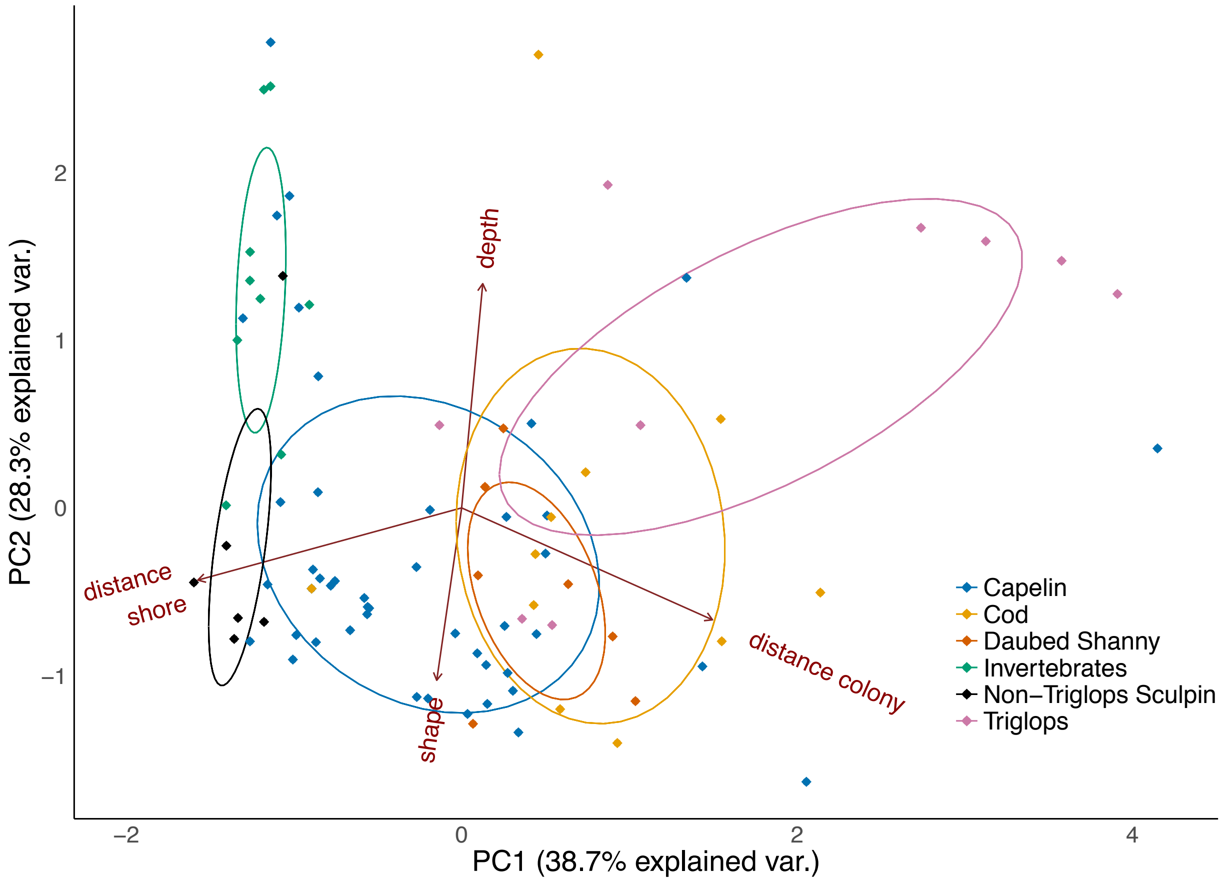


Fig 3.1: Principal components analysis of dive characteristics for thick-billed murres at Coats Island, including maximum depth (depth), percentage of bottom dives in a dive bout (shape), distance from the colony (distance colony) and distance to shore (distance shore). Colour represents the prey type recorded at the colony following each dive bout, with the assumption that the prey was caught in the final dive bout prior to the bird returning to the colony.

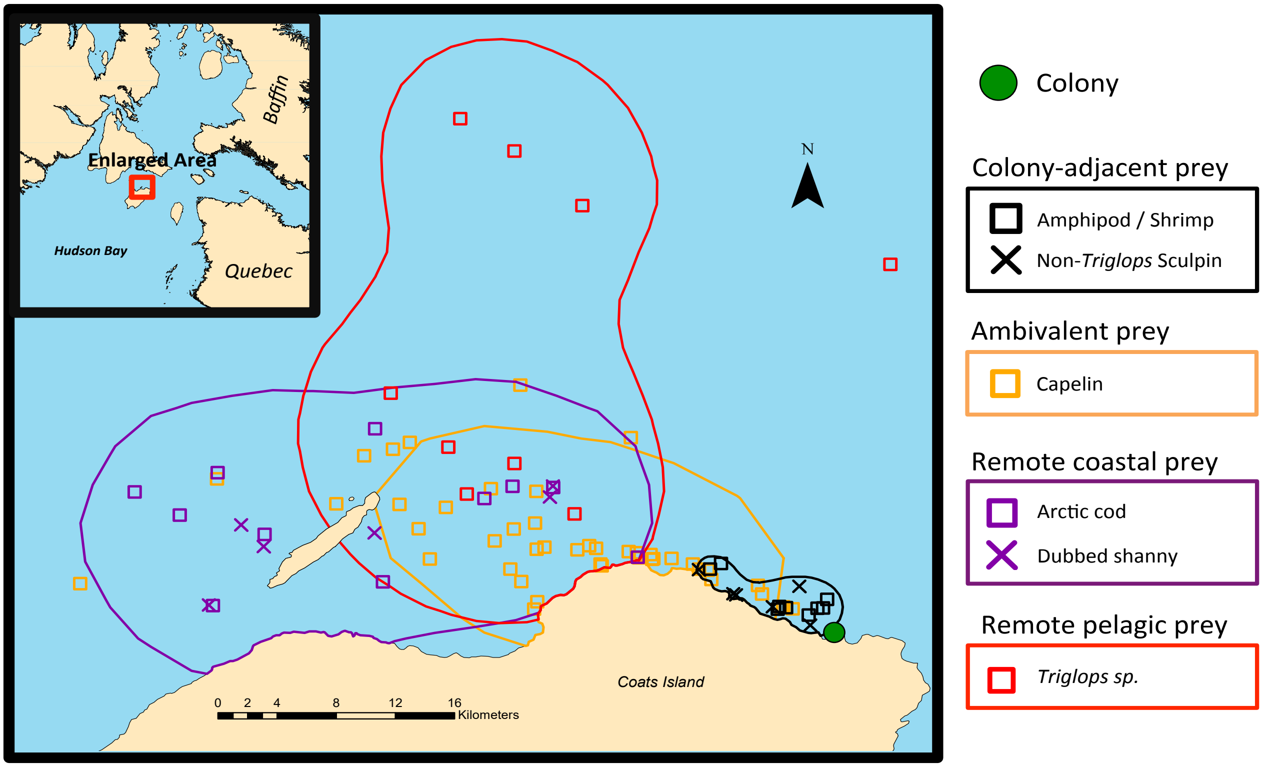


Fig 3.2: Map of prey capture locations for thick-billed murres feeding near the Coats Island colony. Each point represents the location of the final dive bout prior to the return of an individual to the colony with a particular prey item, and assumes the prey item was caught in the final dive bout. Two prey capture events occurred well outside the area shown.

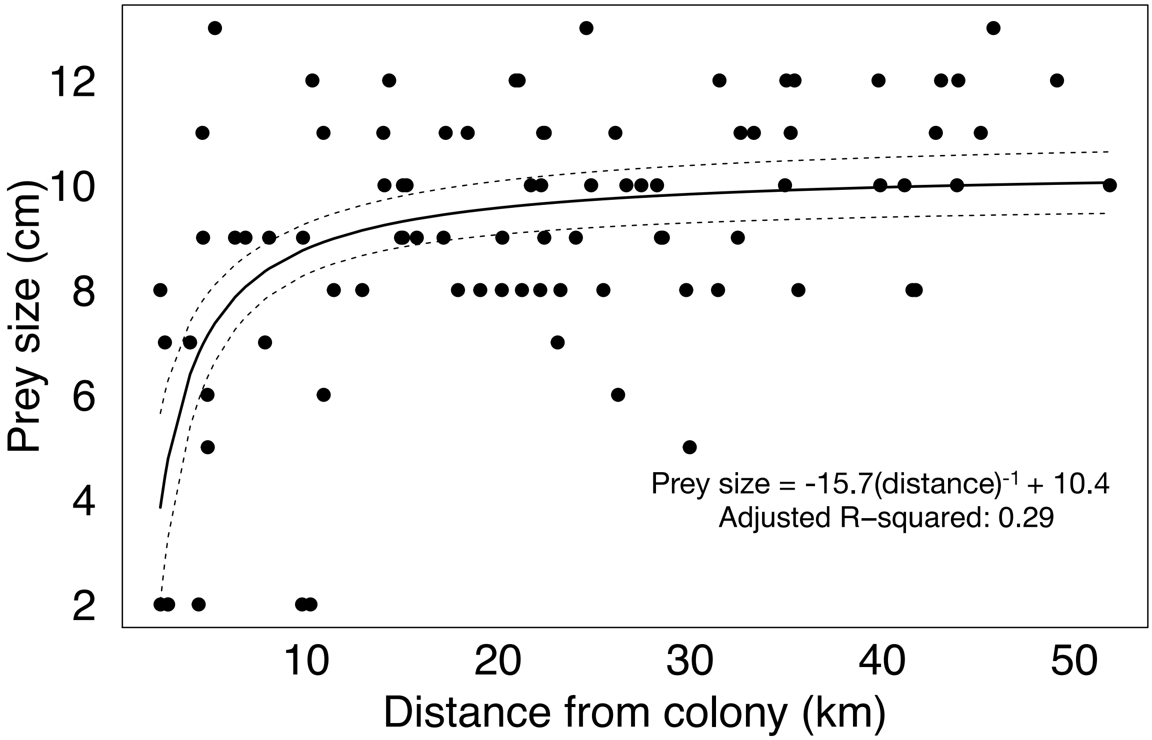


Fig 3.3: Prey size (all species) increases with return distance to the colony for thick-billed murres foraging near Coats Island in 2017. The full line is a fitted linear model, while the dashed lines represent the 95% confidence interval. Distance from the colony represents the distance between the colony and the final dive bout prior to the return of each murre to the colony, under the assumption that the prey item was caught in the final dive bout.

Tab 3.1: Average characteristics of final dive bouts prior to the arrival of thick-billed murres to the colony with each prey type.

Prey type	n	Distance to colony (km)	Distance to shore (km)	Depth (m)	Percentage of bottom dives
Invertebrates	9	5.0 ±3.0	1.3 ±0.5	-97 ±31	22
Capelin	45	21.4 ±10.4	3.4 ±5.2	-50 ±33	51
Arctic Cod	11	34.2 ±11.1	5.7 ±3.1	-72 ±50	55
Daubed Shanny	7	32.2 ±9.4	4.1 ±2.0	-65 ±37	71
Non-Triglops Sculpin	6	6.5 ±3.0	0.8 ±0.9	-54 ±17	83
Triglops sp.	9	31.9 ±8.0	15.1 ±10.4	-85 ±36	22

Dive characteristics according to breeding stage

Dives during the chick-rearing period were deeper (47±30m) than dives during incubation (27±15m, t_{132} = 5.28, P < 0.001). There was no difference between the percentages of bottom dives for both periods, as 19% of dives were bottom dives during incubation and 21% during chick-rearing (Fisher's exact test P = 0.84). Both maximum depth and ratio of bottom dives were different between camera-equipped birds during the chick-rearing period and GPS-equipped birds. Maximum depth was 63±38m (t_{163} = 2.9, P = 0.004) for GPS-equipped birds while the percentage of bottom dives was 49% (Fisher's exact test P < 0.001).

Diet specialization

In the surveyed plot, 30 birds were observed feeding their chicks at least five times. Four birds specialized on invertebrates, 15 on capelin, 5 on cod, 1 on daubed shanny, 3 on non-*Triglops* sculpin, 2 on *Triglops* and 1 was a generalist. To obtain sufficient statistical power, we clumped colony-adjacent specialists (invertebrate or sculpin) and remote prey specialists (cod, shanny or *Triglops*). The sole generalist was removed from analysis. Capelin was the most common prey and was brought back by all individuals (48.5% of all feeds). As capelin was also caught in various geographic conditions, near the centroid of Fig. 1, we investigated if capelin could have been an opportunistic prey sometimes caught by specialists. We therefore tested if capelin caught by colony-adjacent prey specialists were captured in different locations than those caught by remote prey specialists or capelin specialists. Capelin caught by colony-adjacent specialists were caught closer to the colony and closer to shore than the ones caught by remote prey specialists, which follows the same tendency as the prey for which these birds are specialised on (fig. 4). Capelin caught by capelin specialists were overlapping with both groups.

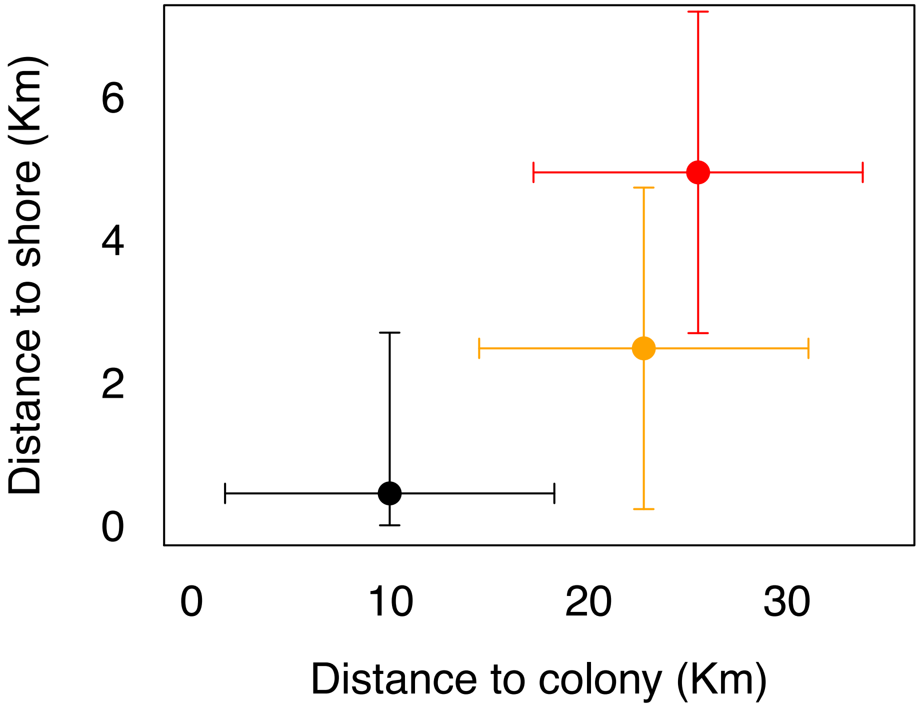


Fig 3.4: Distance to shore increases with distance to colony for capelin caught by colony-adjacent prey specialists (black), compared with those caught by capelin specialists (orange) and remote-prey specialists (red).

Discussion

Our results showed that breeding period influences foraging behaviour, with individuals diving deeper during the chick-rearing period. As for prey type captured during a dive, it is mainly described by foraging spot selection rather than diving behaviour, which is ideal to obtain prey distribution maps using GPS-equipped birds.

Foraging behaviour during incubation and chick rearing period

Chick-rearing birds dived deeper than incubating birds, as has been found in other studies of auks (Benvenuti et al.; Davoren and Burger, 1999; Elliott et al., 2008c; Ito et al., 2010). Central place foraging theory predicts that individuals should increase their load size compared with self-feeding individuals, and chick-rearing birds likely increased their effort to capture larger and more energetically profitable prey for their chick by diving deeper (Davoren and Burger, 1999; Elliott et al., 2008c; Ito et al., 2010). Similarly, the deeper and more benthic dives preceding the prey delivery to the chick (recorded by GPS-loggers) could again be due to an increase in searching effort when foraging for the chick compared to self-feeding (the latter recorded abundantly on the camera-equipped birds). The diet of adults detected by the camera loggers was dominated by amphipods while chicks were mostly fed with fish, an observation consistent with isotopic analysis (Hobson, 1993) and stomach contents (Provencher et al., 2013). However, the effect of self vs chick feeding on diving characteristic may also be inflated due to a heavier load on the camera-equipped birds (20% heavier), which usually results in reduced diving abilities (Ludynia et al., 2012) with the impossibility to dive as deep as the more lightly equipped GPS-logger birds.

Associating foraging behaviour with prey type

Elliott et al. (2008a) found that the behaviour of a bird while diving can be useful to determine what prey type is more likely going to be caught. In contrast, our results suggest that, even before a murre starts diving, the location where the bird is foraging provides a better estimate and narrows down the possible prey type caught to one or two (but up to four in small high diversity pockets, see fig. 2).

Our results corresponded with the expected patterns based on the life history of the fish species and the energetic requirements of murres. Smaller, less energetically-profitable prey, like sculpin and invertebrates, were caught closer to the colony. While these prey might have been common farther from the colony (invertebrates were visible in all dives by every one of our camera-equipped birds), it would not be advantageous for an individual that makes a longer trip to come back to feed its chick until the individual catches a more energetically profitable prey. Those energetically profitable preys, however, might be depleted in the vicinity of the colony (Elliott et al., 2009a), necessitating longer trips. Fish habitat preference might drive the rest of the variation observed. Triglops can be found in deeper water than young cod and daubed shanny, which prefer coastal areas (Andriyashev, 1954; Craig et al., 1982; Mecklenburg and Sheiko, 2004; Pietsch, 1993). The same logic applies to colony-adjacent prey, with small invertebrates being more abundant in the middle of the water colomn (Iken et al., 2005), and sculpin near the bottom closer to shore (Vanier, 1996).

Woo et al. (2008) showed a high level of dietary specialisation among individuals at our study site, with some individuals coming back to their nest with otherwise rare prey types year after year. Our results suggest individuals specialize by having preferences for particular locations when foraging, while underwater behaviour has little effect on the bird's diet. For example, even capelin, the most widespread prey, was caught further from the colony by remote-prey specialists than by colony-adjacent specialists. This highlights the fact that individuals have stereotyped foraging location preference. All birds will likely capture the most energetically-profitable prey available at a given location, but the location chosen will change among individuals. Those foraging in the vicinity of the colony will have reduced travelling effort for each foraging trip. However, they will capture more frequently the less energetically-profitable prey and will need to compensate by increasing the number of trips. For example, we recorded adults feeding their chicks with invertebrates up to fours times in less than an hour (the average for all prey types combined was 2.4 times per day). On the other hand, other individuals will forage farther, increasing the chance of capturing a bigger prey, but making fewer trips per day.

In all cases, the geographic association of murres with their prey could give us great insight into the distribution of the marine fauna in the Arctic. Thick-billed murres can travel more than a hundred kilometers from the colony to forage for their chick. By simply equipping a certain number of murres with GPS tags coupled with feeding watches, a fish species map can quickly be established around the colony. A boat survey of the same area would be much more costly, and only provide a snapshot in time. The idea of using seabirds as indicator of the aquatic fauna is not new (Brisson-Curadeau et al., 2017a; Cairns, 1988; Piatt et al., 2007), but using their foraging behaviour to obtain insights of aquatic species distributions has not been exploited to its full potential. Whereas fish maps based on murre captures could be biased towards the energetically-profitable prey (recall that amphipods are probably present far from the colony for example), murres sample a larger spectrum of the food chain, from benthic to pelagic prey. Boat samples, on the contrary, are often restricted to particular prey. At the very least, seabirds could provide a cheaper complement to traditional sampling.

Research needs

While diving behaviour (maximum depth and dive type) were only weakly related to prey type in our experiment, more research needs to be done to completely rule out the importance of underwater behaviour. For example, all fish captures recorded with camera loggers occurred in the ascending phase, sometimes centimeters below the surface regardless of dive type. However, our study focused on the information of the deepest phase, where it was previously believed prey captures occurred (Elliott et al., 2008a). Our results suggest finer information should be used to provide better insights into underwater behaviour than maximum depth and dive type. The next step would be to use acceleration and identify where the last prey capture event occurred, using algorithms similar to the ones proposed by recent research (Chimienti et al., 2016; Watanabe and Takahashi, 2013). Perhaps individuals seeking amphipods would capture them more often during the descending phase, as supported by the observations made from camera loggers (many captures during descent, all of which were invertebrates). Birds seeking fish would catch their last prey in a dive at the deepest phase for deep water fish like *Triglops*, and during the ascent phase for pelagic fish like capelin (although we did record on camera one sculpin caught near the surface). Therefore, the acceleration profile could be used to identify when in the dive the prey was capture, and the associated parameter (depth, etc.) could be extracted at that moment rather than at the deepest point.

Another surprising behaviour that could potentially add error to the analysis is the observation of a bird that kept diving after it caught a fish for its chick. Probably, the individual was assessing the possibility of catching a bigger prey (exploration dive), increasing the energy gain of the chick while only slightly increasing foraging effort. Although the bird only dove at very superficial depth (<2m), barely detectable by the depth-logger, it is likely that if this behaviour is common, some individuals could dive pass the threshold of what we considered a dive. Since the bird in question sometimes flew between those exploration dives, it would mean that both geographic location variables and underwater variables might contain error if only the last dive bout is considered (Elliott et al., 2008a). A temporary solution would be to increase the depth criterion used to identify dives, eliminating all exploration dives without removing active foraging dives. More observations of exploration dives would be needed to determine the minimum depth to use in this case. Furthermore, accelerometers could again provide a solution to the problem, as considering the last catching event before the prey delivery to the chick would eliminate all those capture-less dives. However, a good validation of the algorithm determining prey capture using acceleration needs to be realized on thick-billed murres before this methodology is implemented.

General Conclusion

While there is still much work to be done before thick-billed murres are used as indicators of the changes of the Arctic marine ecosystem at a circumpolar scale, my work will facilitate future attempts to link the behaviour of this seabird with prey availability. The place of drones in the monitoring of at-colony information is more promising than ever, as their accuracy and efficiency to monitor cliff-nesting seabirds is now quantified. Furthermore, the impact they have on the behaviour of murres can be greatly reduced with the recommendations presented in my thesis. While the exact way in which at-colony measures can be related to prey availability is yet to be determined in the thick-billed murre, the use of drones is likely to facilitate future studies aiming to answer these questions.

As for at-sea behaviours, the pattern observed at large-scale, with individuals converging on particular foraging hotspots, implies that there is a correlation between foraging murres and their prey. In other words, movement of predator can be used to obtain information on prey distribution. At small scales, social associations probably drive the distribution patterns, so that associations with prey might be more difficult to quantify. On the other hand, the mechanisms of prey type selection, with different prey species being caught at different locations, implies that it is possible to use murres to obtain distribution maps of the different fish species preyed upon by the seabird. Of particular interest would be the use of magnetometers and accelerometers to record prey capture events, and possibly even assign prey size and type. The coupling of camera loggers and magnetometers/accelerometers could lead to such validations.

It will probably take many years before murres are efficiently used as sentinels of the sea, but the results of this thesis suggest that the avenue is promising. Hopefully, more research is done on this peculiar seabird species before climate change has affected too much of the fragile Arctic environment.

Literature cited

Ainley, D.G., Spear, L.B., Tynan, C.T., Barth, J.A., Pierce, S.D., Glenn Ford, R., and Cowles, T.J. (2005). Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. Deep Sea Res. Part II Top. Stud. Oceanogr. *52*, 123–143.

Ambrose, E.E., Solarin, B.B., Isebor, C.E., and Williams, A.B. (2005). Assessment of fish by-catch species from coastal artisanal shrimp beam trawl fisheries in Nigeria. Fish. Res. *71*, 125–132.

van Andel, A.C., Wich, S.A., Boesch, C., Koh, L.P., Robbins, M.M., Kelly, J., and Kuehl, H.S. (2015). Locating chimpanzee nests and identifying fruiting trees with an unmanned aerial vehicle: Locating Chimpanzee Nests With UAVs. Am. J. Primatol. *77*, 1122–1134.

Anderson, K., and Gaston, K.J. (2013). Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Front. Ecol. Environ. *11*, 138–146.

Andriyashev, A.P. (1954). Fishes of the northern seas of the USSR Keys to the fauna of the USSR Published by the Zoological Institute of the USSR. Acad. Sci. 266–269.

Angel, L.P., Barker, S., Berlincourt, M., Tew, E., Warwick-Evans, V., and Arnould, J.P.Y. (2015). Eating locally: Australasian gannets increase their foraging effort in a restricted range. Biol. Open *4*, 1298–1305.

Bairos-Novak, K.R., Crook, K.A., and Davoren, G.K. (2015). Relative importance of local enhancement as a search strategy for breeding seabirds: an experimental approach. Anim. Behav. *106*, 71–78.

Bayer, R.D. (1981). Arrival and Departure Frequencies of Great Blue Herons at Two Oregon Estuarine Colonies. The Auk *98*, 589–595.

Bednarz, J.C. (2018). Cooperative Hunting Harris' Hawks. 4.

Benvenuti, S., Dall'Antonia, L., and Falk, K. Diving behaviour differs between incubating and brooding Bru¨ nnich's guillemots, Uria lomvia. 5.

Berlincourt, M., and Arnould, J.P.Y. (2014). At-Sea Associations in Foraging Little Penguins. PLoS ONE *9*, e105065.

Bertrand, S., Joo, R., Smet, C.A., Tremblay, Y., Barbraud, C., and Weimerskirch, H. (2012). Local depletion by a fishery can affect seabird foraging. J. Appl. Ecol. *49*, 1168–1177.

Bock, C.E., and Webb, B. (1984). Birds as Grazing Indicator Species in Southeastern Arizona. J. Wildl. Manag. *48*, 1045–1049.

Boé, J., Hall, A., and Qu, X. (2009). September sea-ice cover in the Arctic Ocean projected to vanish by 2100. Nat. Geosci. *2*, 341–343.

Boyd, C., Castillo, R., Hunt, G.L., Punt, A.E., VanBlaricom, G.R., Weimerskirch, H., and Bertrand, S. (2015). Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. J. Anim. Ecol. *84*, 1575–1588.

Brisson-Curadeau, E., Patterson, A., Whelan, S., Lazarus, T., and Elliott, K.H. (2017a). Tracking Cairns: Biologging Improves the Use of Seabirds as Sentinels of the Sea. Front. Mar. Sci. *4*.

Brisson-Curadeau, É., Bird, D., Burke, C., Fifield, D.A., Pace, P., Sherley, R.B., and Elliott, K.H. (2017b). Seabird species vary in behavioural response to drone census. Sci. Rep. *7*.

Brown, C.R. (1986). Cliff Swallow Colonies as Information Centers. Science *234*, 83–85.

Brown, R.G.B., Nettleship, D.N., Germain, P., and Tull, C.E. (1975). Atlas of eastern Canadian seabirds.

Bryant, R., Jones, I.L., and Hipfner, J.M. (1999). Responses to changes in prey availability by Common Murres and Thick-billed Murres at the Gannet Islands, Labrador. *77*, 10.

Buckley, N.J. (1997a). Spatial-Concentration Effects and the Importance of Local Enhancement in the Evolution of Colonial Breeding in Seabirds. Am. Nat. *149*, 1091–1112.

Buckley, N.J. (1997b). Experimental tests of the information-center hypothesis with black vultures (Coragypsatratus) and turkey vultures (Cathartesaura). Behav. Ecol. Sociobiol. *41*, 267–279.

Burger, A.E. (1997). Arrival and Departure Behavior of Common Murres at Colonies: Evidence for an Information Halo? Colon. Waterbirds *20*, 55–65.

Burger, A.E., and Shaffer, S.A. (2008). Application of tracking and data-logging technology in research and conservation of seabirds. The Auk *125*, 253–264.

Burnham, K.P., Anderson, D.R., and Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. *65*, 23–35.

Cairns, D.K. (1988). Seabirds as Indicators of Marine Food Supplies. Biol. Oceanogr. *5*, 261–271.

Cairns, D.K., and Schneider, D.C. (1990). Hot spots in cold water: feeding habitat selection by thick-billed murres. Stud. Avian Biol. *14*, 52–69.

Campobello, D., and Hare, J.F. (2007). Information transfer determined by association of neighbours in European bee-eater (*Merops apiaster*) colonies. Ethol. Ecol. Evol. *19*, 237–243.

Casale, P. (2011). Sea turtle by-catch in the Mediterranean: Sea turtle by-catch in the Mediterranean. Fish Fish. *12*, 299–316.

Casey, S. (2010). The Wave: In the Pursuit of the Rogues, Freaks and Giants of the Ocean.

Catry, P., Phillips, R., Phalan, B., Silk, J., and Croxall, J. (2004). Foraging strategies of grey-headed albatrosses Thalassarche chrysostoma: integration of movements, activity and feeding events. Mar. Ecol. Prog. Ser. *280*, 261–273.

Chabot, D., and Bird, D.M. (2015). Wildlife research and management methods in the 21st century: Where do unmanned aircraft fit in? J. Unmanned Veh. Syst. *3*, 137–155.

Chabot, D., Craik, S.R., and Bird, D.M. (2015). Population Census of a Large Common Tern Colony with a Small Unmanned Aircraft. PLOS ONE *10*, e0122588.

Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I.M., Travis, J.M.J., and Scott, B.E. (2016). The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. Ecol. Evol. *6*, 727–741.

Cohen, L., Pichegru, L., Grémillet, D., Coetzee, J., Upfold, L., and Ryan, P. (2014). Changes in prey availability impact the foraging behaviour and fitness of Cape gannets over a decade. Mar. Ecol. Prog. Ser. *505*, 281–293.

Cook, L.M., Brower, L.P., and Croze, H.J. (1967). The Accuracy of a Population Estimation from Multiple Recapture Data. J. Anim. Ecol. *36*, 57–60.

Cook, T.R., Gubiani, R., Ryan, P.G., and Muzaffar, S.B. (2017). Group foraging in Socotra cormorants: A biologging approach to the study of a complex behavior. Ecol. Evol. *7*, 2025–2038.

Coulson, J.C. (2001). Colonial breeding in seabirds. In Biology of Marine Birds, pp. 87–113.

Craig, P.C., Griffiths, W.B., Haldorson, L., and McElderry, H. (1982). Ecological Studies of Arctic Cod (Boreogadus saida) in Beaufort Sea Coastal Waters, Alaska. Can. J. Fish. Aquat. Sci. *39*, 395–406.

Crawford, R.J.M., Barham, P.J., Underhill, L.G., Shannon, L.J., Coetzee, J.C., Dyer, B.M., Leshoro, T.M., and Upfold, L. (2006). The influence of food availability on breeding success of African penguins Spheniscus demersus at Robben Island, South Africa. Biol. Conserv. *132*, 119–125.

Croll, D.A., Demer, D.A., Hewitt, R.P., Jansen, J.K., Goebel, M.E., and Tershy, B.R. (2006). Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (Pygoscelis antarctica). J. Zool. *269*, 506–513.

Cury, P.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J.M., Furness, R.W., Mills, J.A., Murphy, E.J., Osterblom, H., Paleczny, M., et al. (2011). Global Seabird Response to Forage Fish Depletion--One-Third for the Birds. Science *334*, 1703–1706.

Daufresne, M., Lengfellner, K., and Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. Proc. Natl. Acad. Sci. *106*, 12788–12793.

Davoren, G.K., and Burger, A.E. (1999). Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. Anim. Behav. *58*, 853–863.

Davoren, G.K., Montevecchi, W.A., and Anderson, J.T. (2003). Search strategies of a pursuit-diving marine bird and the persistence of prey patches. Ecol. Monogr. *73*, 463–481.

Ditmer, M.A., Vincent, J.B., Werden, L.K., Tanner, J.C., Laske, T.G., Iaizzo, P.A., Garshelis, D.L., and Fieberg, J.R. (2015). Bears Show a Physiological but Limited Behavioral Response to Unmanned Aerial Vehicles. Curr. Biol. *25*, 2278–2283.

Dutilleul, P. (2011). Spatio-temporal heterogeneity: Concepts and analyses.

Elliott, K.H., and Gaston, A.J. (2008). Mass–length relationships and energy content of fishes and invertebrates delivered to nestling thick-billed murres uria lomvia in the canadian arctic, 1981–2007. 10.

Elliott, K.H., and Gaston, A.J. (2014). Dive behaviour and daily energy expenditure in thick-billed murres uria lomvia after leaving the breeding colony. 8.

Elliott, K., Woo, K., Gaston, A., Benvenuti, S., Dall'Antonia, L., and Davoren, G. (2008a). Seabird foraging behaviour indicates prey type. Mar. Ecol. Prog. Ser. *354*, 289–303.

Elliott, K.H., Davoren, G.K., and Gaston, A.J. (2007). The influence of buoyancy and drag on the dive behaviour of an Arctic seabird, the Thick-billed Murre. Can. J. Zool. *85*, 352–361.

Elliott, K.H., Davoren, G.K., and Gaston, A.J. (2008b). Time allocation by a deep-diving bird reflects prey type and energy gain. Anim. Behav. *75*, 1301–1310.

Elliott, K.H., Jacobs, S.R., Ringrose, J., Gaston, A.J., and Davoren, G.K. (2008c). Is mass loss in Brünnich's guillemots Uria lomvia an adaptation for improved flight performance or improved dive performance? J. Avian Biol. *39*, 619–628.

Elliott, K.H., Woo, K.J., Gaston, A.J., Benvenuti, S., Dall'Antonia, L., and Davoren, G.K. (2009a). Central-place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. The Auk *126*, 613–625.

Elliott, K.H., Bull, R.D., Gaston, A.J., and Davoren, G.K. (2009b). Underwater and above-water search patterns of an Arctic seabird: reduced searching at small spatiotemporal scales. Behav. Ecol. Sociobiol. *63*, 1773–1785.

Elliott, K.H., Woo, K.J., and Benvenuti, S. (2009c). Do activity costs determine foraging tactics for an arctic seabird? Mar. Biol. *156*, 1809–1816.

Elliott, K.H., Gaston, A.J., and Crump, D. (2010). Sex-specific behavior by a monomorphic seabird represents risk partitioning. Behav. Ecol. *21*, 1024–1032.

Elliott, K.H., Le Vaillant, M., Kato, A., Gaston, A.J., Ropert-Coudert, Y., Hare, J.F., Speakman, J.R., and Croll, D. (2014a). Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. J. Anim. Ecol. *83*, 136–146.

Elliott, K.H., Chivers, L.S., Bessey, L., Gaston, A.J., Hatch, S.A., Kato, A., Osborne, O., Ropert-Coudert, Y., Speakman, J.R., and Hare, J.F. (2014b). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. Mov. Ecol. *2*.

Eschmeyer, W.N., and Herald, E.S. (1999). A field guide to Pacific coast fishes: North America (Houghton Mifflin Harcourt).

ESRI (2011). ArcGIS Desktop: Release 10 (Environmental Systems Research Institute).

Fauchald, P., and Tveraa, T. (2006). Hierarchical Patch Dynamics and Animal Movement Pattern. Oecologia *149*, 383–395.

Fauchald, P., Erikstad, K.E., and Skarsfjord, H. (2000). Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology *81*, 773–783.

Gaston, A. (2002). Thick-billed Murre populations in the Eastern Canadian Arctic, 1976-2000.

Gaston, A.J. (1998). The auks: alcidae (USA).

Gaston, A.J. (2003). Synchronous fluctuations of thick-billed murre (uria lomvia) colonies in the eastern canadian arctic suggest population regulation in winter. The Auk *120*, 362.

Gaston, A.J., and Nettleship, D.N. (1981). The thick-billed murres of Prince Leopold Island (Ottawa).

Gaston, A.J., and Nettleship, D.N. (1982). Factors Determining Seasonal Changes in Attendance at Colonies of the Thick-Billed Murre Uria lomvia. The Auk *99*, 468–473.

Gaston, A.J., Decker, R., Cooch, F.G., and Reed, A. (1986). The Distribution of Larger Species of Birds Breeding on the Coasts of Foxe Basin and Northern Hudson Bay, Canada. Arctic *39*, 285–296.

Gaston, A.J., Smith, P.A., Tranquilla, L.M., Montevecchi, W.A., Fifield, D.A., Gilchrist, H.G., Hedd, A., Mallory, M.L., Robertson, G.J., and Phillips, R.A. (2011). Movements and wintering areas of breeding age Thick-billed Murre Uria lomvia from two colonies in Nunavut, Canada. Mar. Biol. *158*, 1929–1941.

Gaston, A.J., Mallory, M.L., and Gilchrist, H.G. (2012). Populations and trends of Canadian Arctic seabirds. Polar Biol. *35*, 1221–1232.

Gaston, A.J., Elliott, K.H., Ropert-Coudert, Y., Kato, A., Macdonald, C.A., Mallory, M.L., and Gilchrist, H.G. (2013). Modeling foraging range for breeding colonies of thick-billed murres

Uria lomvia in the Eastern Canadian Arctic and potential overlap with industrial development. Biol. Conserv. *168*, 134–143.

Gerritsen, J., and Strickler, J.R. (1977). Encounter Probabilities and Community Structure in Zooplankton: a Mathematical Model. J. Fish. Res. Board Can. *34*, 73–82.

Gilchrist, H.G. (1999). Declining thick-billed murre Uria lomvia colonies experience higher gull predation rates: an inter-colony comparison. Biol. Conserv. *87*, 21–27.

Giraldeau, L.A., and Caraco, T. (2000). Social foraging theory.

Goebel, M.E., Perryman, W.L., Hinke, J.T., Krause, D.J., Hann, N.A., Gardner, S., and LeRoi, D.J. (2015). A small unmanned aerial system for estimating abundance and size of Antarctic predators. Polar Biol. *38*, 619–630.

Grant, J.W.A. (1993). Whether or not to defend? The influence of resource distribution. Mar. Behav. Physiol. *23*, 137–153.

Grémillet, D., Lewis, S., Drapeau, L., van Der Lingen, C.D., Huggett, J.A., Coetzee, J.C., Verheye, H.M., Daunt, F., Wanless, S., and Ryan, P.G. (2008). Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? J. Appl. Ecol. *45*, 610–621.

Grémillet, D., Puech, W., Garçon, V., Boulinier, T., and Maho, Y.L. (2012). Robots in Ecology: Welcome to the machine. Open J. Ecol. *02*, 49–57.

Grenzdörffer, G.J. (2013). UAS-based automatic bird count of a common gull colony. ISPRS - Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci. *XL-1/W2*, 169–174.

Guigueno, M.F., and Sealy, S.G. (2011). Aggression towards egg-removing cowbird elicits clutch abandonment in parasitized yellow warblers, Dendroica petechia. Anim. Behav. *81*, 211–218.

Häder, D.-P., Kumar, H.D., Smith, R.C., and Worrest, R.C. (2007). Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. Photochem Photobiol Sci *6*, 267–285.

Halliday, T.R. (1980). The extinction of the passenger pigeon ectopistes migratorius and its relevance to contemporary conservation. Biol. Conserv. *17*, 157–162.

Halliwell, B., Uller, T., Wapstra, E., and While, G.M. (2017). Resource distribution mediates social and mating behavior in a family living lizard. Behav. Ecol. *28*, 145–153.

Harding, A., Piatt, J., and Schmutz, J. (2007). Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. Mar. Ecol. Prog. Ser. *352*, 269–274.

Harding, A., Paredes, R., Suryan, R., Roby, D., Irons, D., Orben, R., Renner, H., Young, R., Barger, C., Dorresteijn, I., et al. (2013). Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep Sea Res. Part II Top. Stud. Oceanogr. *94*, 178–191.

Hatch, S.A., and Hatch, M.A. (1989). Attendance Patterns of Murres at Breeding Sites: Implications for Monitoring. J. Wildl. Manag. *53*, 483–493.

Hipfner, J.M. (2005). Population status of the common murre uria aalge in british columbia, canada. 4.

Hipfner, J.M., Gaston, A.J., and Smith, B.D. (2006). Regulation of provisioning rate in the Thick-billed Murre (Uria lomvia). Can. J. Zool. *84*, 931–938.

Hobson, K. (1993). Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Mar. Ecol. Prog. Ser. *95*, 7–18.

Hodgson, A., Kelly, N., and Peel, D. (2013). Unmanned Aerial Vehicles (UAVs) for Surveying Marine Fauna: A Dugong Case Study. PLoS ONE *8*, e79556.

Iken, K., Bluhm, B., and Gradinger, R. (2005). Food web structure in the high Arctic Canada Basin: evidence from ?13C and ?15N analysis. Polar Biol. *28*, 238–249.

Ito, M., Takahashi, A., Kokubun, N., Kitaysky, A., and Watanuki, Y. (2010). Foraging behavior of incubating and chick-rearing thick-billed murres Uria lomvia. Aquat. Biol. *8*, 279–287.

Junda, J., Greene, E., and Bird, D.M. (2015). Proper flight technique for using a small rotary-winged drone aircraft to safely, quickly, and accurately survey raptor nests. J. Unmanned Veh. Syst. *3*, 222–236.

Junda, J.H., Greene, E., Zazelenchuk, D., and Bird, D.M. (2016). Nest defense behaviour of four raptor species (osprey, bald eagle, ferruginous hawk, and red-tailed hawk) to a novel aerial intruder – a small rotary-winged drone. J. Unmanned Veh. Syst. *4*, 217–227.

Kampp, K. (1990). The Thick-Billed Murre Population of the Thule District, Greenland. Arctic *43*, 115–120.

Kleiber, P., and Maunder, M.N. (2008). Inherent bias in using aggregate CPUE to characterize abundance of fish species assemblages. Fish. Res. *93*, 140–145.

Koh, L.P., and Wich, S.A. (2012). Dawn of Drone Ecology: Low-Cost Autonomous Aerial Vehicles for Conservation. Trop. Conserv. Sci. *5*, 121–132.

Kokubun, N., Yamamoto, T., Sato, N., Watanuki, Y., Will, A., Kitaysky, A., and Takahashi, A. (2015). Foraging segregation of two congeneric diving seabird species (common and thick-billed murres) breeding on St. George Island, Bering Sea. Biogeosciences Discuss 18151–18183.

Krebs, J.R. (1974). Colonial Nesting and Social Feeding as Strategies for Exploiting Food Resources in the Great Blue Heron (Ardea herodias). Behaviour *51*, 99–134.

Le Maho, Y., Whittington, J.D., Hanuise, N., Pereira, L., Boureau, M., Brucker, M., Chatelain, N., Courtecuisse, J., Crenner, F., Friess, B., et al. (2014). Rovers minimize human disturbance in research on wild animals. Nat. Methods *11*, 1242–1244.

Lescroël, A., Mathevet, R., Péron, C., Authier, M., Provost, P., Takahashi, A., and Grémillet, D. (2016). Seeing the ocean through the eyes of seabirds: A new path for marine conservation? Mar. Policy *68*, 212–220.

Linchant, J., Lisein, J., Semeki, J., Lejeune, P., and Vermeulen, C. (2015). Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. Mammal Rev. *45*, 239–252.

Linnebjerg, J.F., Huffeldt, N.P., Falk, K., Merkel, F.R., Mosbech, A., and Frederiksen, M. (2014). Inferring seabird activity budgets from leg-mounted time–depth recorders. J. Ornithol. *155*, 301–306.

Linnebjerg, J.F., Reuleaux, A., Mouritsen, K.N., and Frederiksen, M. (2015). Foraging Ecology of Three Sympatric Breeding Alcids in a Declining Colony in Southwest Greenland. Waterbirds *38*, 143–152.

Litzow, M.A., and Piatt, J.F. (2003). Variance in prey abundance influences time budgets of breeding seabirds: evidence from pigeon guillemots Cepphus columba. J. Avian Biol. *34*, 54–64.

Lønne, O.J., and Gulliksen, B. (1989). Size, age and diet of polar cod, Boreogadus saida (Lepechin 1773), in ice covered waters. Polar Biol. *9*, 187–191.

Lovvorn, J.R. (2004). Stroke patterns and regulation of swim speed and energy cost in free-ranging Brunnich's guillemots. J. Exp. Biol. *207*, 4679–4695.

Ludynia, K., Dehnhard, N., Poisbleau, M., Demongin, L., Masello, J.F., and Quillfeldt, P. (2012). Evaluating the Impact of Handling and Logger Attachment on Foraging Parameters and Physiology in Southern Rockhopper Penguins. PLoS ONE *7*, e50429.

Marchand, C., Simard, Y., and Gratton, Y. (1999). Concentration of capelin (Mallotus villosus) in tidal upwelling fronts at the head of the Laurentian Channel in the St. Lawrence estuary. Can. J. Fish. Aquat. Sci. *56*, 1832–1848.

Marris, E. (2013). Fly, and bring me Data. Science *498*, 153–156.

Mcclelland, G.T.W., Bond, A.L., Sardana, A., and Glass, T. (2016). Rapid population estimate of a surface-nesting seabird on a remote island using a low-cost unmanned aerial vehicle. 6.

McEvoy, J.F., Hall, G.P., and McDonald, P.G. (2016). Evaluation of unmanned aerial vehicle shape, flight path and camera type for waterfowl surveys: disturbance effects and species recognition. PeerJ *4*, e1831.

McFarlane Tranquilla, L., Montevecchi, W.A., Hedd, A., Regular, P.M., Robertson, G.J., Fifield, D.A., and Devillers, R. (2015). Ecological segregation among Thick-billed Murres (*Uria lomvia*) and Common Murres (*Uria aalge*) in the Northwest Atlantic persists through the nonbreeding season. Can. J. Zool. *93*, 447–460.

Mecklenburg, C.W., and Sheiko, B.A. (2004). Family Stichaeidae Gill 1864 - pricklebacks (California Academy of Sciences).

Meehan, R., and Divoky, G. (1998). Implications of climate change for Alaska's seabirds. Assess. Consequences Clim. Change Alsk. Bering Sea Reg. *29*, 75–89.

Mehlum, F., Hunt, G.L., Decker, M.B., and Nordlund, N. (1998). Hydrographic Features, Cetaceans and the Foraging of Thick-Billed Murres and Other Marine Birds in the Northwestern Barents Sea. Arctic *51*, 243–252.

Meier, H.E.M., Döscher, R., and Halkka, A. (2004). Simulated Distributions of Baltic Sea-ice in Warming Climate and Consequences for the Winter Habitat of the Baltic Ringed Seal. AMBIO J. Hum. Environ. *33*, 249–256.

Mock, D.W., Lamey, T.C., and Thompson, D.B.A. (1988). Falsifiability and the Information Centre Hypothesis. Ornis Scand. Scand. J. Ornithol. *19*, 231–248.

Monaghan, P., Walton, P., Wanless, S., Uttley, J.D., and Bljrns, M.D. (2008). Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots Uria aalge. Ibis *136*, 214–222.

Montevecchi, W.A. (1993). Birds as indicators of change in marine prey stocks. In Birds as Monitors of Environmental Change, (Dordrecht: Springer), p.

Montevecchi, W.A., Hedd, A., McFarlane Tranquilla, L., Fifield, D.A., Burke, C.M., Regular, P.M., Davoren, G.K., Garthe, S., Robertson, G.J., and Phillips, R.A. (2012). Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. Biol. Conserv. *156*, 62–71.

Mori, Y., Takahashi, A., Mehlum, F., and Watanuki, Y. (2002). An application of optimal diving models to diving behaviour of Brünnich's guillemots. Anim. Behav. *64*, 739–745.

NOAA (2017). National Oceanic and Atmospheric Administration (USA).

Oro, D., and Furness, R.W. (2002). Influences of food availability and predation on survival of kittiwakes. Ecology *83*, 2516–2528.

Österblom, H., Casini, M., Olsson, O., and Bignert, A. (2006). Fish, seabirds and trophic cascades in the Baltic Sea. Mar. Ecol. Prog. Ser. *323*, 233–238.

Paredes, R., Orben, R., Roby, D., Irons, D., Young, R., Renner, H., Tremblay, Y., Will, A., Harding, A., and Kitaysky, A. (2015). Foraging ecology during nesting influences body size in a pursuit-diving seabird. Mar. Ecol. Prog. Ser. *533*, 261–276.

Patricelli, G.L., Uy, J.A.C., Walsh, G., and Borgia, G. (2002). Male displays adjusted to female's response. Nature *415*, 279–280.

Peterken, G.F. (1974). A method for assessing woodland flora for conservation using indicator species. Biol. Conserv. *6*, 239–245.

Piatt, J., Harding, A., Shultz, M., Speckman, S., van Pelt, T., Drew, G., and Kettle, A. (2007). Seabirds as indicators of marine food supplies: Cairns revisited. Mar. Ecol. Prog. Ser. *352*, 221–234.

Pichegru, L., Gremillet, D., Crawford, R.J.M., and Ryan, P.G. (2010). Marine no-take zone rapidly benefits endangered penguin. Biol. Lett. *6*, 498–501.

Pietsch, T.W. (1993). Systematics and distribution of cottid fishes of the genus Triglops Reinhardt (Teleostei: Scorpaeniformes). Zool. J. Linn. Soc. *109*, 335–393.

Poff, N.L., Brinson, M.M., and Day, J.W. (2002). Aquatic ecosystems and global climate change. Pew Cent. Glob. Clim. Change Arlingt. 1–36.

Provencher, J.F., Elliott, K.H., Gaston, A.J., and Braune, B.M. (2013). Networks of prey specialization in an Arctic monomorphic seabird. J. Avian Biol. *44*, 551–560.

R Development Core Team (2014). R: A language and environment for statistical computing (Vienna, Austria: R Foundation for Statistical Computing).

Ratcliffe, N., Guihen, D., Robst, J., Crofts, S., Stanworth, A., and Enderlein, P. (2015). A protocol for the aerial survey of penguin colonies using UAVs. J. Unmanned Veh. Syst. *3*, 95–101.

Richards, L.J., and Schnute, J.T. (1986). An experimental and statistical approach to the question: is CPUE an index of abundance? Can. J. Fish. Aquat. Sci. 1214–1227.

Rolstad, J., Gjerde, I., Gundersen, V.S., and Saetersdal, M. (2002). Use of Indicator Species to Assess Forest Continuity: a Critique. Conserv. Biol. *16*, 253–257.

Rose, G.A., and Kulka, D.W. (1999). Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (Gadus morhua) declined. Can. J. Fish. Aquat. Sci. *56*, 118–127.

Ruiz-Olmo, J., and Jiménez, J. (2009). Diet diversity and breeding of top predators are determined by habitat stability and structure: a case study with the Eurasian otter (Lutra lutra L.). Eur. J. Wildl. Res. *55*, 133–144.

Salthaug, A., and Godø, O.R. (2000). Analysis of CPUE from the Norwegian bottom trawl fleet. 14.

Sardà-Palomera, F., Bota, G., ViñOlo, C., PallaréS, O., Sazatornil, V., Brotons, L., GomáRiz, S., and Sardà, F. (2012). Fine-scale bird monitoring from light unmanned aircraft systems: *Bird monitoring from UAS*. Ibis *154*, 177–183.

Sasse, D.B. (2001). Monitoring of biological diversity in space and time. Trends Ecol. Evol. *16*.

Schnabel, Z.E. (1938). The Estimation of Total Fish Population of a Lake. Am. Math. Mon. *45*, 348–352.

Schuttler, S.G., Ruiz-López, M.J., Monello, R., Wehtje, M., Eggert, L.S., and Gompper, M.E. (2015). The interplay between clumped resources, social aggregation, and genetic relatedness in the raccoon. Mammal Res. *60*, 365–373.

Scott, B., Sharples, J., Ross, O., Wang, J., Pierce, G., and Camphuysen, C. (2010). Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. Mar. Ecol. Prog. Ser. *408*, 207–226.

Silverman, E., Veit, R., and Nevitt, G. (2004). Nearest neighbors as foraging cues: information transfer in a patchy environment. Mar. Ecol. Prog. Ser. *277*, 25–36.

Simard, Y., Lavoie, D., and Saucier, F.J. (2002). Channel head dynamics: capelin (Mallotus villosus) aggregation in the tidally driven upwelling system of the Saguenay - St. Lawrence Marine Park's whale feeding ground. Can. J. Fish. Aquat. Sci. *59*, 197–210.

Slagstad, D., Ellingsen, I.H., and Wassmann, P. (2011). Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: An experimental simulation approach. Prog. Oceanogr. *90*, 117–131.

Spiegel, O., Leu, S.T., Bull, C.M., and Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecol. Lett. *20*, 3–18.

Spieler, M. (2003). Risk of predation affects aggregation size: a study with tadpoles of Phrynomantis microps (Anura: Microhylidae). Anim. Behav. *65*, 179–184.

Suryan, R., Irons, D., Kaufman, M., Benson, J., Jodice, P., Roby, D., and Brown, E. (2002). Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake Rissa tridactyla. Mar. Ecol. Prog. Ser. *236*, 273–287.

Takahashi, A., Matsumoto, K., Hunt, G.L., Shultz, M.T., Kitaysky, A.S., Sato, K., Iida, K., and Watanuki, Y. (2008). Thick-billed murres use different diving behaviors in mixed and stratified waters. Deep Sea Res. Part II Top. Stud. Oceanogr. *55*, 1837–1845.

Thiebault, A., Mullers, R.H.E., Pistorius, P.A., and Tremblay, Y. (2014). Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. Behav. Ecol. *25*, 1302–1310.

Timmermans, M.L. (2015). Sea Surface Temperature.

Vader, W., Barrett, R.T., Erikstad, K.E., and Strann, K.B. (1990). Differential responses of common and thick-billed murres to a crash in the capelin stock in the southern Barents Sea. Stud. Avian Biol. *14*, 175–180.

Vanier, B. (1996). Répartition des ressources spatiale et alimentaire chez quatre espèces de cottidés, Myoxocephalus quadricornis, M. scorpius, M. scorpioides et Gymnocanthus tricuspis, cohabitant la cṭ̥e orientale de la baie de James, Canada. National Library of Canada = Bibliothq̈ue nationale du Canada.

Vas, E., Lescroel, A., Duriez, O., Boguszewski, G., and Gremillet, D. (2015). Approaching birds with drones: first experiments and ethical guidelines. Biol. Lett. *11*, 20140754–20140754.

Vermeulen, C., Lejeune, P., Lisein, J., Sawadogo, P., and Bouché, P. (2013). Unmanned Aerial Survey of Elephants. PLoS ONE *8*, e54700.

Ward, P., and Zahavi, A. (2008). The importance of certain assemblages of birds as “information-centres” for food-finding. Ibis *115*, 517–534.

Watanabe, Y.Y., and Takahashi, A. (2013). Linking animal-borne video to accelerometers reveals prey capture variability. Proc. Natl. Acad. Sci. *110*, 2199–2204.

Watanuki, Y., Daunt, F., Takahashi, A., Newell, M., Wanless, S., Sato, K., and Miyazaki, N. (2008). Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers. Mar. Ecol. Prog. Ser. *356*, 283–293.

Waters, W.E. (1959). A Quantitative Measure of Aggregation in Insects1. J. Econ. Entomol. *52*, 1180–1184.

Weimerskirch, H., Gault, A., and Cherel, Y. (2005). Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. Ecology *86*, 2611–2622.

Wessel, P., and Smith, W.H.F. (1996). A global, self-consistent, hierarchical, high-resolution shoreline database. J. Geophys. Res. Solid Earth *101*, 8741–8743.

White, G.C. (1996). NOREMARK: Population Estimation from Mark-Resighting Surveys. Wildl. Soc. Bull. 1973-2006 *24*, 50–52.

Wilschut, L.I., Laudisoit, A., Hughes, N.K., Addink, E.A., de Jong, S.M., Heesterbeek, H.A.P., Reijniers, J., Eagle, S., Dubyanskiy, V.M., and Begon, M. (2015). Spatial distribution patterns of plague hosts: point pattern analysis of the burrows of great gerbils in Kazakhstan. J. Biogeogr. *42*, 1281–1292.

Wittenberger, J.F. (1985). The adaptive significance of coloniality in birds. Avian Biol. 1–78.

Woo, K.J., Elliott, K.H., Davidson, M., Gaston, A.J., and Davoren, G.K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. J. Anim. Ecol. *77*, 1082–1091.

Wyllie-Echerrieva, T., and Wooster, W.S. (1998). Year-to-year variations in Bering Sea ice cover and some consequences for ®sh distributions. Fish Ocean. 12.

Yoccoz, N.G., Nichols, J.D., and Boulinier, T. (2001). Monitoring of biological diversity in space and time. Trends Ecol. Evol. *16*, 446–453.

Zamon, J.E., Phillips, E.M., and Guy, T.J. (2014). Marine bird aggregations associated with the tidally-driven plume and plume fronts of the Columbia River. Deep Sea Res. Part II Top. Stud. Oceanogr. *107*, 85–95.

Zippin, C. (1958). The Removal Method of Population Estimation. J. Wildl. Manag. *22*, 82–90.

Zmarz, A., Korczak-Abshire, M., Storvold, R., Rodzewicz, M., and Kędzierska, I. (2015). Indicator species population monitoring in antarctica with uav. ISPRS - Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci. *XL-1/W4*, 189–193.