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How seabirds respond to a changing oceanic environment: A biologging approach

Thesis presented by

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for the degree of

Doctor of Philosophy

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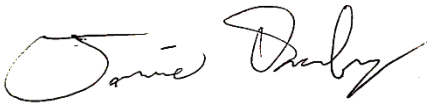
Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property.

Signed: 

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Go raibh míle maith agaibh go léir.

ABSTRACT

Marine habitats are undergoing rapid change due to human influences. The intensity and diversity of human impacts on oceanic habitats are increasing with rising demand for energy and resources. For example, fisheries operate in over 90% of the ocean, harvesting marine life and directly affecting ecosystem functions and resilience. Climate change is also changing the physical and chemical properties of the ocean and altering storm frequency and intensity at a global scale. Seabirds are a group of marine predators that are sensitive to such changes, with impacts contributing to global population declines. We broadly understand how stressors affect different species through effects on life histories and physiological traits, and where seabirds are most impacted based on spatiotemporal overlap of seabirds with human activities. However, finer scale behavioural data are required to understand the functional response of seabirds to different stressors.

Biologging devices are continuously improving and miniaturising, being applied to collect fine-scale behavioural information for smaller species and for more protracted durations. In this thesis, biotelemetry is used to investigate the at-sea behaviour of three North Atlantic seabird species in order to understand the drivers of distribution. A better understanding of such drivers sheds light on the challenges facing seabird species when far from land, susceptibility to stressors, and provides insights into more effective monitoring and conservation efforts.

Chapter 1 provides a broad introduction to seabird ecology, the application of biologging, and identifies model species for investigating seabird responses to a range of environmental stressors. Chapter 2 investigates the diving behaviour of Manx shearwaters (*Puffinus puffinus*) and how this correlates with water clarity, which is predicted to deteriorate with increasing urbanisation, eutrophication, and climate impacts. Chapter 3 highlights the relative importance of commercial fisheries compared to other environmental variables in driving the foraging distribution and behaviour of northern fulmars (*Fulmarus glacialis*) during the breeding season. Chapter 4 expands on this by identifying fulmar-vessel encounters in the non-breeding season, showing how nocturnal vessel attendance is increasing over time, and the apparent relationship with migration effort and time-activity budgets.

Chapter 5 identifies unusual levels of variability in the moult period of Atlantic puffins (*Fratercula arctica*), when they are flightless and more susceptible to climate impacts that may prevent them from foraging. Variability in moult strategy is tied to susceptibility of populations to risks posed by severe winter storms.

Chapter 6 provides a synthesis of findings from previous chapters, highlighting how the methods and principles developed may be built upon to further improve our knowledge of seabird ecology and design appropriate conservation measures. Building on insights from previous chapters, I discuss how seabirds are likely to functionally respond to several stressors in the marine environment, including fisheries practices, climate change, and shifting prey availability. Several recommendations are made for further research, including exploring mitigative measures that can be employed to tackle the negative effects of changes to their environment.

CHAPTER 1: INTRODUCTION TO THE MARINE ENVIRONMENT, SEABIRDS, AND BIOLOGGING

1.1 Changing oceanic habitats

The world's oceans are being influenced by human industry, with studies suggesting almost all oceanic habitats are being altered by impacts such as climate change, fisheries, pollution, disturbance, among others (Halpern et al. 2008). The diversity and intensity of human activity at sea is ever-increasing, while our understanding of the consequences for marine life often lags behind these industrial developments. Impacts vary in their extent, from altering singular populations, to affecting whole ecosystems.

The accumulation of stressors now present in the ocean has a widespread damaging effect on the biota that inhabit it. Continuously rising human populations and the accompanying demand for resources mean that these pressures are unlikely to abate, despite efforts to monitor and mitigate against associated negative impacts, such as through improved monitoring of fisheries (Kroodsma et al. 2018) or multinational pledges to limit the extent of climate change (UNFCCC 2015). As a consequence, over 40% of marine species studied are threatened or near threatened according to International Union for the Conservation of Nature (IUCN) classification (O' Hara et al. 2019). Seabirds are one group of marine species that has undergone rapid declines in recent decades, in large parts due to changes in the marine environment (Dias et al. 2019).

1.2 Seabirds and their marine environment

Pelagic seabirds are defined as bird species that spend a considerable portion of their life on the open ocean, far from land, often only venturing onshore to breed (Brooke 2018) and are well-adapted for a life at sea. Seabirds are a key component of oceanic and coastal ecosystems that transfer nutrients from the open ocean back to their terrestrial breeding colonies (Ellis et al. 2006).

For some species, impressive flight capabilities and endurance often help to navigate and find food over a vast oceanic habitat where food can be patchily distributed, and

many can cover huge distances. Gadfly petrels cover thousands of kilometres in a single foraging trip, opportunistically stopping to feed along the way (Clay et al. 2018). Albatrosses use dynamic soaring, combining large wingspans with predictable and strong winds to remain airborne for protracted periods and cover huge distances to find food (Weimerskirch et al. 2000). Frigatebirds use thermals and associated updrafts at sea to gain altitude, then glide in the desired direction of travel, an extremely efficient means of travel that allows them to exploit scarce resources in tropical pelagic habitats (Weimerskirch et al. 2003).

Other pelagic seabirds tend not to cover such huge above-water distances in the search for food, specialising in other means of locating prey patches. Large auk species are adapted for deep dives in pursuit of their prey, with Brünnich's guillemots (*Uria lomvia*) recorded diving up to 140m depth, with longer dives lasting over 4 minutes (Elliott et al. 2008). Species regularly diving to such great depths tend to have adapted shorter wings for more powerful underwater propulsion, resulting in a higher cost of flight (Thaxter et al. 2010). Penguins are the extreme example of this adaptation, completely flightless, with emperor penguins (*Aptenodytes forsteri*) known to dive to over 400m depth (Zimmer et al. 2010). A broad spectrum exists between the extremes of diving and flying capabilities, with many pelagic species, such as the Manx shearwater, being both far ranging (Wischnewski et al. 2019) and competent divers (Shoji et al. 2016). Both above and below water mobility have historically made the at-sea ecology of seabirds quite difficult to study.

Seabirds are typically long-lived, with delayed maturity and a low fecundity (Lack 1968), making them K-selected to varying degrees (MacArthur & Wilson 1967). This paradigm would also suggest that seabirds are adapted to occupy and compete for resources within a relatively stable environment. However, the habitats that pelagic seabirds exploit for food are in fact dynamic and changeable. Prey are often patchily distributed (Fauchald 2009), and the spatial availability of prey may change relatively rapidly (e.g. Jessopp et al. 2013). Seabirds must use a variety of cues to find food efficiently in such an environment. Tubenose seabirds (order: *Procellariiformes*) appear to use olfaction for detection of areas of enhanced food availability. They are known to react to indicator compounds, such as pyrazines and dimethyl sulphide

released by zooplankton grazing, in minute concentrations in the air (Nevitt 2008). Many tubenose species have a high flight efficiency, so in theory they can follow these scents over large distances without incurring major energetic costs. At finer spatial scales, visual indicators are likely important cues of food availability for most seabirds. Often, it seems that cues visible above the surface are most useful when deciding where to concentrate foraging effort, because foraging conspecifics and other marine predators at or above the water surface will often be easier to detect than prey itself (Michel et al. 2022, Votier et al. 2013). How prey capture is informed below the water is still a mystery in many cases, but binocular vision centred around the bill in most seabirds suggests that vision plays a vital role (Martin 2009).

Besides direct sensory detection of prey availability, most pelagic seabirds also possess navigation abilities that can direct them to productive foraging habitat, as well as back to their breeding colony. These areas may consistently provide food during the breeding season (Wakefield et al. 2015) or form stopovers during non-breeding migratory phases (Guilford et al. 2009). The underlying mechanisms are likely as diverse and varied as those used for prey capture, and photoperiod (Padgett et al. 2018), olfaction (Pollonara et al. 2015), magnetoreception (Wynn et al. 2020), and infrasound (Patrick et al. 2021) have all been linked to seabird navigation. Knowledge of the direction to these productive zones is possibly either inherited, genetically (Yoda et al. 2017) or culturally (Harrison et al. 2010), or may be developed over time, through exploration and refinement of migration routes or foraging areas (Guilford et al. 2011). The diversity of cues seabirds use for foraging and navigation means identifying the drivers of their distribution can be difficult without detailed information about their behaviour. These behaviours primarily occur far from land, which hinders direct observation.

This thesis investigates the behaviours that drive the distribution of seabirds, using three model species that breed in Ireland. Ireland sits on an expansive and productive shelf area, bordered to the west by a steep and topographically complex shelf edge, providing upwelling currents and associated enhanced nutrient availability offshore (Raine et al. 1990). A diversity of islands and steep cliffs around the coast of Ireland support nesting and breeding sites for 24 species of seabird, with half to three-

quarters of a million breeders occurring in the summer breeding season (Cummins et al. 2019). Some, such as northern gannets (*Morus bassanus*), European storm petrels (*Hydrobates pelagicus*), and Manx shearwaters (*Puffinus puffinus*), are present in internationally important numbers (Mitchell et al. 2004). Others including northern fulmars (*Fulmarus glacialis*) and great skua (*Catharacta skua*) began to breed in Ireland in the early and late 20th century respectively, providing these species with breeding outposts in the southern extent of their European ranges (Fisher 1952, Cummins et al. 2019). A lone Cory's shearwater (*Calonectris diomedia*) has held residence at a nest site in Skellig Michael in Kerry, southwest Ireland, since the 1990s (Alyn Walsh, pers. comms.), and while their efforts to attract a mate have failed so far, its persistence highlights the potential for other species to colonise the islands and exploit the surrounding productive waters.

1.3 Seabird responses to changing oceans

Seabirds are key indicators of ocean health, as they are known to be sensitive to changes in food supply and marine pollution (Cairns 1988, Furness & Camphuysen 1997). Typically, direct conservation and monitoring of seabirds occurs on land at their breeding sites/colonies (Paleczny et al. 2015). This is important, as land-based threats such as introduced predators and disturbance can heavily impair reproductive success and even adult survival (Wanless et al. 2007, Watson et al. 2014), and estimates of breeding population and output are possibly the best metrics currently available for assessing population health (JNCC 2020). To fully understand the population trends of seabirds, it is critical to understand what impacts survival and foraging success when at sea. Most monitored seabird populations are negatively impacted the changes at sea brought about by human industry (Dias et al. 2019), though we know relatively about the behavioural response of seabirds to such impacts.

The Industrial Revolution saw the development of engine-powered fishing vessels in the 1880s, accelerating the intensification of commercial fisheries and increasing reported global fish landings until their 1996 maximum (Swartz et al. 2010). Commercial fisheries can lead to the severe depletion of targeted catch through overfishing (Myers et al. 1996) or non-target species through incidental bycatch

(Lewison et al. 2004). Many seabirds are vulnerable to bycatch in commercial fishing gears, especially those that can locate and direct towards fishing vessels from large distances to scavenge on fisheries waste or bait (Bodey et al. 2014, Pirotta et al. 2018), with many scavenging species undergoing steep declines where they overlap with more bycatch-prone fisheries (Clay et al. 2019). Whether the fisheries themselves drive this overlap by providing a consistent food source to scavenging species, or whether fisheries and seabirds simply target the same productive areas, remains to be seen. Fisheries may also have broader indirect impacts on marine life through competition, through the removal or reduction of key prey species that sustain populations of higher predators (Rindorf et al. 2000). Seabird diet has been shown to shift in response to decreases in previously dominant prey species, often because those species have been heavily overfished (Wanless et al. 2018). This depletion of fish stocks has consequences for fisheries themselves, with the majority now returning much smaller yields per distance travelled, while the global footprint of fisheries has reached up to 90% of the world's ocean area (Tickler et al. 2018).

The energy industry at sea introduces risks to marine life, with offshore oil and gas extraction altering habitats and resulting in the addition of harmful pollutants to marine environments (Cordes et al. 2015). Seismic surveys used to locate and monitor oil and gas deposits create extremely high noise levels, which can disrupt marine life that relies on hearing for communication or prey location (Kavanagh et al. 2019). As more of our energy is generated using renewable sources, associated risks for marine biota are also changing. The construction of large offshore wind turbines can lead to disruption of marine habitats (Bailey et al. 2014), introducing disturbance in the form of novel structures or the associated increased noise (Russell et al. 2016, Fox & Petersen 2006). Above water, turbines may pose a collision risk for seabirds that travel within the sweep height of the blades (Furness et al. 2013). Some seabirds have shown avoidance responses to turbines, though in such cases, they may be excluded from feeding grounds, or require more flight time to reach them (Fox & Petersen 2006).

Intensifying at-sea industry is accompanied by the pollution of many marine ecosystems, through oil spills (Castège et al. 2007), discharge of oily bilgewater (Dong

et al. 2022), use and disposal of harmful chemicals (Jamieson et al. 2017), and discarded fishing gears (Gilman et al. 2021) to name a few. Products of land-based human industry also commonly reach the ocean, often carried by freshwater pathways. Plastic pollution is pervasive and has found its way into marine food chains, even those far from the surface and from land (Wieczorek et al. 2018). Seabirds often interact quite heavily with the ocean surface for social rafting, resting, feather preening, or foraging (Carter et al. 2016, Richards et al. 2019), leaving them at higher risk from the many pollutants for which their low density keeps them at the top of the water column, such as petroleum oils (O' Hara & Morandin 2010) and plastic (van Franeker 1985).

Climate change is altering the chemical and physical properties of the oceans at an unnatural rate (IPCC 2022). Many of these changes bring about additional challenges for marine life. Species' climatic envelopes are often temperature dependant (e.g. Fort et al. 2012), so their distributions may shift towards the poles in warming oceans (e.g. Clairbaux et al. 2021). Changes in storm intensity are forecast due to climate change, with extreme storm events already becoming more frequent in some areas, such as the North Atlantic (2014). These storm events are often catastrophic for marine life, with large wrecks of seabirds washing ashore emaciated after winter storms (e.g. Morley et al. 2017). The exact cause of mortality in such events is likely to vary, but starvation due to struggling to feed in adverse weather conditions has been proposed as a cause (Clairbaux et al. 2021). Acidification and carbon enrichment of seawater, alongside runoff from agricultural processes in coastal areas (Beman et al. 2005), are altering the timing and intensity of planktonic blooms, altering the light and nutrient availability of oceanic habitat, often over vast areas (Signorini & McClain 2009).

National or international directives, such as the EU Birds Directive (2009/147/EC), oblige countries to maintain favourable conservation status of wild bird populations. Often, the mechanism used to achieve this is the designation of protected areas. Improving our knowledge of species' behavioural ecology and distribution is essential for effectively locating and maintaining these protected areas. Commonly, protected areas have been established at breeding colonies and waters immediately adjacent

to them, but rarely extend far enough to cover important foraging sites to maximise their effectiveness (Critchley et al. 2018). In order to establish suitable protected areas, more information is required to identify important high-use areas for seabirds at sea (Davies et al. 2021). Further to this, more detailed at-sea behavioural data may identify areas of conservation concern, where the behaviour of seabirds may place them at risk, leading to more directed mitigative conservation efforts (e.g. O' Keefe et al. 2021). Better behavioural data can also inform the planning of marine-based infrastructure and activity, by conducting *a priori* risk assessments based on detailed knowledge of seabird at-sea ecology (e.g. Searle et al. 2022).

1.4 The use of biologging in seabird ecology

One of the greatest challenges in biology is the study of species without direct observation. This is a prohibitive factor when studying the at-sea ecology of seabirds. At very coarse scales, observational monitoring of seabirds at their breeding colony can tell us about productivity and interannual survival, and how these respond to variables such as climate, based on broad ocean-wide descriptors (Thompson & Ollason 2001). This approach provides some insight into the processes that may affect species when out of view, though it requires massive timeseries of observational effort, and assumptions about the mechanistic effects of environmental variables on individual fitness. The development of telemetry for tracking seabirds has rapidly accelerated our understanding of their at-sea behaviour and distribution, and how they interact with their environment (Brooke 2018). Early tracking studies in the late 1980s focussed on species large enough to carry the bulky satellite tags available at the time. As a result, Jouventin & Weimerskirch (1990) showed that wandering albatrosses (*Diomedea exulans*) could cover up to 15,000km on a single foraging trip. Tracking technology has continuously miniaturised since, with some recent high resolution GPS tags weighing less than 1 gram, small enough to attach to a 28-gram European storm petrel and gain similar insights into their foraging range (Bolton 2021). Types of location tracking have also diversified, with lightweight light-level geolocator devices small and efficient enough to attach to birds for years at a time, albeit with low spatial and temporal resolution (Phillips et al. 2004).

Location tracking data can tell us in the simplest terms what areas are important for seabirds. Once enough of these data are generated, protected areas can be proposed based on consistent seabird abundance and diversity (e.g. Davies et al. 2021). Hotspots can also be identified through boat-based or aerial observer effort (Rogan et al. 2018, Merkel at 2002), though many such hotspots are so far from land that regular observation is impractical (Bennison & Jessopp 2015). Beyond simple information on location, tracking data can be used to infer seabird behaviour based on patterns of movement, using the distance and angle between successive locations to estimate whether a seabird is resting on water, searching for food, or engaged in straight-line flight (Bennison et al. 2018). Collecting these data is usually only possible in the breeding season, but can provide insights into habitat associations, movement, and foraging cues that likely hold true year-round. For instance, Manx shearwaters have been shown to begin search-type behaviour when in areas of elevated chlorophyll-a concentration (Kane et al. 2020), often considered a proxy for primary productivity and higher trophic-level prey availability (Tremblay et al. 2009). Reactions to dynamic stimuli can also be measured, such as attraction to fishing vessels for scavenging seabirds (Bodey et al. 2014) or navigating storm systems to avoid extreme weather (Lempidakis et al. 2022).

Understanding seabird behaviour can be complemented by using other forms of biologging devices. Time-depth recorders (TDRs) are used to investigate the diving behaviour of seabirds. For seabirds that tend to dive and not feed on the surface, this gives us a reliable indication of effort spent foraging and energy expended for a given time (Dunn et al. 2020). These data can also help us to relate diving behaviour to environmental factors, such as mixing fronts (Cox et al. 2016) or light availability (Wilson et al. 1993), which may influence whether an individual dives, or the style of dive performed. Leg-mounted immersion switches can't distinguish whether a bird is on or under water, but they are useful when looking at long-term patterns of flight versus non-flight behaviour (Cherel et al. 2016). Triaxial accelerometers are being used to investigate extremely fine-scale changes in behaviour, down to individual wingbeats (Krishnan et al. 2022). The energetic cost of different behaviours can also be calculated using accelerometers by looking at dynamic body acceleration

(Shepard et al. 2008) and investigating the impact of external factors, such as wind speed and directional offset to a flight path (Elliott et al. 2014). Bird-borne cameras have also been used to determine what visual cues precede foraging, such as presence of fishing vessels, conspecifics, or other marine predators (Votier et al. 2013, Michel et al. 2022). These tools offer a novel perspective into how seabirds respond to extreme weather events, fishing vessels, and wind turbines, for example. They also offer insights into formerly cryptic aspects of seabird ecology, such as means of prey capture.

Information on seabird behaviour from biologging can be used to tease apart the environmental drivers of their distribution (Wakefield et al. 2009). This in turn facilitates species distribution modelling, based on environmental associations from tracked individuals and expanded to wider populations (Cleasby et al. 2020, Wakefield et al. 2017). Distribution and behaviour may also be driven by life histories of species and the current stage of an individual within this. Biologging can be used to describe cryptic life history stages that occur at sea, such as moult (Grissot et al. 2020) and migration (Amélineau et al. 2021), by looking at changes in behaviour over relatively protracted timeseries. Pre-existing knowledge of the life history can also help to explain temporal changes in behaviour, for instance the protracted foraging trips undertaken by female tubenose seabirds during their pre-laying exodus to assist egg development (Gatt et al. 2019).

To complement improvements in seabird tracking technology, remote sensing of environmental conditions and human industry at sea are developing rapidly. Tracking the global footprint of commercial fisheries is possible thanks to legislation requiring that vessels carry transponders to report their location, with collation of data at national, international, or global levels (Kroodsma et al. 2018). Satellite imagery can be used to identify where vessels are present but not reporting their activity via transponders, giving us a more complete knowledge of the distribution of fisheries (Kroodsma et al. 2022). Remote sensing data also present opportunities to track oceanographic surface variables, such as temperature, salinity, and primary productivity, while the tools now available to handle these data are becoming more open and accessible (Dodge et al. 2013). Weather forecast reanalysis also provides

historical datasets of weather variables, relating to wind, precipitation, and cloud cover for example (Hersbach et al. 2020).

In addition to the diversity of data now available using biologging technologies, we are increasingly cognisant of the potential for attached devices to negatively impact our study individuals. This may alter their behaviour and mobility, so that the results of tracking are not representative of the animal's natural behaviour (Vandenabeele et al. 2014). In ethical terms, the study of an animal should not impair individuals ability to feed or reproduce, and also aim to impact as few individuals as possible. Conversely, the impact of logger attachement on the at-sea behaviours of seabirds is difficult to quantify without sufficient numbers of birds equipped (Cleasby et al. 2021). With improved knowledge of device effects, both researchers and device manufacturers aim towards light and streamlined tags without compromising functionality, progressively reducing impact on our study species. However, the fine-scale effects of devices on movement and foraging success are still largely unknown. For instance, studies such as Vandenabeele et al. (2014) have shown how loggers may impact the powered flight of seabirds, though none so far have explored their effects on underwater propulsion of diving species. The weight of a device may not be as important as its buoyancy or drag when underwater. Increasing consideration of impacts in all aspects of seabird ecology, alongside miniaturisation of devices, progressively allows us to record behaviour and distribution reliably without compromising the health of study animals.

There is a wealth and diversity of data now available. The responses of seabirds to environmental change can be studied using a range of remote sensing and tracking techniques. In this thesis, I use biotelemetry, alongside environmental data obtained by remote-sensing, to investigate the fine-scale behaviour of seabirds to explore the drivers of their distribution. This is accomplished through the use of three model seabird species with contrasting foraging modes and diet.

1.5 Study species

The first model species is the Manx shearwater (*Puffinus* puffinus). Shearwater species use wind and waves to travel efficiently via dynamic soaring and are

potentially sensitive to severe weather when commuting to feeding grounds as a result (Lempidakis et al. 2022). Below the water, the foraging capabilities of many seabird species is likely dependent on local conditions, such as light availability (Wilson et al. 1993), though how this functionally affects the foraging behaviour is poorly understood. The Manx shearwater provides an excellent study candidate to assess how diving is impacted by environmental conditions that affect light availability, as they dive up to 50m (Shoji et al. 2016), and the placement of their eyes suggests that prey capture is visually guided (Martin & Brooke 1991). They can cover huge distances in a single foraging trip (Wischnewski et al. 2019, Padget et al. 2019), encountering highly varied conditions within a relatively short time period, facilitating the study of behavioural responses to environmental conditions.

The second study species is the northern fulmar (*Fulmarus glacialis*). Like many seabird species, fulmars have been shown to scavenge for fisheries by-products behind vessels (Bicknell et al. 2013). This supplementary food source is likely to impact both behaviour and distribution of scavenging species (de la Cruz et al. 2022), while also placing them at risk from bycatch in fishing gears. Fulmars colonised Ireland in the early 20th century, having spread southwards through the Faroes and Scotland (Burg et al. 2003). This southward expansion is often attributed to the fulmars' scavenging of fisheries waste, which became more available due to the intensification of fisheries around the time of their expansion (Fisher 1952). The fulmar is now the most heavily bycaught species in North Atlantic fisheries (Fangel et al. 2015). In this thesis, the fulmar is used as a model species to develop our understanding of seabirds' fine-scale behavioural responses to fishing vessels, and how the distribution of fishing vessels, alongside other environmental variables, can impact seabird distribution at broader spatial and temporal scales.

The third study species is the Atlantic puffin (*Fratercula arctica*). Puffins, like other larger members of the *Alcidae* family, shed and regrow all of their primary wing feathers at once during the non-breeding season (Peery et al. 2008). This is known as catastrophic moult, which leaves these seabirds flightless (Gaston & Jones 1998) and impairs their diving abilities (Bridge 2004). The timing and location of this sensitive life history stage has been difficult to identify from direct observation of puffins

(Harris et al. 2014). Biologging provides an opportunity to not only detect this stage from behavioural analysis, but also discuss how puffins may develop a strategy to undergo moult in areas of predictable weather and prey availability. Puffins are commonly washed ashore in storm wrecks (Morley et al. 2017, Anker-Nilssen et al. 2018), and are suffering declines across much of their range (BirdLife International, 2015). Understanding the timing and location of moult, which likely increases their sensitivity to adverse impacts, may help to explain some of the drivers of their declines.

1.6 Thesis aims and knowledge gaps

Using the three identified model species, this thesis sets out to fill knowledge gaps in our understanding of seabird ecology. Tracking technologies are applied to investigate seabird behaviour and distribution, with a specific focus on how aspects of their ecology are responding, or may yet respond, to human-driven changes in the marine environment including fisheries practices and intensity, changes in the distribution and availability of prey, and climate-driven changes in environmental conditions at both coarse and fine spatiotemporal scales.

Chapter 2 focusses on the fine-scale foraging and diving behaviour of Manx shearwaters in response to variability in water turbidity. Increased turbidity as a result of human industry and climate may have negative consequences for visual hunters such as the Manx shearwater (Martin & Brooke 1991). Findings are likely to be relevant to many other marine species relying on visual detection of prey.

Chapter 3 explores the relationship between commercial fishing activities and the behaviour and distribution of the northern fulmar. This chapter investigates how fulmars are currently affected by fisheries, in terms of behavioural response and foraging distribution during the breeding season. In turn, the distribution of fishing effort is tested as a suitable variable to predict the foraging distribution of this species.

Chapter 4 expands on fulmar-fisheries interactions to include the entire annual cycle and colonies from Ireland, UK, Iceland, and Norway. This chapter uses protracted timeseries of comparable data, from 2006 to 2021, to explore trends in fishing vessel

attendance, winter migration effort, and associated foraging effort, and how each may correlate. Understanding trends in fisheries interactions is vital to understanding how seabird bycatch risk may be changing over time.

Chapter 5 focuses on the flightless moult and non-breeding distribution of Atlantic puffins and how these may covary on an individual basis. Using similar light level loggers to those used in chapter 4, in combination with saltwater immersion loggers, a new method is developed in this chapter to define fine scale behaviours over annual timeseries to detect flightless moult. Even though the method had limited success, it still provides vital insights into puffin ecology, giving context to risks from climate change and shifting prey availability, and sets a foundation for future studies.

CHAPTER 2: UNDERWATER VISIBILITY CONSTRAINS THE FORAGING BEHAVIOUR OF A DIVING PELAGIC SEABIRD

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Abstract

Understanding the sensory ecology of species is vital if we are to predict how they will function in a changing environment. Visual cues are fundamentally important for many predators when detecting and capturing prey. However, many marine areas have become more turbid through processes influenced by climate change, potentially affecting the ability of marine predators to detect prey. We performed the first study that directly relates a pelagic seabird species' foraging behaviour to oceanic turbidity. We collected biologging data from 79 foraging trips and 5472 dives of a visually dependent, pursuit diving seabird, the Manx shearwater (*Puffinus puffinus*). Foraging behaviour was modelled against environmental variables affecting underwater visibility, including water turbidity, cloud cover, and solar angle. Shearwaters were more likely to initiate area restricted search and foraging dives in clearer waters. Underwater visibility also strongly predicted dive rate and depth, suggesting that fine scale prey capture was constrained by the detectability of prey underwater. Our novel use of dynamic descriptors of underwater visibility suggests that visual cues are vital for underwater foraging. Our data indicate that climate change could negatively impact seabird populations by making prey more difficult to detect, compounded by the widely reported effects of reduced prey populations.

2.1 Introduction

The chemical and physical properties of the planet's oceans are changing at an unnatural rate (IPCC 2014), bringing about challenges for marine life. A changing climate is exaggerating the physical processes that increase ocean turbidity, such as wave action and seabed shear stress. These forces accelerate the rate of sediment resuspension in productive shelf sea regions (Thompson et al. 2011), leading to lower light transmissibility through seawater over broad spatiotemporal scales (Wilson & Heath 2019, Capuzzo et al. 2015, Dupont & Aksnes 2013). This suspension of non-algal particulate matter can negatively affect primary producers (Jiang et al. 2021), potentially impacting the base of marine food webs. Climate-driven physical and chemical changes, including warming, stratification, and carbon enrichment of seawater, are also affecting the timing and intensity of plankton blooms, altering the light and nutrient availability of oceanic habitat, often over vast areas (Signorini & McClain 2009).

An increasingly turbid ocean may have negative consequences for oceanic consumers that use visual cues for prey capture. Some fishes have reduced movement efficiency when foraging in turbid conditions (Sørnes & Aksnes 2004, Newport et al. 2021), and one study found that fish biomass in the North Sea was 76-85% positively correlated with water visibility alone (Aksnes 2007), suggesting that visibility is pivotal in the habitat preference of many fish species. In addition, species compositions can be altered by elevated turbidity in coastal systems, where visual predators are put at a disadvantage compared to chemosensory predators (Lunt & Smee 2015). The effect of such visibility/turbidity on prey detection and foraging has been widely explored in freshwater (Cezilly 1992, Abrahams & Kattenfeld 1997) and estuarine systems (Grecay & Targett 1996), where turbidity levels are often higher, but where prey capture and foraging usually occur over small scales. While many marine species have been shown to rely on light levels and visual cues for foraging (Wilson et al. 1993, Doyle et al. 2015, Gardiner et al. 2014, Elliott & Gaston 2015), the effect of turbidity and reduced visibility on foraging efficiency has received little attention in oceanic systems.

Seabirds rely on a sensory array for prey detection over an expansive and seemingly featureless ocean. Chemoreception and olfaction are thought to influence the broad-scale search behaviour of tubenose seabirds (order: *Procellariiformes*), with indicator compounds (e.g. dimethyl sulphide, pyrazines) likely to attract these birds towards areas of high productivity and prey availability (Nevitt 2008, Kane et al. 2020), or to fishing vessels beyond the range of visual detection (Pirotta et al. 2018, Darby et al. 2021, Haney et al. 1992). Great cormorants (*Phalacrocorax carbo*) have been shown to utilise acoustic cues underwater for prey capture in highly turbid coastal regions (Hansen et al. 2017) where low visibility may benefit non-visual methods of prey detection. Acoustic communication between conspecifics has also been observed during gregarious feeding in foraging Cape gannets (*Morus capensis*, Thiebault et al. 2016), and three penguin species (Thiebault et al. 2019), though it is unclear whether hearing is involved in prey detection and capture in these species.

For many seabirds, visual cues are likely essential for foraging. Cameras attached to Scopoli's shearwaters (*Calonectris diomedea*) showed that individuals targeted aggregations of conspecifics, often in association with other marine predators, before engaging in foraging behaviour (Michel et al. 2022). Bird-borne cameras on Cape gannets led one study to conclude that broad scale search for food mostly relied on stimuli visible above the water, such as fishing vessels, conspecifics, or other predators (Tremblay et al. 2014). On a finer scale, gannet species are also thought to use sight to locate conspecifics before diving, either to avoid collisions or attempt to steal their prey (Machovsky Capuska et al 2011). The importance of underwater vision for prey capture by seabirds is more difficult to quantify (Haney & Stone 1988), though some studies would suggest that foraging capabilities of diving seabirds are limited by underwater visibility (Henkel 2006). A study on penguin species suggested that diel patterns in maximum dive depth were dependent on light availability due to solar angle, rather than on the vertical distribution of prey (Wilson et al. 1993). Captive little penguins (*Eudyptula minor*) were shown to reduce prey capture attempts with decreasing light availability (Cannell & Cullen 2008). Hundreds of thousands of short-tailed shearwaters (*Puffinus tenuirostris*) starved to death in 1997 during an anomalous coccolithophore bloom in their Bering Sea wintering grounds

that drastically reduced light transmission through the water (Vance et al. 1998). The shearwaters' preferred prey shifted their vertical distribution towards deeper waters, likely to avoid anomalous surface temperatures. This reduced prey availability may have been compounded by the widespread increases in turbidity, further impairing their ability to detect prey (Stockwell et al. 2001). One study suggests that these die-offs occurred due to difficulty in visually detecting prey from above water, though this study was based on modelled prey capture strategies rather than empirical measurements of foraging effort or dive depth (Lovvorn et al. 2001).

Understanding the sensory ecology of a species is vital if we are to predict how sensitive it is to changes in its environment. Increasingly turbid oceans due to climate change are likely to constrain the foraging abilities of visual pursuit hunters, with knock-on effects on annual survival and reproductive output. The Manx shearwater (*Puffinus puffinus*) is an excellent model species for investigating the effects of turbidity on foraging; they are highly mobile, undertaking foraging trips up to thousands of kilometres from their colony (Padget et al. 2019, Wischnewski et al. 2019) ranging over an area of continental shelf that has become increasingly turbid in recent decades (Wilson & Heath 2019). While Manx shearwaters probably use olfactory cues for broad-scale search behaviour (Kane et al. 2020), the physiology and placement of their eyes indicate that prey capture relies on visual guidance (Martin & Brooke 1991). Manx shearwaters actively pursue prey underwater at depths down to 50 metres, with dives limited to daylight hours, suggesting that light availability is important for the pursuit of their prey (Shoji et al. 2016), which consist of small schooling baitfist, squid, and crustaceans. Here we investigated the role of variables that determine underwater visibility including solar angle, cloud cover and turbidity on the broad scale search patterns, dive rate, and maximum dive depth of foraging Manx shearwaters.

2.2 Methods

2.2.1 Data collection

A total of 36 breeding adult Manx shearwaters were successfully tracked from Little Saltee (52.138, -6.586), Ireland, from June to August 2021. All capture, handling and

tagging was completed under licence from the National Parks and Wildlife Service (54/2021, C155/2021) and the British Trust for Ornithology (CO/6143). Birds were either caught by hand using nest access chambers, or purse nets at the nest entrance (Brooke 1991). Pathtrack nanoFix Geo (3.5g) with integrated time-depth recorder (TDR, n = 14) or CatLog genII+ (~10.5g) tags (n = 32) were attached to feathers on the centre of the bird's back using Tesa® 4651 waterproof tape. Both tag types were set to record high accuracy GPS fixes at 5-minute intervals. CatLog GPS tags were paired with Cefas G5 TDRs (2.5g) on 8 individuals. PathTrack TDRs recorded depth every 2 seconds when underwater and had an accuracy of ±1% up to 50m and a resolution of 1cm. Cefas TDRs were set to record depth every 2 seconds constantly, and 4 times per second when underwater, and had an accuracy of ±1% and a resolution of <4cm. All depth data were subsampled to 0.5Hz to match the temporal resolution of the PathTrack TDRs. Total weight of devices and attaching material were 3% or less of the bird's total mass (mean ± SD = 2.5 ± 0.1%). Tags were mounted on the bird's back, slightly behind the highest point, to mitigate against negative aerodynamic and hydrodynamic impacts of tag attachment (Vandenabeele et al. 2014, Cleasby et al. 2021).

2.2.2 Foraging trips and dive locations

All analyses were completed using R version 4.1.2 (R Core Team 2022). Tracks were linearly interpolated to consistent 5-minute intervals using *PathInterpolatR* (Long 2022) to correct for any delayed or missing GPS fixes (typically when a bird was underwater at the time of the location fix attempt). Where gaps of > 1 hour were present in the raw GPS data, tracks were split into sections to avoid interpolating over large time intervals. Foraging trips were defined as when an individual spent at least 6 hours > 5km from the colony, with track points at the colony (1km radius) removed from further analysis (Bodey et al. 2014). Concurrent GPS and TDR data were recorded for 15 individuals across 29 foraging trips. Dives were identified as a sequence of consecutive depth data for which depth was > 1m. Dives were further grouped into bouts of diving activity, split by time intervals between dives, and the bout ending criterion defined with non-linear least-squares regression using the *diveMove* package (Luque 2007). Locations were appended to dives from the closest

track point timewise, and similarly number of dives was calculated for each track point interval.

2.2.3 Environmental variables

Environmental variables that directly measure or affect water visibility were appended to track and dive data by date, time, and location. Solar angle (°) was calculated using the *oce* package (Kelley & Richards 2020) and used as a proxy for light availability. Solar angle was taken as the angle between the sun and horizon, with positive values above the horizon, negative values below, and 0 at rising or setting. Secchi disk depth (Zsd) was used as a metric of light transmissibility through the water column, i.e. turbidity (Aksnes 2007, Luck et al. 2020). Zsd was provided in metres, where greater Zsd corresponds to clearer water, and sourced at daily temporal and 4km spatial resolution from the Copernicus Marine Service Ocean Products database (resources.marine.copernicus.eu/). Cloud cover (%) data were sourced from MoveBank's Env-DATA service (www.movebank.org/), which accesses the European Centre for Medium-range Weather Forecasts' ERA5 dataset (Dodge et al. 2013). These data are provided at 0.25x0.25 degrees spatial and hourly temporal resolution and were appended using bilinear interpolation. Water depth (m) was calculated using the *marmap* package at 2 arc-minute resolution (Pante et al. 2022). Time of day was calculated as hours from midnight in Universal Time Zone.

2.2.4 Informing hidden Markov models using Secchi disk depth

We investigated whether water Zsd could improve model fit for a behavioural classification method currently used for marine top predators. Hidden Markov models (HMMs) can be used to distinguish between 3 putative behavioural states using step length and turning angle in seabird tracking data: rest, area-restricted search (ARS) and transit (Bennison et al. 2018, Giménez et al. 2021). ARS is thought to represent the movement mode most likely to include prey capture attempts, usually with steep turning angles and intermediate distances between points (Kareiva & Odell 1987). Environmental variables that may affect the decision of an animal to engage in one of these behaviours can be included in these models to improve fit (Clay et al. 2020). Initial values for these parameters were taken from a previous study (Kane et al. 2020), who fit HMMs using Manx shearwater tracks at the

same temporal resolution from colonies on the west coast of Ireland. Two HMMs were run using the *MomentuHMM* package (McClintock & Michelot 2018), one with and one without Zsd as a model covariate. The AIC of these models were compared to assess how Zsd affected model fit. For tracks with concurrent TDR data, the proportion of dives within each state of each HMM (with and without turbidity as a covariate) was also calculated to assess behavioural prediction accuracy, comparing hit rate, miss rate and precision across models. Stationary state and state-switching probabilities were calculated as a response to Zsd using the *plotStationary* function in *momentuHMM*.

2.2.5 Modelling dive rate

Dive rate was modelled using a generalised additive mixed-effects model (GAMM) with bird identity included as a random effect to account for variation caused by tagging effects and/or individual differences in target prey or maximum dive depth. We used the *bam* function in the *mgcv* package (Wood 2011) which allows for the efficient fitting of generalised additive models (GAMs) with an autoregressive order 1 (AR(1)) structure. An autocorrelation function (ACF) was used to establish a coefficient (*rho*) to describe serial correlation between track points. Thin-plate regression splines with shrinkage were used for all predictor variables, which return the simplest effective spline. The model gamma parameter was set to 1.2, which increases the null-space penalty to avoid overfitting of model terms (Wood 2003). Model selection was performed using an inbuilt feature in *mgcv*'s model fitting infrastructure, which uses spline shrinkage to regress a covariate's effect to 0 where it has no significant effect on the model response. The response variable, dive rate, was presented as dive count per 5 minutes using a negative binomial model structure with a log link to account for overdispersion. Solar angle, cloud cover and Zsd were included as explanatory variables, as all will affect water visibility. Time of day was also included to account for diel patterns in dive rate not attributable to light levels and was fit using a cyclic cubic spline. A 2-dimensional spline was chosen to represent solar angle and Zsd, as both work in combination to regulate light transmission through water. A tensor product spline was used for this 2D relationship because of the differing scales of these two variables. This method was validated by comparing

Akaike's information criterion (AIC) values for two models, one with the 2-dimensional spline and one with two individual splines. Model goodness of fit (GOF) was described using deviance explained. Area under the receiver operating characteristic curve (AUC) was also calculated as a secondary measure of GOF using the *caret* package (Kuhn et al. 2019). We predicted a binomial response (dives present or absent) using the fitted model and compared the prediction to the presence or absence of dive behaviour for each track location as a Boolean object to calculate AUC.

2.2.6 Modelling dive depth

Maximum dive depth was also modelled as a response to environmental covariates using a GAMM. The model response was maximum depth per dive bout (n = 1358), to account for fine-scale variation in dive depths within bouts of diving behaviour. Bird identity was again included as a random effect. No serial correlation was observed in the ACF plot of this model's residuals, so no autocorrelation structure was implemented. A gaussian error structure with an identity link was used based on the distribution of model residuals. Zsd, solar angle, and cloud cover were included, considering these variables regulate light levels, which are likely to influence dive depth (Wilson et al., 1993). Zsd and solar angle were again tested as both a 2-dimensional tensor product spline and two individual splines using AIC to select the better descriptor. Time of day was included to capture any changes in dive depth based on vertical distribution of prey and how that may change throughout the day irrespective of light levels (Elliot & Gaston 2015). Water column depth was also included, as this forms a physical constraint to maximum dive depth that needs to be considered. HMM inferred state was included as a covariate to compare dive depths across different phases of motion, represented as transit, ARS and resting on the water. A second model was also run with the tensor product of solar angle and Zsd fit to each study individual separately, and these effects were then compared superficially to the same tensor product in the overall model.

2.3 Results

2.3.1 Foraging trips and dive locations

A total of 79 foraging trips were recorded from 36 breeding Manx shearwaters on Little Saltee. 5472 individual dives were recorded from the 15 study individuals also equipped with TDRs, with a mean ± SD of 67 ± 33 dives per day (range 5-134). Mean ± SD dive depth was 8m ± 6.5, ranging up to 42m. Mean ± SD Zsd encountered on each foraging trip was 7.5m ± 2.6. Tracks were mostly distributed along the south and east coasts of Ireland (figure 1). Dives almost all occurred during daylight hours, with peaks of occurrence around dawn and dusk (appendices, figure S1).

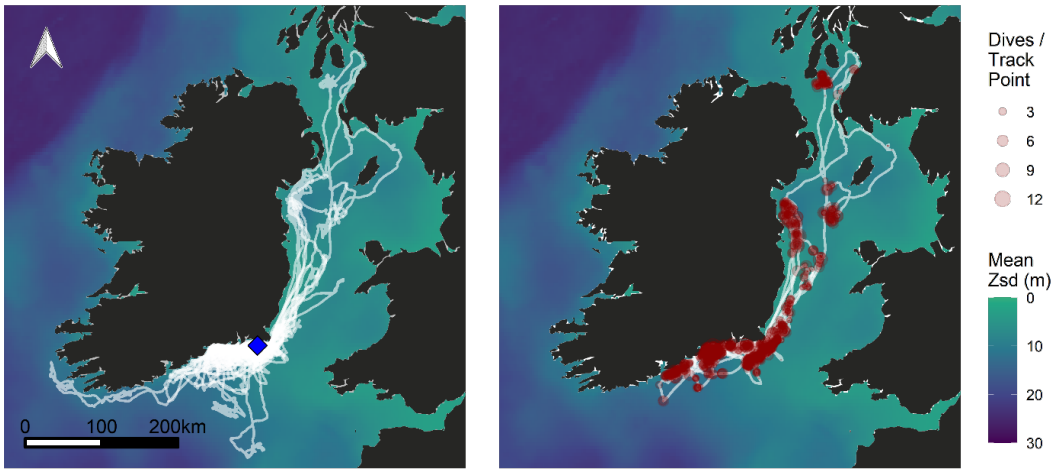

Figure 1: Left: Manx shearwater foraging trips (n = 79) from Little Saltee. Colony shown by the blue point. Right: Recorded dives of Manx shearwaters. Each point represents a track location with dives associated with it. The size of the point corresponds to the number of dives per track location, and all are 30% opaque to better visualise spatial overlap. Only trips with associated dive data (n = 30) are retained in this map. The background shows the mean Zsd (m) across the study period. This mean is only used for visualisation, and dynamic daily values were instead used for all analysis.

2.3.2 Informing hidden Markov models using turbidity

The fit of the 3-state HMM was improved by including Zsd as a covariate according to AIC. The states assigned by each model (with and without Zsd) were 99.5% similar. Model prediction hit rate stayed the same with the inclusion of Zsd, though miss rate and precision were both negatively affected, suggesting that Zsd improved model fit based on movement phases alone, but did not improve the prediction of diving behaviour (appendices, table S1). Increasing Zsd led to a higher likelihood of switching from transit to ARS states, and individuals were also more likely to remain

in an ARS state when Zsd was higher (figure 2). Of the track points that contained dives, 75.5% occurred in an inferred ARS state (appendices, table S2), and the stationary probabilities indicate that ARS behaviour was more likely to occur in areas of high Zsd (appendices, figure S2).

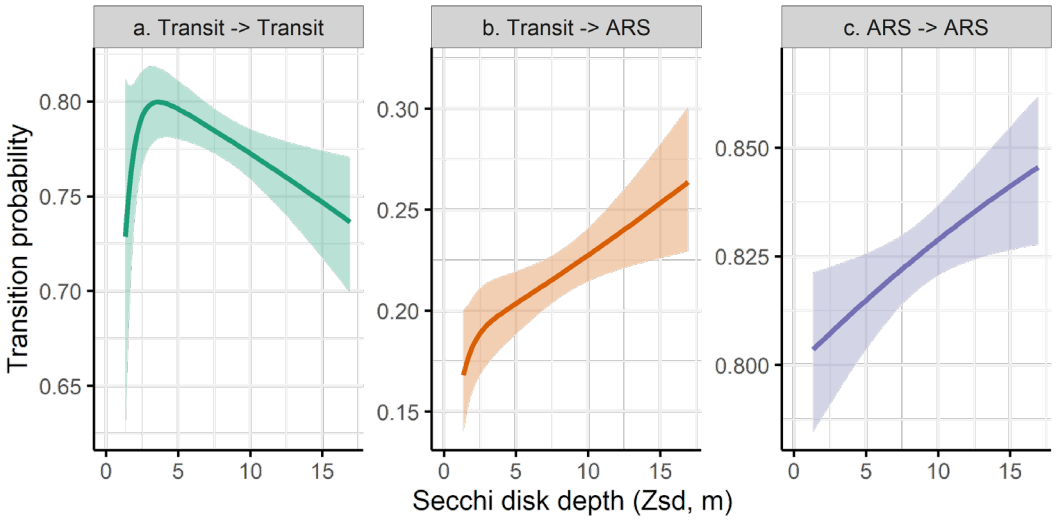

Figure 2: Transition probabilities between behavioural states affected by Secchi disk depth (m) according to the 3-state HMM. Shaded areas represent 95% confidence intervals. See appendices, figure S3, for a full matrix of transition probabilities in relation to Secchi disk depth.

2.3.3 Modelling dive rate

Table 1: Dive rate GAMM covariates. Response is dive count per location at 5-minute intervals. Estimated degrees of freedom (EDF) is a measurement of term complexity, F-statistic represents effect on the model output, and terms with a p-value < 0.05 are taken to be significant (bold text, * symbol after p-value).

Model covariate	**EDF**	**F-statistic**	**p-value**
Tensor product (Solar angle x Zsd)	**12.4**	**6.9**	**<0.001***
Time of day	**0.8**	**1.9**	**0.027***
ID (Random)	**7.5**	**1.4**	**<0.001***
Cloud cover	<0.01	0	0.77

Dive rate was predicted by the 2-dimensional tensor product of solar angle and Zsd, as well as time of day and individual ID. Cloud cover did not have a significant effect (table 1). The effect of solar angle and Zsd on dive rate clearly reflects a diurnal pattern of diving behaviour, with a peak around lower positive values of solar angle corresponding to dawn and dusk (figure 3a). Moderate Zsd led to higher dive rates,

particularly in the dawn/dusk peak (figure 3a). Time of day suggests that dive rate increases during the evening, with higher rates in the latter half of the day (figure 3b). The significant effect of individual identity indicates between individual variation in dive rate. This model explained 22% of deviance in dive rate, while the AUC for dive prediction was 74%, signifying moderate to good model GOF.

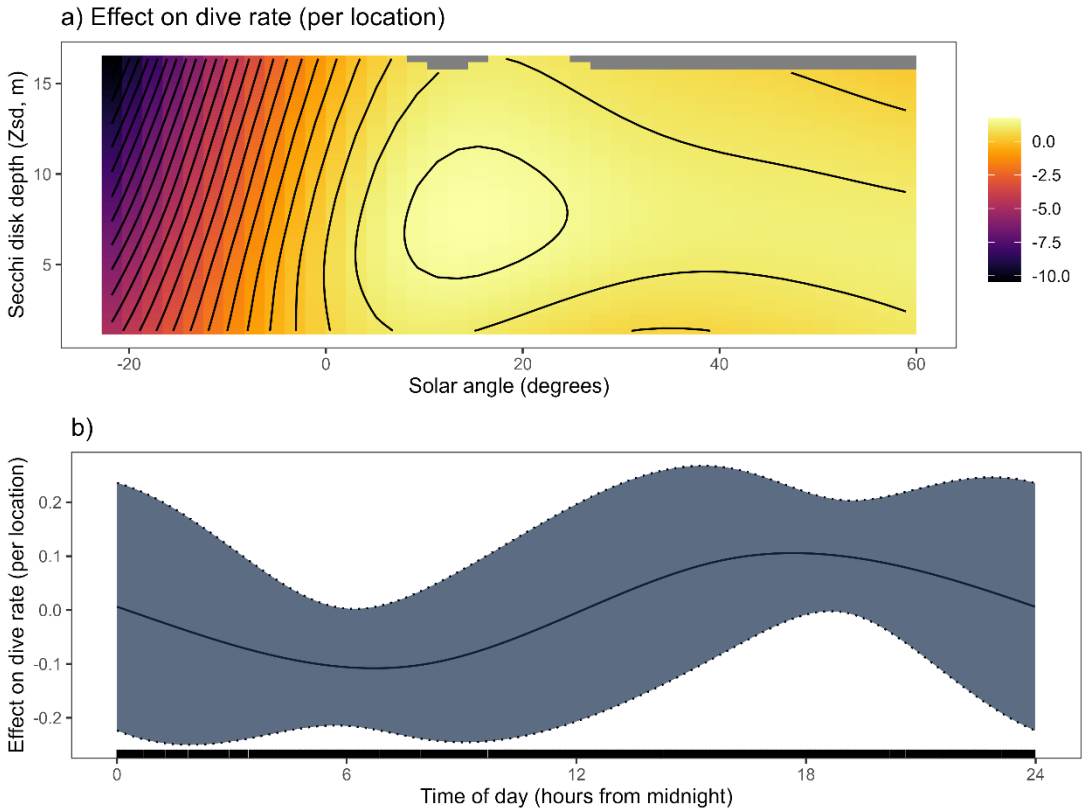

Figure 3: Significant GAMM covariates describing the dive rate of Manx shearwaters. For the 2D effect of Secchi disk depth (Zsd) and solar angle, plot a), the fill colour represents covariate effect on dive rate. A log link function was used to fit the negative binomial distribution, so true effect on dive rate is calculated as the exponential of the displayed effect. For plot b), the effect of time of day, the y-axis represents the effect on dive rate. The 95% confidence interval of the time of day term is shaded.

2.3.4 Modelling dive depth using water turbidity

The tensor product of solar angle and Zsd, as well as cloud cover and individual ID predicted maximum dive depth per bout of diving behaviour (table 2). When this effect was tested on a per-individual basis, a similar effect was observed where the individual tensor product was significant (appendices, figure S5), which suggests that the relationship is robust and consistent across individuals. Water depth was selected against, as this model term was regressed to 0 by the selection process and had no

detectable effect on maximum dive depth per bout. High solar angle and Zsd together led to greater dive depths, suggesting that maximum dive depth is constrained by light levels available underwater (figure 4a). This is reinforced by the lack of diving at night, with < 1% of dives occurring after civil twilight (solar angle < -6 degrees) throughout the entire dataset (appendices, figure S1). Cloud cover had a negative effect on dive depth overall, though the relationship was not fully linear, with dive depth increasing slightly between moderate and high total cloud cover (figure 4b). Time of day did not have a significant effect, but the term was retained by the model selection process and had a non-zero effect (table 2), indicating that the dive depth may increase later in the day, as was observed for dive rate (figure 3b), though the effect is weak. The random effect of individual identity was also significant, likely due to variation in individual fitness, tagging effects, and/or depth of preferred prey (table 2). The deviance explained by this model was 12.5%, increasing to 15% when the tensor product of solar angle and Zsd was split according to individual.

Table 2: Maximum dive depth GAMM covariates included as smooth terms. Response is maximum dive depth per bout of diving behaviour (m). Estimated degrees of freedom (EDF) is a measurement of term complexity, F-statistic represents effect on the model output, and terms with a p-value < 0.05 are taken to be significant (bold text, * symbol after p-value).

Model covariate	**EDF**	**F-statistic**	**p-value**
Tensor product (Solar angle x Zsd)	**3.8**	**2.4**	**<0.001***
Cloud cover	**2.2**	**4.4**	**0.002**
ID (Random)	**10.5**	**3.8**	**<0.001***
Time of day	0.3	0.3	0.18
Depth	<0.01	0	0.59

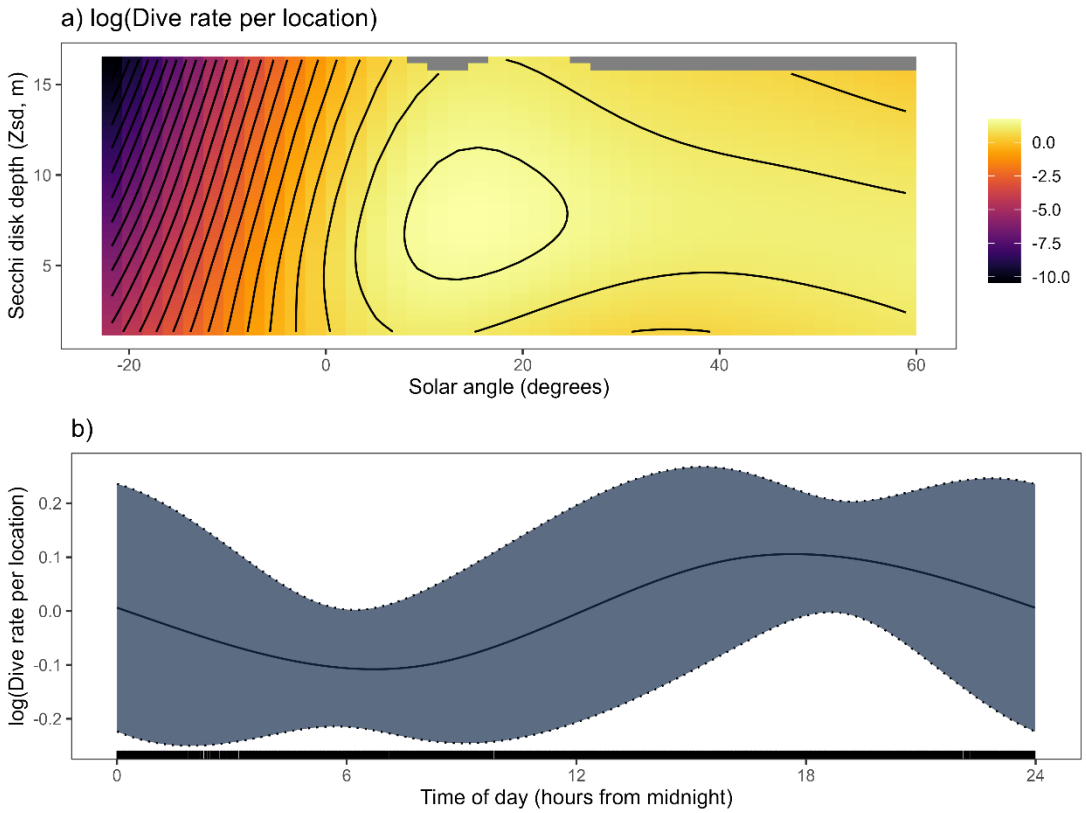

Figure 4: Model covariates describing the dive depth of Manx shearwaters. For the 2D effect of Secchi disk depth (Zsd) and solar angle, plot a), the fill colour represents covariate effect on dive depth. For 1D effect of cloud cover b), the y-axis represents the covariates' effect on dive depth, and the rug plot beneath reflects the distribution of values. The 95% confidence interval of the effect of cloud cover is shaded.

Behaviour inferred by the HMM had a significant effect on dive depth (appendices, table S3, figure S4). There was no significant difference between dive depths in inferred rest or ARS states, but dives were 2.9m shallower when they occurred in inferred transit states (p-value = 0.004).

2.4 Discussion

Using a detailed spatio-temporal analysis, we demonstrated that Manx shearwater foraging behaviour is affected by water visibility. At fine scales, high solar angles, clear waters, and low cloud cover all lead to greater maximum dive depths. Both dive depth and rate were best explained when solar angle and turbidity were combined into a single 2-dimensional covariate, which strongly infers that diel dive patterns observed are limited by light availability. Less than 1% of dives occurred when the sun was more than 6 degrees below the horizon. This also suggests that dives were preceded by visual detection of either prey or indicators of prey, such as other predators (Michel et al. 2022, Veit & Harrison 2017). Cloud cover had no effect and turbidity had a minimal effect on dive rate, reinforcing the hypothesis that visual stimuli for dives probably occur at or close to the water surface (Tremblay et al. 2014). Dive rate decreased slightly at very low turbidity levels, though this may simply reflect deeper, longer, and more energetically costly dives undertaken due to elevated visibility, resulting in a reduced capacity for dives within the 5-minute window. Dive rate increased before dusk, which may have coincided with an increased availability of prey, or increased foraging effort prior to returning to the colony to provision their chick at night. This late peak in diving behaviour is not limited to the final day of each foraging trip before returning to the colony (appendices, figure S1), and is most likely driven by temporal increases in prey availability. Nonetheless, further data on foraging success during dives, e.g. from bird-borne cameras (Michel et al. 2022), are necessary to investigate this temporal trend.

The 3-state hidden Markov model fit was improved by including Secchi disk depth as a measure of turbidity. Switching from transit to ARS was more likely over low turbidity waters, as was remaining in ARS. This model also inferred a slightly higher stationary probability of ARS in areas of low turbidity, meaning that movement patterns consistent with broad-scale search behaviour and more likely in clearer waters overall. These models are not infallible predictors of behaviour (Bennison et al. 2018), and 24.5% of track points with dives were not within the inferred ARS state. Dives during inferred rest behaviour may reflect periods of preening and maintaining

feathers between dives over good quality habitat which will confound behavioural classification based on 2-dimensional GPS track data alone. Dives that occurred while the bird was inferred to be in transit between prey patches were significantly shallower than during other modes of movement, consistent with opportunistic visual detection of prey or prey indicators during directed flight (Clay et al. 2018, Weimerskirch et al. 2005).

Cloud cover had a mostly negative effect on dive depth. Clear skies led to the greatest maximum depths, which is intuitive when light availability is taken to be a limiting factor (Wilson et al. 1993). High cloud cover also led to slightly greater dive depths than intermediate cloud cover, suggesting that complete cloud cover may covary with prey availability at certain depths. This could occur through mixing at ocean front systems for instance (Cox et al. 2016), as sea-surface temperature gradients at frontal mixing zones can create dense cloud cover through accelerated atmospheric convection (Tokinaga et al. 2009). Manx shearwaters possess either violet sensitive (VS) or ultraviolet sensitive vision (UVS) (Lind et al. 2014, Olsson et al. 2021). Clouds don't attenuate these shorter wavelengths of light to the same degree as longer wavelengths in the visible spectrum (Nann & Riordan 1991), so complete cloud cover may not limit availability of Manx shearwater's visible spectra as much as we might expect. However, violet and ultraviolet light are attenuated at a much greater rate in turbid waters compared to other visible wavelengths (Moser 1992, Tedetti et al. 2007). Therefore, while VS or UVS vision may confer an advantage in heavy cloud cover, it might also be impaired to a greater degree in turbid water, giving further context to the restrictive effect of turbidity on dive depths in Manx shearwaters.

The relatively coarse spatial and temporal resolution of environmental variables may account for some of the unexplained variation in our models, along with other unknown factors, the most obvious of which are vertical prey distribution and varying effects of device attachment. Despite this, the results described here are biologically logical. Manx shearwaters possibly also capture prey at the water surface, which we can't confidently identify using the existing data streams. This behaviour might be identified using additional data streams, such as from accelerometers (Cianchetti-Benedetti et al. 2017). While quantifying surface prey capture may provide additional

insight into the foraging ecology of Manx shearwaters, the findings of this study pivot specifically around their diving behaviour, so this potential knowledge gap is not critical to our conclusions.

Turbidity limiting the foraging ability of marine visual predators has wide-ranging conservation implications. Large marine areas have become more turbid in recent decades, driven by increased wave action and seabed shear stress associated with climate change (Thompson et al. 2011, Wilson & Heath 2019). This affects both shallow coastal and deeper offshore shelf waters (Capuzzo et al. 2015, Dupont & Aksnes 2013). Such a widespread decrease in light transmissibility through water is certain to have a negative effect on visual foragers occupying many trophic levels in these areas (Aksnes 2007, Weiffen et al. 2006), as well as reducing light availability for primary producers (Jiang et al. 2021). Extreme storms events, which are already becoming more frequent in areas such as the North Atlantic (IPCC 2014) and forecast to increase in frequency in some of the most biodiverse oceanic areas (Murakami et al. 2017, Zhao et al. 2009), may also acutely reduce visibility. Such storms are responsible for mass mortality events in seabirds, especially those with reduced mobility due to high wing loading or flight feather moult, that can't easily avoid the storm track (Harris et al. 2014, Morley et al. 2017). It has been suggested that such storms starve seabirds, with their inability to feed cited as a cause of starvation (Clairbaux et al. 2021). A sharp temporary increase in turbidity brought about by intensified wave action and seabed shear stress may contribute to this incapacity, compounded by reduced ambient light levels and turbulence in the upper water column that accompany storms. Similarly, climate change is altering the location, timing, and intensity of planktonic blooms, which can severely limit visibility for months at a time over vast areas (Kopelevich et al. 2020). Anomalous blooms occurring in important seabird habitat have resulted in mass die-offs due to starvation (Vance et al. 1998), with associated turbidity likely to compromise seabirds' ability to locate prey. Increased turbidity has also been linked with elevated bycatch rates of seals by static gillnet fisheries (Luck et al. 2020). Though this connection has not been investigated in other marine predators or fisheries, turbidity

could contribute to bycatch risk for other species, and this topic deserves further attention.

Turbidity is currently overlooked as a dynamic descriptor of oceanic habitats, despite its potential to constrain the foraging abilities of many marine species. A changing climate brings with it altered physical attributes of ocean habitats including pH, temperature, and optical properties of seawater. Understanding species' sensory perception is vital to understanding how they function and their sensitivity to change, and as biologging technology continues to improve, we can improve our understanding of sensory cues that animals use to navigate and forage.

2.5 Appendices

Timing of dives

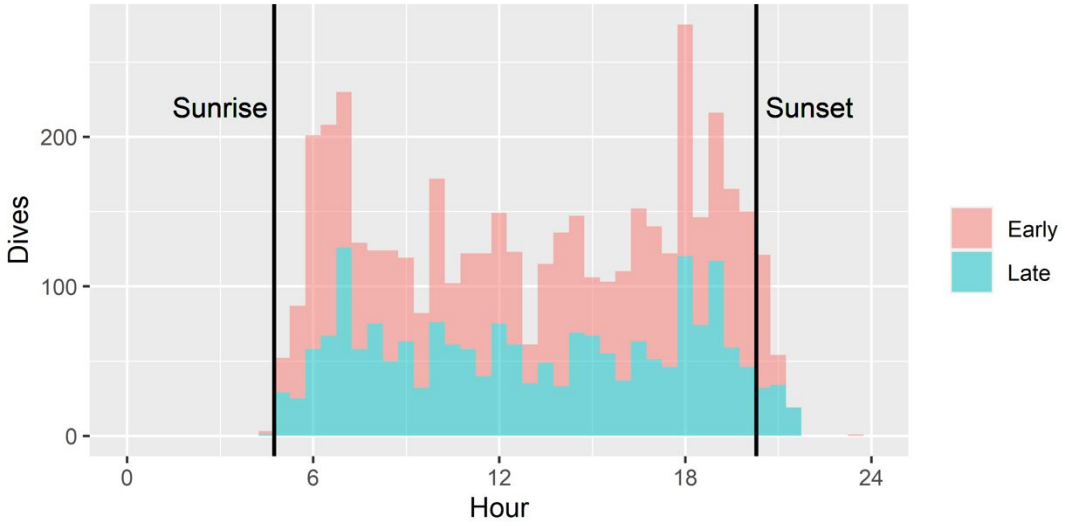

Figure S5: Histogram of dives recorded by bird-borne TDRs for which GPS data were available (n = 4488) against time of day (hours). The black vertical lines represent average sunrise and sunset times across the dive dataset. Areas shaded blue (Late) represent dives that occurred on the final day of a foraging trip, i.e. during the final day before returning to the colony. Areas shaded red (Early) represent dives that occurred earlier in the foraging trip.

Hidden Markov model outputs

Table S3: Hidden Markov model metrics. Akaike's Information Criteria (AIC) are a metric of model fit, with lower values signifying better fit. Hit rate is the percentage of inferred ARS track intervals that contain dives. Miss rate is the percentage of inferred non-ARS track intervals that contain dives. Precision is the proportion of true positives (hit rate) over the total proportion of positives (hit rate + miss rate).

Model	AIC	Hit rate	Miss rate	Precision
3-state HMM	618079	23.2%	5.9%	79.6%
3-state HMM ~ Zsd	618054	23.2%	6.1 %	79.3%

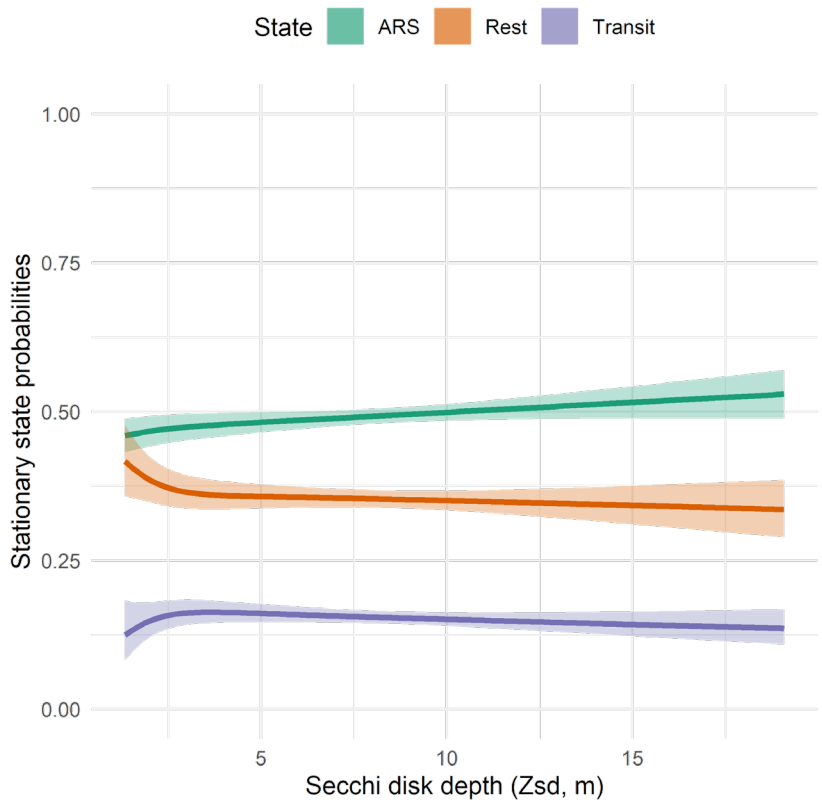

Figure S6: Stationary state probabilities (y-axis) estimated by the hidden Markov model for each inferred behavioural state in relation to Secchi disk depth (x-axis). The behavioural states are rest, area restricted search (ARS) and transit. The shaded area around each trend line correspond to the 95% confidence interval.

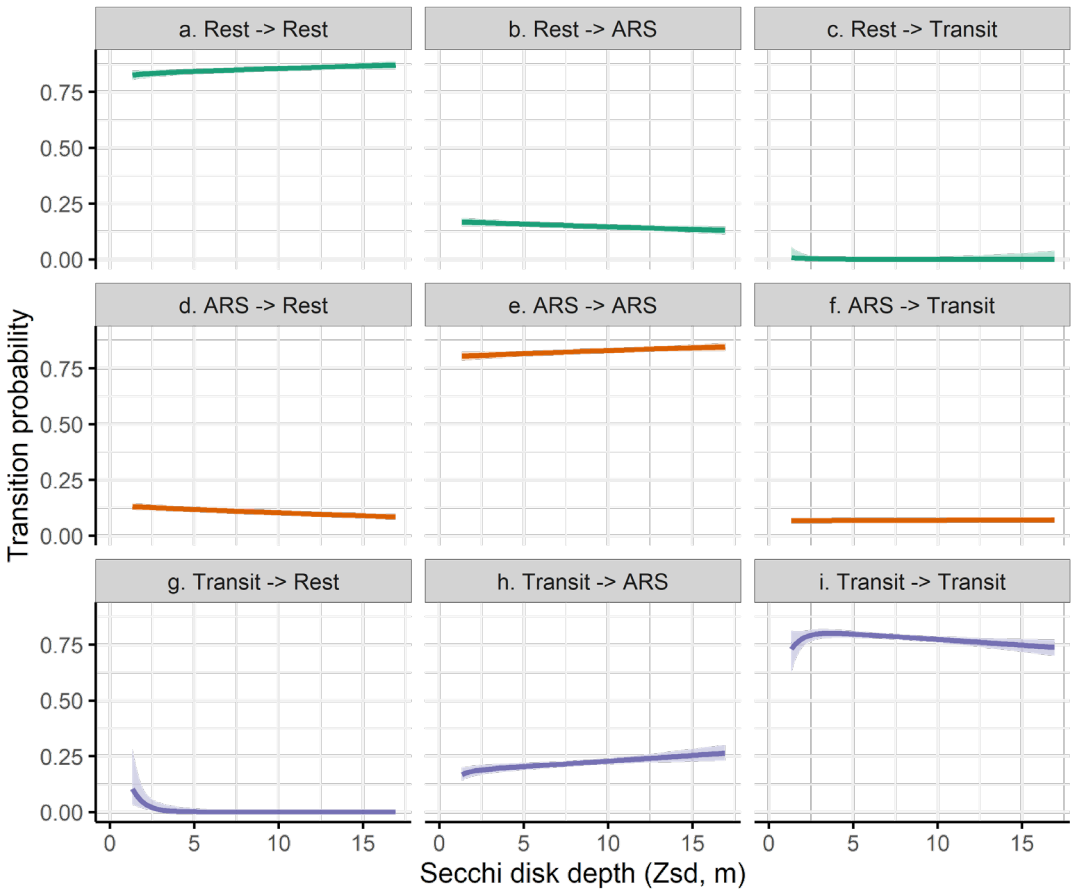

Figure S7: Transition probabilities between all 3 behavioural states as a function of Secchi disk depth (m) according to the 3-state HMM. Shaded areas represent 95% confidence intervals.

Table S4: Distribution of total track points and track points containing dives within the 3 described behaviours of Manx shearwaters, inferred using a 3-state HMM with Secchi disk depth (m) as a covariate.

HMM state	**Rest**	**ARS**	**Transit**
Track points (% of total)	5671 (35.3%)	7593 (47.9%)	2601 (16.4%)
Track points with dives (% of total)	257 (13.5%)	1434 (75.5%)	207 (10.9%)

Dive depth and hidden Markov model state

Table S5: Effect of HMM-inferred behavioural state on the maximum dive depth per bout. Note that the estimate for rest is contained within the intercept, while the estimates for ARS and transit states are true model effects and represent differences in dive depth from rest state. Standard error of the term estimate is also included, and terms with a p-value < 0.05 are taken to be significant (bold text, * symbol after p-value).

HMM-inferred state	Estimate	Standard Error	p-value
Intercept (Rest)	**12.96**	**0.93**	**<0.001***
ARS	-0.19	0.78	0.7
Transit	**-2.87**	**1.02**	**0.004***

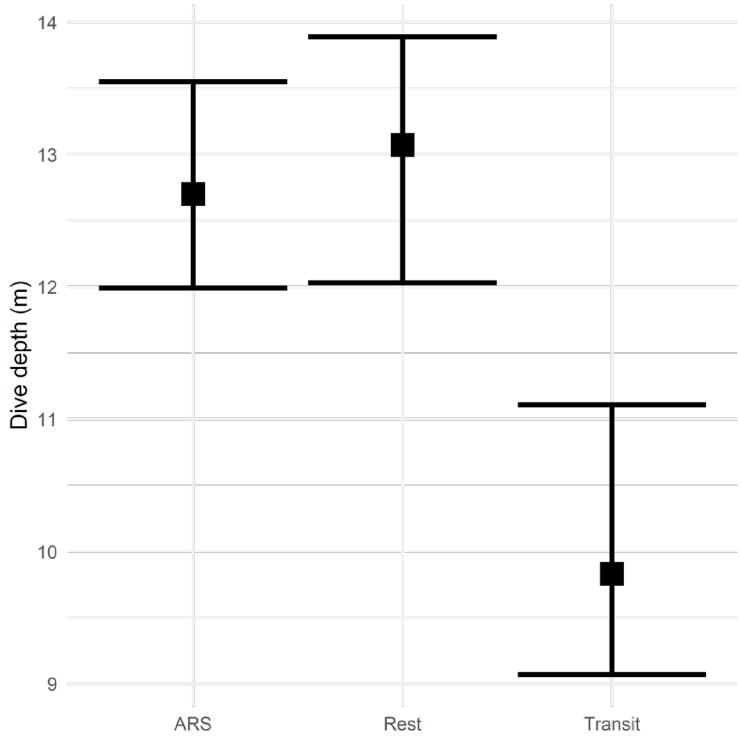

Figure S8: Residual relationship between dive depth and HMM-inferred state. This is according to the dive depth GAMM and based on a net-zero effect of all other covariates.

Dive depth effect split by individual

There was a non-zero effect of solar angle and Secchi disk depth on dive depth in 8 of the 15 individuals for which dive data were available. The effects of these individual-specific 2-dimensional tensor product splines were similar to the same effect in the overall model, with greater dive depths generally occurring with higher solar angles and higher Secchi disk depths (Figure S5).

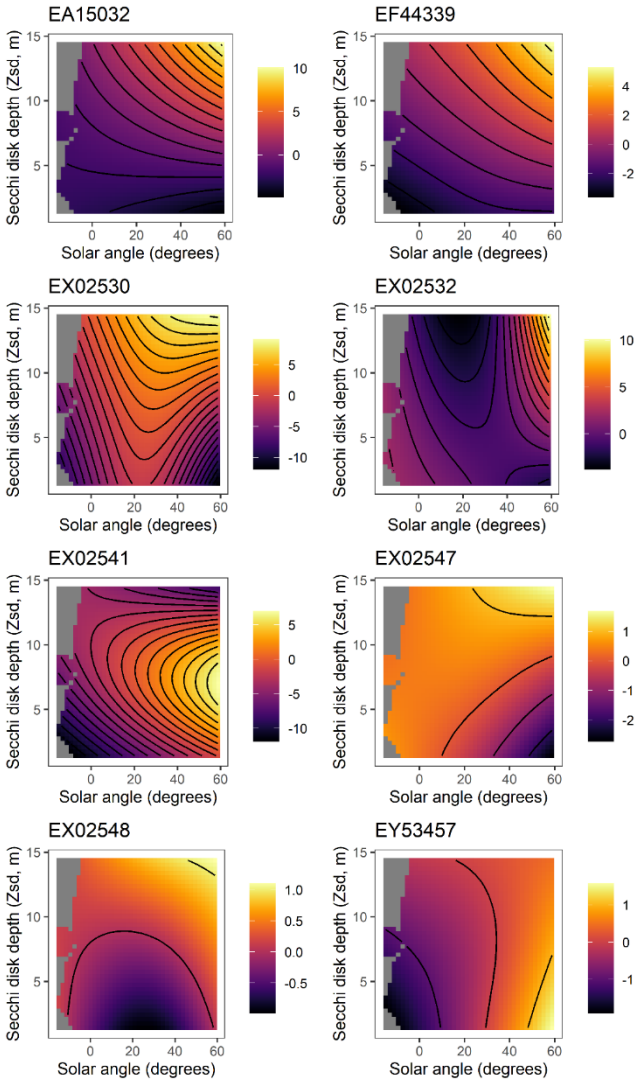

Figure S9: Each plot represents a tensor product spline combining solar angle and Secchi disk depth, and its effect on the dive depth of an individual Manx shearwater. The effect is represented by the colour gradient of the plots, with darker colours corresponding to generally shallower dives, and brighter colours to deeper dives. Secchi disk depth is on the y axis, and solar angle is on the x axis. Only individuals with a non-zero model coefficient are shown (8 of 15).

CHAPTER 3: THE FORAGING DISTRIBUTION OF BREEDING NORTHERN FULMARS IS PREDICTED BY COMMERCIAL FISHERIES

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Abstract

Habitat-use and distribution models are essential tools of conservation biology. For wide-ranging species, such models may be challenged by the expanse, remoteness, and variability of their habitat, and are often compounded by their mobility. In marine environments, direct observations and sampling are usually impractical over broad regions, and instead remotely sensed proxies of prey availability are often used to link species abundance or foraging behaviour to areas that are expected to provide food consistently. One source of food consumed by many marine top predators is fisheries waste, however habitat-use models rarely account for this interaction. We assessed the utility of commercial fishing effort as a covariate in foraging habitat models for northern fulmars (*Fulmarus glacialis*), a species known to exploit fisheries waste, during their summer breeding season. First, we investigated the prevalence of fulmar-vessel interactions using concurrently tracked fulmars and fishing vessels. We infer that over half of our study individuals associate with fishing vessels while foraging, mostly with trawl type vessels. We then used hidden Markov models to explain the spatio-temporal distribution of putative foraging behaviour as a function of a range of covariates. Persistent commercial fishing effort was a significant predictor of foraging behaviour, and more important than commonly used environmental covariates retained in the model. This study demonstrates the effect of commercial fisheries on the foraging distribution behaviour of a marine top predator and supports the idea that, in some systems, incorporating human activities into distribution studies can improve model fit substantially.

3.1 Introduction

Understanding the drivers of species' distributions is a key objective in conservation biology. Statistical modelling allows us to identify these drivers (Elith & Leathwick 2009) and to subsequently predict distribution patterns (e.g. Scales et al. 2016). Ideally, habitat use models incorporate environmental covariates that are known to reflect food availability – for example, vegetation type in terrestrial systems (Vynne et al. 2011) and primary productivity in marine environments (Nur et al. 2011). In terrestrial systems, these descriptors work well because the associated producers are commonly fixed in space and time (e.g. Fryxell et al. 2004, Smit 2011). In marine environments, equivalent descriptors are more elusive because prey patches are transient and less predictable (Fauchald 2009). For example, chlorophyll-a concentration and sea-surface temperature are often used as a proxy for productivity and prey abundance (e.g. Serratosa et al. 2020, Domalik et al. 2018, Tremblay et al. 2009) but with low predictive power for higher predator behaviour or distribution (e.g. Kane et al. 2020). This is possibly due to spatio-temporal lags between environmental conditions that promote productivity and prey aggregations targeted by marine top predators (e.g. Whitehead et al. 2010, McGowan et al. 2013, Torres et al. 2015). It may also be that these variables predict prey biomass rather than availability (Boyd et al. 2015, Waggitt et al. 2018). As a result, static variables such as water depth, distance to colony and seabed slope are often found to better represent marine predator distribution (Amorim et al. 2009, Warwick-Evans et al. 2016, Critchley et al. 2020). Such habitat descriptors may function in combination to enhance prey availability (e.g. Stevick et al. 2008, Scott et al. 2013). Although many studies have examined the predictive power of these oceanographic features in explaining marine distributions (Tremblay et al. 2009), the extent to which these effects are moderated by human activities has scarcely been investigated.

Human activities have the potential to repel or attract species, for example through persistent habitat disturbance (Sauvajot et al. 1998) or provisioning of an extra food source (Newsome et al. 2015). In a marine setting, food sources derived from human activity usually originate from the fishing industry, either through depredation (e.g. Cosgrove et al. 2013) or through scavenging of offal and discards (Bicknell et al. 2013,

Giménez et al. 2021). This association with human activity and waste can lead to negative effects, including plastic-ingestion in urban scavengers (Caldwell et al. 2020), higher likelihood of human-wildlife conflicts (Cronin et al. 2016, Newsome & Van Eeden 2017), and the intake of food of lower nutritional value than natural prey (Grémillet et al. 2008).

Seabirds are widely distributed marine predators but are experiencing global declines (Paleczny et al. 2015). Habitat-use and distribution models are essential tools in seabird conservation as they can be used to identify areas of concern where seabirds and human activities co-occur (Critchley et al. 2018, Waggitt et al. 2020), and to prioritise areas for protection (Lascelles et al. 2012, McGowan et al. 2013). Many previous studies have focussed on the potentially harmful overlap between fisheries and seabirds in terms of bycatch risk (e.g. Zador et al. 2008, Taylor & Small 2009, Tuck et al. 2011, Torres et al. 2013, Clay et al. 2019). However, approximately 100 seabird species utilise fishing vessels as a source of food, through scavenging of discards or offal (Bicknell et al. 2013), or depredation of bait from baited gears (Dunn & Steel 2001), with studies showing how seabirds actively associate with vessels to forage on these products of fisheries (e.g. Bodey et al. 2014, Soriano-Redondo et al. 2016, Pirotta et al. 2018). Therefore, distribution of commercial fishing effort might be a suitable predictor of foraging distribution for these marine predators. This could be through individuals co-occurring in the same productive areas as fishing vessels, though is more likely through vessel-attending species targeting areas of known vessel intensity in order to exploit fisheries waste (Collet & Weimerskirch 2020) or depredate catches.

The northern fulmar (*Fulmarus glacialis)*, hereafter “fulmar”, is a far-ranging, pelagic-foraging seabird that both benefits and suffers from fisheries interactions. It is one of the most commonly bycaught seabird species in the North Atlantic (Fangel et al. 2015, Hedd et al. 2016, Bærum et al. 2019), and Alaskan fisheries (Dietrich et al. 2009). Fulmars are also vulnerable to other human activities and by-products, such as oil extraction (Fox et al. 2016) and plastic pollution (Trevail et al. 2015, Acampora et al. 2017). Prior to the recognition of these negative impacts, fulmars underwent a dramatic range expansion over the last two centuries, spreading from Iceland and St

Kilda through the UK, Ireland and on to the north coast of Europe (Burg et al. 2003). The drivers underlying this expansion likely include both the exploitation of fisheries waste (Fisher 1952, Phillips et al. 1999) and changing patterns of human exploitation (Gordon 1936, Thompson 2006). Currently, however, fulmars are in decline throughout much of their recently established range, observed both in colonies (Cordes et al. 2015, SMP Report, 1986-2018, JNCC 2020) and at sea (Sherley et al. 2020). There is therefore an urgent need to better understand the drivers of their distribution when foraging at sea, and to investigate the causes of their recent declines.

We hypothesised that the foraging distribution of adult breeding fulmars could be better predicted using commercial fishing effort alongside a range of static and dynamic environmental variables. Using tracking data from fulmars and fishing vessels in Ireland and the UK, we estimated the prevalence of fulmar-fisheries interactions during the summer breeding season by looking at direct associations between the vessel and fulmar tracks. We then examined how fulmar foraging distribution was associated with commercial fishing effort over a broad spatio-temporal scale, comparing its importance as a habitat descriptor to other environmental variables. Finally, we incorporated fishing data and other significant environmental descriptors into models of fulmar foraging distribution over the range covered by our empirical data. The aim of this study was to test whether fulmar foraging distribution is influenced by commercial fishing effort, and that distribution models can be improved by acknowledging links between marine predators and human activity.

3.2 Materials & Methods

3.2.1 Data collection

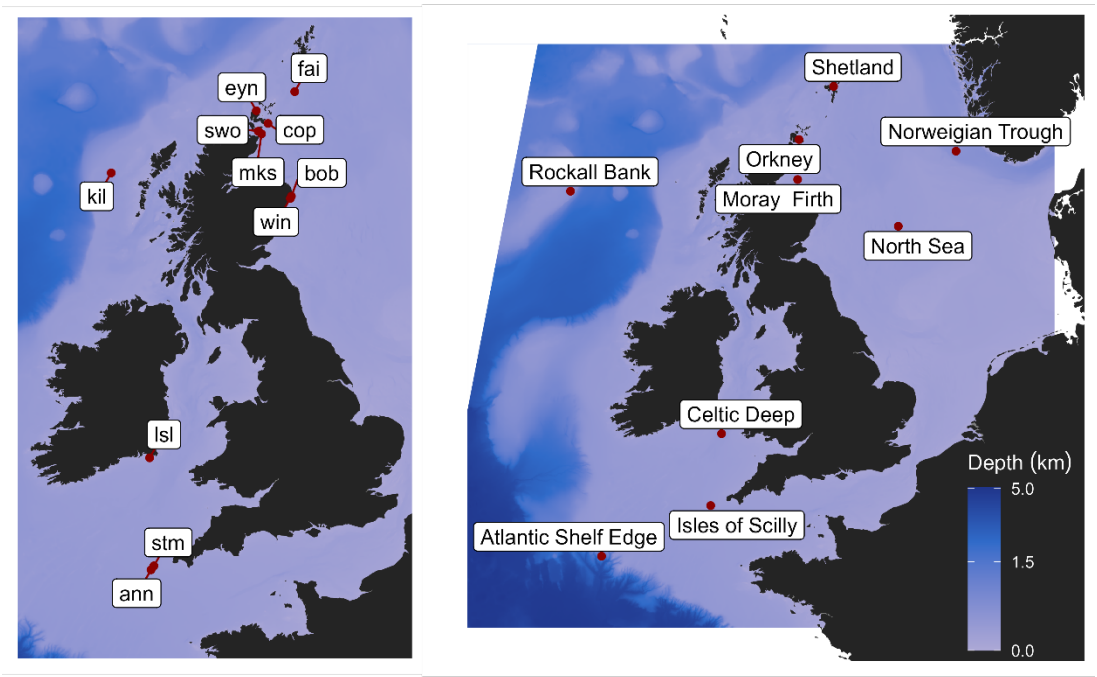


Figure 1: Locations of colonies (left) and major geographic features referenced in the text (right). Colonies are Annet (ann), Bullers of Buchan (bob), Copinsay (cop), Eynhallow (eyn), Fair Isle (fai), Hirta, St. Kilda (kil), Little Saltee (lsl), Muckle-Skerry (mks), St. Martin (stm), Swona (swo), and Whinnyfold (win).

A total of 102 breeding adult fulmars were successfully tracked from Little Saltee, Ireland, the Isles of Scilly, England, and several Scottish mainland and island colonies between 2009 and 2019 (table 1, figure 1). Fulmars were caught by hand, hand-net or noose-pole from the nest. PathTrack Nanofix wireless enabled (10g), Pathtrack Nanofix archival (15g) or MobileAction iGotU gt-120 tags (~17g) were attached to feathers on the centre of the bird's back using Tesa® 4651 waterproof tape. All tag types record the same high accuracy (~3m) GPS fixes. To mitigate potential negative impacts of tag attachment, total weight of the tag and attaching material were up to 3% of the bird's total mass (2.19 $\pm$ 0.39%, max 3.2%), and tags were mounted on the bird's back, directly above their centre of gravity. Despite these considerations, we acknowledge that negative effects remain difficult to detect, control and quantify and could still lead to behavioural anomalies (Vandenabeele et al. 2014, Cleasby et al. 2021).

Table 6. Deployment sites and number of individuals/trips at each site. Stages are early chick rearing (ECR) and incubating (INC).

Colony	**Year(s)**	**Birds**	**Trips**	**Stage**
Annet, Isles of Scilly, England	2010	1	1	ECR
Bullers of Buchan, Aberdeenshire, Scotland	2012	4	10	ECR
Copinsay, Orkney, Scotland	2010-13	9	20	ECR
Eynhallow, Orkney, Scotland	2009-11, 2017	23	42	INC & ECR
Fair Isle, Shetland, Scotland	2011-14	9	11	ECR
Little Saltee, Co. Wexford, Ireland	2018-19	10	29	INC
Muckle-Skerry, Orkney, Scotland	2014	8	18	ECR
Hirta, St. Kilda, Scotland	2011-12	35	48	ECR
St. Martin, Isles of Scilly, England	2011	1	1	ECR
Swona, Orkney, Scotland	2012	1	1	ECR
Whinnyfold, Aberdeenshire, Scotland	2012	1	2	ECR

Tags were programmed to record locations at regular intervals. Depending on tag type and the intended duration of the deployment, this interval ranged from 1.5 to 10 minutes in the majority of birds, as well as a small subset of birds on Hirta, St. Kilda, with tags set to record every 15 or 20 minutes. Nests of tagged individuals were monitored, and data from tags were either remotely downloaded (PathTrack Nanofix wireless enabled) or retrieved after several days when the tagged bird had undertaken at least one foraging trip. All work was conducted under licences from the British Trust for Ornithology (BTO) and Irish National Parks and Wildlife Service (NPWS). All data analyses were undertaken using R version 3.6.3 (R Core Team, 2022). Foraging trips were originally defined as periods of > 1 hour that the bird spent > 3 km from the colony. Distance from the colony and total distance travelled were calculated using the *raster* package (Hijmans 2020, appendices, tables S1 and S2). Data were further filtered to include foraging trips that contained > 100 GPS fixes where birds travelled > 10 km from the colony to exclude small trips that may have

occurred because of disturbances at the colony. Points within 5 km of the colony were also removed as they likely encompassed colony-related behaviours (Bodey et al. 2014).

3.2.2 Fulmar-vessel foraging interactions

First, we aimed to establish the extent to which adult fulmars tracked in this study foraged in association with fishing vessels during the breeding season. Fishing vessel tracking data were sourced from the Vessel Monitoring System (VMS). Irish VMS data sourced from the Irish Marine Institute, while UK VMS data were sourced from Marine Scotland Science. VMS provides GPS locations of fishing vessels > 12 m long, approximately every 2 hours. UK VMS data consisted of almost exclusively UK-flagged vessels, not detecting non-UK vessels in the UK Exclusive Economic Zone, likely leading to underestimates in fulmar-vessel encounters in these waters. Concurrent vessel and fulmar tracks were available from 2009 to 2018, and were linearly interpolated to the same resolution, either 3- or 10-minute intervals depending on the resolution of the fulmar tracks from each colony. The co-ordinates of the nearest fishing vessel were extracted for each interpolated fulmar location in R, for a subset of complete tracks from 2018 and before (n = 92) for which sufficient VMS data were available. A frequentist implementation of the Pirotta et al. (2018) Bayesian approach, using similar constraints, was then used to fit a 7-state Hidden Markov Model (HMM) in *momentuHMM*. This implementation was based on the fulmar example in the *momentuHMM* vignette (McClintock & Michelot 2018) with the addition of a rest state. Briefly, our method assumes the occurrence of seven states of movement: rest, transit (on outward journey, at fishing vessel or on return journey) and ARS (on outward journey, at fishing vessel or on return journey) (appendices, table S4). These can be identified based on the step length and turning angle between interpolated points, while also incorporating distance and bearing to the nearest vessel and bearing to the colony. ARS is thought to correspond to foraging activity (Kareiva & Odell 1987, Weimerskirch et al. 2007, Bennison et al. 2018). Initial values of the model parameters were selected through k-means clustering of step lengths and turning angles into three clusters, intended to represent rest, ARS, and transit states. The initial values of the parameters of the

state-dependent distribution of distance to the nearest vessel (*d*) were selected based on the histogram of observed distances and previous knowledge that fulmars may direct their movement toward vessels from distances of up to 35 km (Pirotta et al. 2018, appendices, table S3). The outputs of the 7-state HMM were used to estimate the proportion of time spent in vessel-associated ARS on a track-by-track basis, which was compared to the time spent in ARS away from detected vessels. Vessel gear type was not available for all VMS data, but where available, was used to investigate the frequency of occurrence of association with different types of fishing vessels. Gear types were grouped into six categories; trawlers, seines, longlines, gillnets, dredgers, and traps/pots.

3.2.3 Identifying three primary states of fulmar behaviour

Next, we aimed to identify putative foraging behaviour using the features of fulmar tracks. All fulmar tracks were linearly interpolated to 10-minute relocations, as this and subsequent analysis requires regular and uniform track point intervals. Trips were split into sections where gaps of > 1 hour were present in the raw GPS data to avoid interpolating over large time intervals. A separate three-state HMM was fitted to these interpolated tracks to infer rest, ARS (putative foraging) and transit states (appendices, figure S1 and S2) irrespective of fishing vessel associations. In other words, while the 7-state HMM was used to differentiate specific vessel-associated ARS from other forms of ARS, this model was used to differentiate ARS from non-ARS more generally. Step lengths and turning angles between points were used to fit this HMM, with initial values of the parameters chosen using the same k-means procedure as for the 7-state model (table S5). The *viterbi* function from *MomentuHMM* was used to obtain the most likely state sequence for each track. These inferred states were used to represent putative foraging and non-foraging behaviour, and to investigate foraging habitat preferences. One caveat of this approach is that it does not account for differences in search-type behaviour (ARS) during vessel-attendance or natural foraging, though the scales of movement are assumed to be similar (Pirotta et al. 2018).

3.2.4 Fulmar foraging habitat preference modelling

Fulmar foraging habitat preference was modelled using the outputs of the 3-state (rest, travel, and ARS) HMM applied to the full tracking data. The response variable was presence or absence of ARS behaviour on each track point. To increase the accuracy in the absence data, only fixes classified as transit behaviour were retained to represent non-foraging, as rest can be difficult to discern from ARS without additional data, for example from time-depth recorders (Dean et al. 2013, Browning & Freeman 2018, Bennison et al. 2019). This response variable was modelled as a function of a set of fixed and dynamic covariates using binomial Generalised Additive Mixed Models (GAMMs) with a logit link function. Individual ID was included as a random effect. The *mgcv* package was used for model fitting (Wood 2011). The *bam* function was used, because, while the autocorrelation estimation is more flexible in the *gamm* function, the associated computation times were not feasible for this dataset. Skewed covariates were transformed towards normal using an optimised Box Cox transformation factor (table S9, Box & Cox 1964), derived using the package *EnvStats* (Millard 2013).

Covariates highly correlated with one or more other covariates were identified and removed stepwise using the *concurvity* function from *mgcv*. A high acceptable threshold of 0.8 was chosen for this process, as important partial effects may be expressed by related variables (Morrissey & Ruxton 2018). This is especially true in biological settings with large sample sizes. The process by which *mgcv* fits GAMMs also mitigates against the negative impacts of multicollinearity through backfitting of covariates (Wood 2008). The model was initially fit with a correlation parameter (ρ) of 0 (i.e., assuming no autocorrelation among residuals) grouped according to individual trip. The autocorrelation function (ACF) plot of the residuals of this model was then used to identify a suitable ρ, the value of the correlation between consecutive residuals. The shape of the ACF plot was also used to verify that a first-order autoregressive (AR(1)) structure provided a good representation of the autocorrelation present. Thin-plate regression splines with shrinkage were used for all predictor variables, which return the simplest effective spline, with complexity further restricted by setting the *gamma* parameter to 1.2, which increases the null-

space penalty when fitting the model (Wood 2003). This method avoids overfitting without having to arbitrarily constrain splines prior to model fitting. A whole-model approach using Akaike's Information Criterion was used for model selection using the *dredge* function in the *MuMIn* package (Bartoń 2020). Moran's Indice (MI) was calculated on the spatial distribution of residuals to investigate spatial autocorrelation in the model using the *ape* package (Paradis & Schliep, 2019). A low MI value of 0.063 suggests that spatial autocorrelation was minimal, so no corrective spatial smooth was included in the model.

Physical habitat variables that may influence the availability of fulmar prey were chosen following Cox et al. (2018). These variables were depth, seabed terrain ruggedness index (TRI, Wilson et al. 2007), stratification (Hunter-Simpson parameter, Simpson & Hunter 1974) and distance to the coast (km). These static environmental habitat predictors were handled as raster layers using the *raster* package (Hijmans 2020). Bathymetric data (TRI, depth) were sourced from a harmonised Digital Terrain Model (DTM) from the EMODnet database (portal.emodnet-bathymetry.eu). TRI identifies changes in seabed depth creating areas of complex currents, upwellings and internal waves – all known to enhance prey availability (Embling et al. 2012, Scott et al. 2013). Depth was included, as water column mixing is exaggerated in shallower waters, where tides interact more with the seabed (Cox et al. 2018). Stratification index was calculated as the Simpson-Hunter stratification parameter (Simpson & Hunter 1974) formulated from depth and maximum tidal current speed. Current information was provided at 1.5 km resolution sourced from the Copernicus Analysis tool using the Atlantic Marginal Model (AMM15) available from the Marine Environmental Monitoring Service (Tonani et al. 2019). Maximum tidal current speeds were calculated from a 14-day spring-neap cycle. Stratification identifies mixed (< 1.9), frontal (1.9) and stratified waters (> 1.9), with fronts assumed to enhance prey availability (Waggitt et al. 2018, Scales et al. 2014). Prey availability may also be increased by intense mixing of the water column in areas of low stratification (Benjamins et al. 2015, Waggitt et al. 2016). TRI and stratification data were resampled to a 1 km resolution using a bilinear interpolation.

The Global Fishing Watch (GFW) Automatic Identification System (AIS) database was used to calculate commercial fishing effort across the region of interest at a 0.01 x 0.01° spatial resolution. These AIS data differ from the VMS data used to run the 7-state HMM in that they provide the spatial distribution of commercial fishing effort with greater coverage, while VMS returns the tracks of individual and identifiable fishing vessels. Fishing effort was calculated from hours fished only, so excluded vessels that were present but not thought to be engaged in fishing activity by the GFW process, which accurately differentiates fishing from non-fishing in > 90% of cases (Kroodsma et al. 2018). We acknowledge that vessels may release offal/discards when in transit rather than when actively fishing, but this process sought to identify the broad spatial distribution of fisheries activity. The 7-state HMM inferred fulmars foraging in association with all major gear-types (see results). Another model was run with fisheries data split according to gear type, with model selection performed using the same process as for the generalised fishing effort model. The gear type model was compared to the base model using AIC to assess the utility of gear-specific fisheries data in explaining fulmar foraging distribution. Fishing effort was observed to be spatially consistent across summer months (appendices, table S6 and S7, figure S3 and S4), and fishing hours from 2012-2018 were averaged across all of May to August (the breeding season for fulmars) in each grid cell to provide a representation of broad-scale fishing effort. The data were smoothed to 5 x 5 km rolling averages and assigned to track points using the *raster* package. Point-specific monthly SST (°C) and chlorophyll-A ($mg \cdot m^{-3}$) values were sourced from NASA's Ocean Biology Processing Group (OBPG) service, and appended to track points using Movebank's bilinear interpolation and inverse distance-weighted processes, respectively (Dodge et al. 2013).

The goodness of fit (GOF) of the final model was assessed by measuring the area under the receiver operating characteristic (ROC) curve (AUC). A confusion matrix and associated accuracy were also included using the packages *PresenceAbsence* (Freeman & Moisen 2008) and *caret* (Kuhn et al. 2019), because AUC has limitations as a measure of GOF (Lobo et al. 2008). The contribution of each covariate to model GOF was also estimated by removing the variable and calculating the change in AUC.

The suitability of foraging habitat was then predicted over the range of the tracking data in each area by applying the model to a raster stack of static covariates. Chlorophyll-a and SST summer averages from 2002-2020 were used in this prediction and were again sourced from OBPG.

3.3 Results

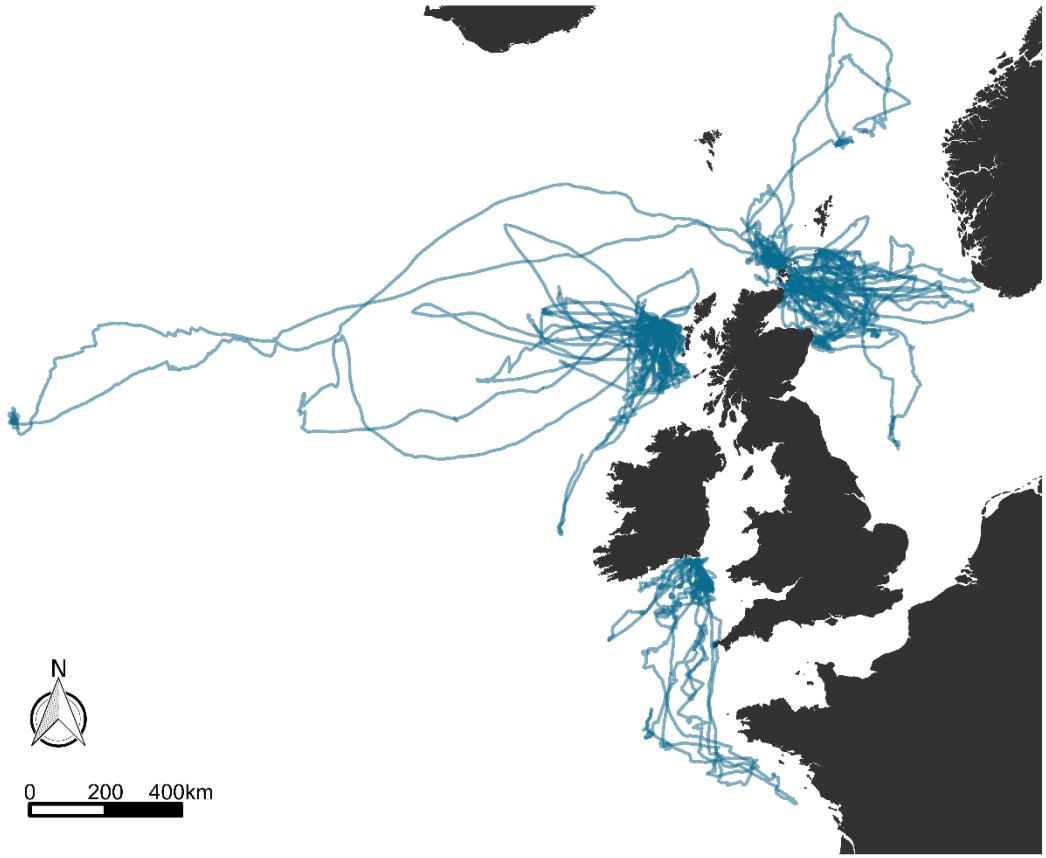


Figure 2: GPS tracks from 102 adult fulmars in Scottish, Irish and Scilly Island colonies, 2009-2019.

We obtained tracking information from 102 breeding fulmars between 2009 and 2019. A total of 184 partial or full foraging trips were recorded from tracked individuals. No distinct differences in distance travelled or proportion of time in Area Restricted Search (ARS) were observed between different geographical areas (appendices, tables S1 and S2). The distribution of tracks covered extensive areas of the southeast Celtic Sea, northwest North Sea, and northeast Atlantic (figure 2).

3.3.1 Fishing vessel association and behaviour

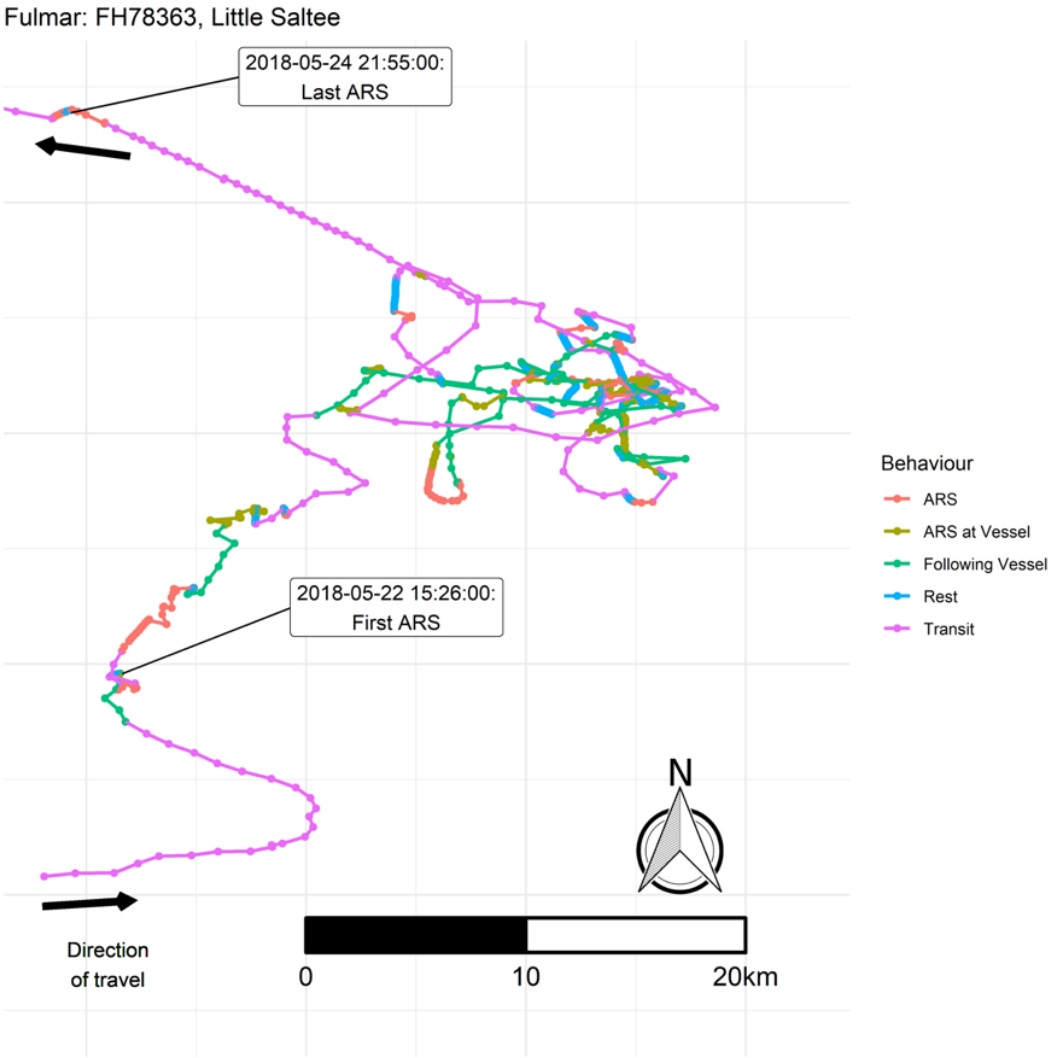


Figure 3: Fulmar track annotated with behaviours inferred by the 7-state HMM. This example has track points identified by the model as ARS in association with fishing vessels, as well as in the absence of detected vessels. It also has examples of vessel-following, rest, and transit states.

Of the 102 tagged birds, 76 had complete foraging trips required for the 7-state HMM to infer direct vessel association. Of these 76 individuals, 41 were identified as engaging in vessel-associated ARS. Figure 3 shows an example of a fulmar track inferred to have engaged in both natural and vessel-associated ARS over the course of 54 hours in the Celtic Deep, a heavily fished area in the Celtic Sea. Within all trips analysed, a greater proportion of time was allocated to non-vessel-associated ARS (29.9%) than vessel-associated ARS (9.5%) (figure 4). Within the trips in which vessel-associated ARS was detected, almost half of the time spent in ARS was spent in association with vessels (46.2 $\pm$ 30.1%). Most of the vessel-associated ARS occurred

in the presence of trawlers (83.2%) consistent with the prevalence of trawler fisheries in the study area and the quantity of discards and offal they produce (Atlas of Demersal Discarding, Anon. 2011). Fulmars showed vessel interactions with all gear types, though longliners (<0.1%), trappers and potters (0.9%) and gillnetters (1.5%) only accounted for a small proportion of interactions (figure 5).

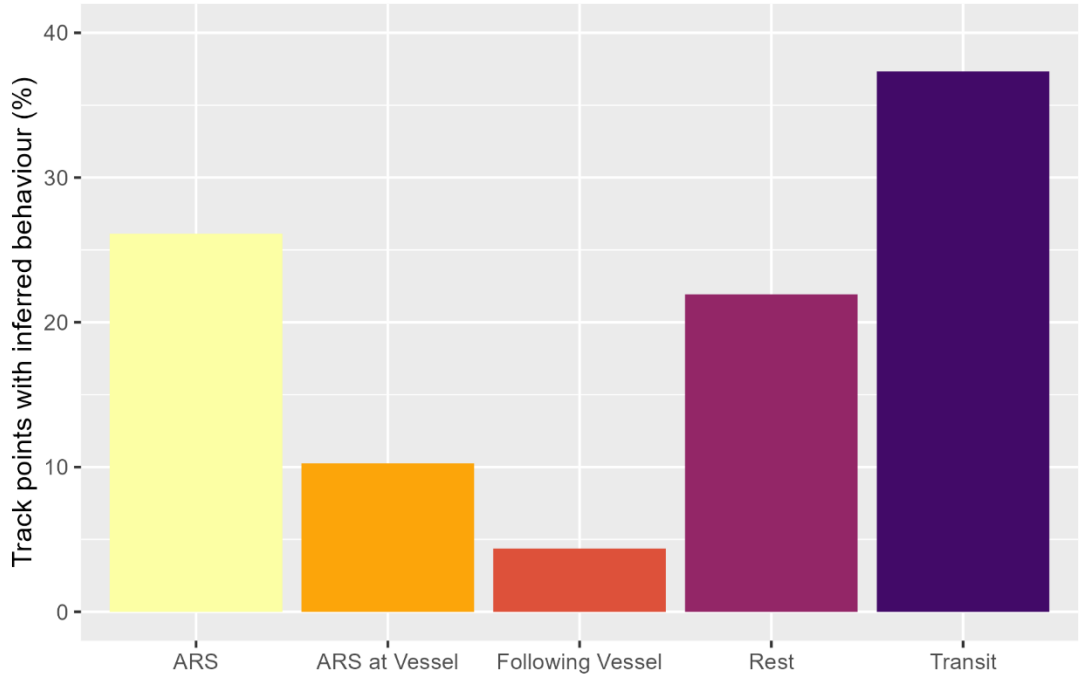


Figure 4: Percentage of time spent in each behaviour according to the 7-state HMM. Transit and ARS states in absence of a detected fishing vessel have been grouped to leave 5 behaviour classes.

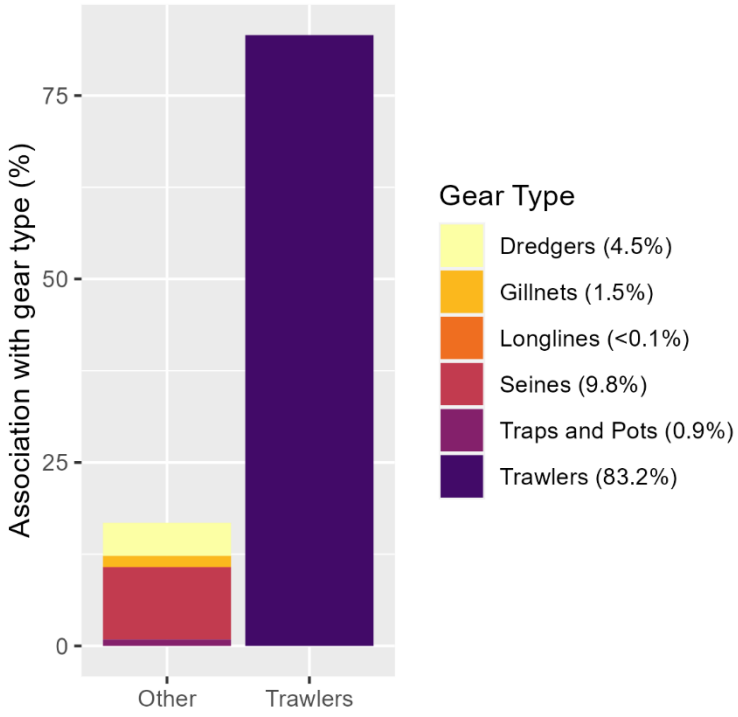


Figure 5: Vessel gear types associated with according to the 7-state HMM. Percentage of points spent in association with each vessel is shown in the legend.

The outputs of the simplified HMM suggested that ARS and non-ARS states were roughly evenly distributed within trips, with 46% ARS (or putative foraging), 32% transit and 22% rest across the full tracking dataset.

3.3.2 Fulmar foraging habitat modelling

Commercial fishing effort was selected as a predictor of putative foraging distribution and behaviour, and environmental variables retained were stratification, seabed roughness, SST, and chlorophyll-A concentration (table 2). Commercial fishing effort made a much greater contribution to model GOF than other variables retained (table 2). The effect of each retained covariate is shown in figure 6. ARS was more likely in poorly stratified/well-mixed waters with a (stratification index < 3) and unlikely in highly stratified waters. The probability of engaging in ARS increased with increasing commercial fishing effort, chlorophyll-a concentration, SST, and seabed roughness. Model AUC was 74.6% and the prediction accuracy was 69%. These values both suggest that the model has a moderate predictive power. A confusion matrix was constructed to compare predicted vs actual values from the model outputs (table 3).

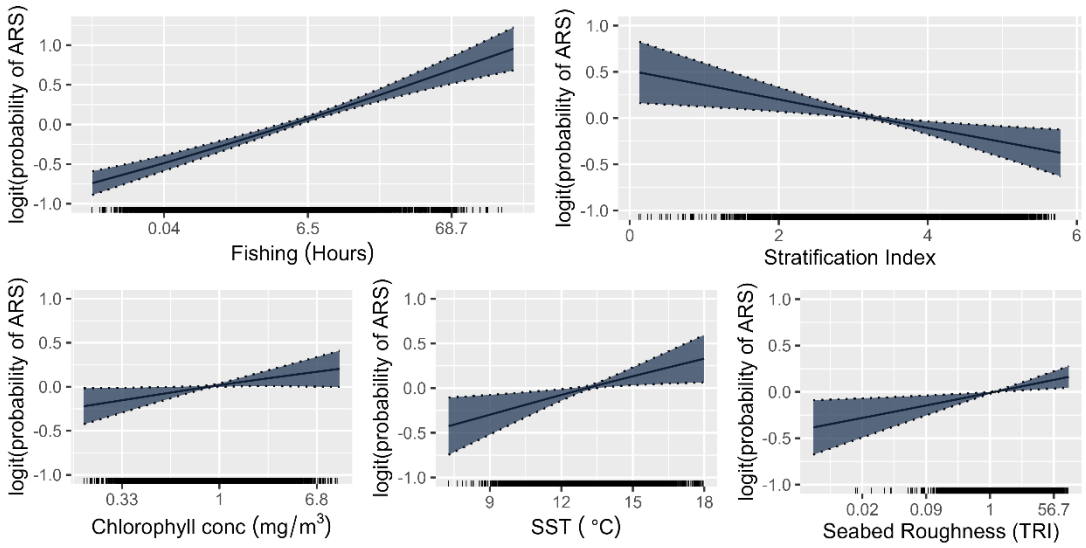


Figure 6: Marginal effects of each model covariate on the probability of ARS behaviour prediction. Dotted lines and shaded grey represent 95% confidence intervals.

Table 7. Retained habitat-preference GAMM covariates that are associated with ARS behaviour of fulmars tracked from Irish, Scottish and Scilly Island colonies. Estimated degrees of freedom (EDF) represents the complexity of the model term, while $\chi 2$ represents the effect the term has on the model output. A p-value of <0.05 is taken as significant. Change in AUC of the model on removal of each variable is also included to represent variable effect on model GOF. This table is ordered by $\chi 2$.

Variable	**EDF**	**$\chi 2$**	**p-value**	**Change in AUC**
Fishing Effort	1.5	199.4	<0.001	1.7%
Sea-Surface Temperature	0.9	25.7	<0.001	0.1%
Stratification	0.9	23.3	0.001	<0.1%
Chlorophyl-a	0.8	9.1	0.015	0.1%
Seabed Roughness	0.9	8.8	0.003	0.3%

Table 8. Confusion Matrix to assess the goodness-of-fit of the foraging habitat preference model by comparing model predictions to HMM-estimated behaviours. The prediction accuracy of this model is 69%.

Confusion Matrix	***HMM-estimated Transit***	***HMM-estimated ARS***
Predicted Transit	5770	3751
Predicted ARS	2715	8641

When commercial fishing effort was split according to gear type, model fit improved according to AIC (11198 with generalised fishing effort, 11174 with fishing effort split by gear types). Trawler and gillnet fishing effort were retained and other fishing gears

dropped by the model selection process (Table S8). Non-trawler fishing effort covariates were heavily positively skewed due to the reduced prevalence of these fisheries within the tracked fulmars' range, leading to high power transformation factors (Box & Cox, 1964) and limiting the utility of these covariates. Generalised fishing effort alone provided a better explanatory variable than retained gear-specific efforts (table 2 & table S8), and because the tracked fulmars were shown to interact with all major fishing gear types, the model including generalised fishing effort was used for subsequent foraging habitat prediction.

The spatial predictions from the model for each study area are shown in figure 7. Large oceanographic features, such as the continental shelf edge, the Rockall Bank and the Norwegian Trench are highlighted as important foraging habitat. Intensely fished areas, such as the Celtic Deep, much of the continental shelf edge and the central North Sea are also highlighted and dense areas of foraging opportunity for breeding fulmars. Closer to shore, areas with a high degree of mixing are identified as important, such as the southeast corner of Ireland (around Little Saltee) and the Pentland Firth between the Scottish mainland and Orkney.

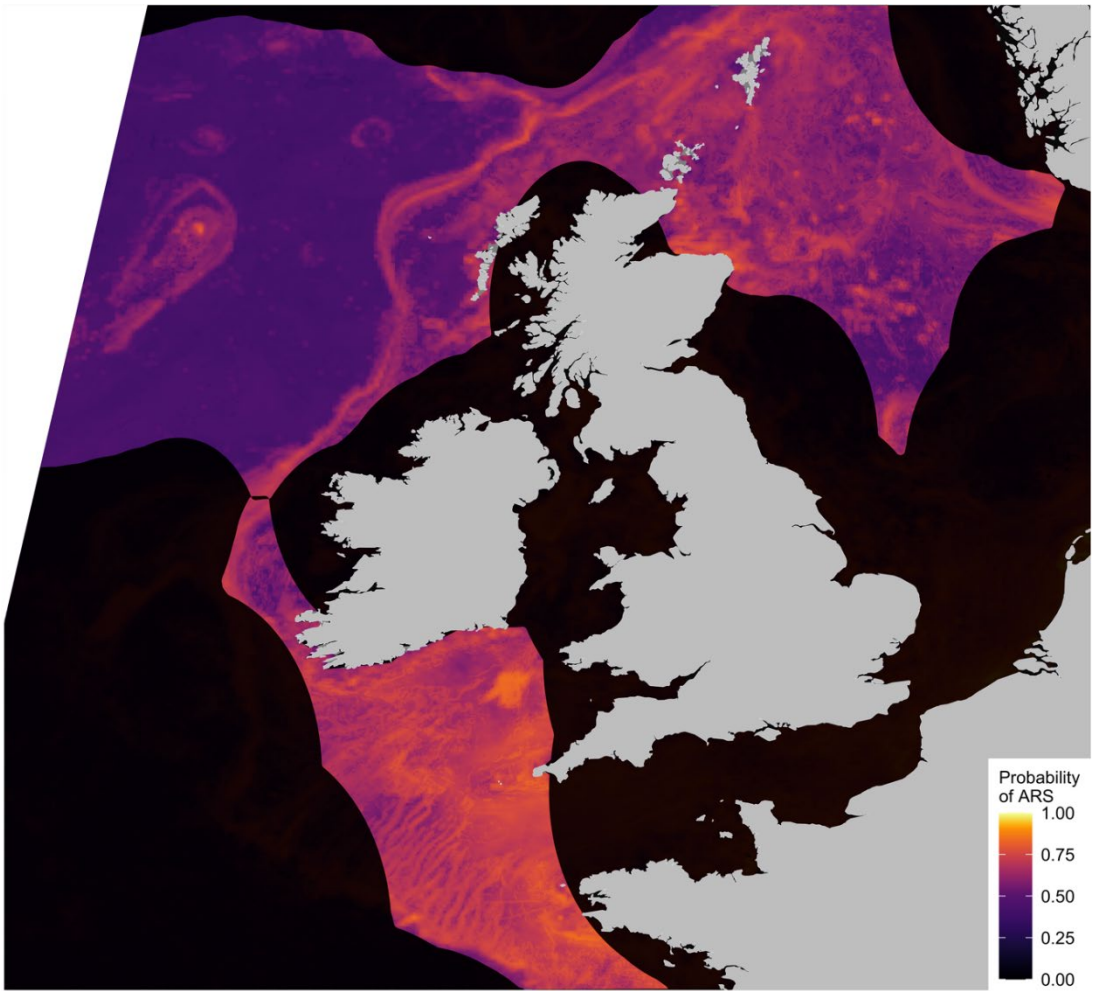


Figure 7: Output of the foraging habitat-preference model extrapolated over the study areas. Care has been taken to avoid predicting across the area for which we do not have tracking data. Values correspond to probability of a fulmar performing ARS in an area if present, from 0 (improbable) to 1 (probable).

3.4 Discussion

Our study highlights high foraging effort in areas of persistently high fishing effort as well as a prevalence of vessel-interactions in breeding fulmars. Fifty-four percent of tracked fulmars associated with vessels on foraging trips, and within those birds known to forage at vessels, roughly half of their time spent in ARS was in the presence of vessels. This provides important context for the elevated bycatch levels for this species (Dunn & Steel 2001, Fangel et al. 2015), as well as their range expansion of the last centuries (Fisher 1952). Not only does this improve our understanding of the fulmars' distribution and use of anthropogenic food subsidies, but it also provides insight into how the foraging distribution of this species may be changing with

shifting fisheries distribution, policies, and practices. On a broader scale, our study also suggests that anthropogenic factors should be considered when discussing the distribution and behaviour of species, such as the fulmar, that alter their habits in response to human activities.

The high degree of putative foraging in association with fishing vessels points to the potential importance of fisheries byproducts (discarded fish, offal, bait) in the diet of this species (Ojowski et al. 2001). This is likely exaggerated in breeding individuals, whose foraging range is central-place constrained by needing to return to the nest for incubation, chick-rearing, and provisioning duties (Edwards et al. 2016). Dupuis et al. (2021) show that fulmars interact with vessels throughout the non-breeding season, but that interactions were more prevalent in parts of their range closer to breeding colonies. This suggests that vessel attendance may be more common when central-place foraging compared to less restricted periods of their annual cycle. It may also simply reflect that fishing effort is concentrated around breeding colonies compared to overwintering areas. Fisheries waste and depredation opportunities may increase food availability within their restricted breeding range (Bicknell et al. 2013) and widen diet to include species otherwise physically out of reach of this surface-feeding species (Hudson & Furness 1988, Thompson et al. 1995, Phillips et al. 1999). However, vessel interactions may also result in bycatch, and rates of vessel-associated foraging noted in this study are consistent with the high incidence of bycatch of fulmars relative to other seabird species (Dunn & Steel 2001, Fangel et al. 2015). Over half of the tracked fulmars associated with vessels, and of all ARS detected in the analysis, 30% was associated with fishing vessels. This is also likely to be an underestimate given that VMS data does not include vessels under 12 m length or those fishing illegally, as well as UK VMS data not capturing non-UK vessels (see methods). There may also be a mismatch in the quantity of VMS data available across different time periods, as proportionally more vessels in the European fleet are fitted with VMS transponders over time (O' Shea & Thompson 2006), with similar patterns apparent in AIS data (appendices, figure S4).

The degree to which fulmars associated with vessels across our tracking dataset is also reflected in persistent fishing effort being a significant predictor of fulmar

foraging habitat. According to model outputs, anthropogenic fishing effort was a better predictor of fulmar habitat preference than oceanographic covariates typically used in species distribution models, including chlorophyll-a concentration, SST, seabed roughness and stratification (e.g. Camphuysen & Garthe 1997, Skov & Durinck 2001, Kane et al. 2020). The recent decline of this species, as well as importance of intensely fished areas for foraging fulmars, highlights the need for targeted conservation that may involve adaptation of fishing gears or fishing practices to mitigate bycatch risk (Løkkeborg 2011, Domingo et al. 2017, Da Rocha et al. 2021). This study would also suggest that negative effects of other threats to fulmars such as oil pollution could be compounded if present in areas of intense fishing activity.

Despite fulmars being known consumers of fishery discards (Ojowski et al. 2001), the described effects of fishing vessels on fulmar foraging behaviour and distribution could arguably be due to both fulmars and fisheries targeting similar areas. While we cannot rule this out entirely, a recent study on the similarly sized, generalist, surface-feeding procellariform Cory's shearwater (*Calonectris borealis*) (Granadeiro et al. 1998) found very little overlap with fishing activity within its range (Pereira et al. 2021). Cory's shearwaters are not thought to habitually associate with fishing vessels, and low overlap would suggest their natural prey is obtained in areas that are not heavily fished. This supports the suggestion that fulmar's foraging habitat being associated with fishing effort is due to fulmars concentrating ARS over areas of known intense fisheries, as Collet & Weimerskirch (2020) demonstrated in black-browed albatrosses (*Thalassarche melanophris*), which were shown to direct foraging effort towards areas where they had previously encountered fishing vessels. Black-browed albatrosses are also known to take fishery discards (Mariano-Jelicich et al. 2014).

Fulmars still directed considerable foraging effort towards natural prey with more foraging occurring in the absence of detected vessels. This is reflected in the contribution of environmental covariates to the foraging habitat preference model. Though fulmars' natural prey species are trophically distinct from primary producers (Furness & Todd 1984), chlorophyll-a concentration was nevertheless identified as a

significant predictor of fulmar foraging behaviour, consistent with studies in other procellariforms (Kane et al. 2020) as well as other marine predators (Russell et al. 1999, Cox et al. 2016). Areas of low stratification, or well-mixed waters, may be of benefit to fulmars through the accumulation and aggregation of zooplankton by complex flow structures (Benjamins et al. 2015). Seabed roughness may also contribute to the complexity of flow structures and increase the availability of prey (Cox et al. 2018) as well as being unsuitable for many demersal fisheries due to risk of loss or damage to fishing gears through snagging on complex seabed terrain.

Fisheries are dynamic, and influenced by governance, market demand, policy, and infrastructure (ports, harbours, *etc*.) as well as fish stock levels and distribution shifts due to climate change (Perry et al. 2005). The foraging distribution of fulmars and other discards-consuming species are therefore linked to the same range of socioeconomic and environmental factors. The European Union initiated a discard ban, or landing obligation, in 2015, calling on fishing vessels to cease the disposal of bycaught non-target species at sea (Borges, 2021). Fulmars are known to take a range of fisheries byproducts, including offal and longline bait (Phillips 1999), though our study has shown that fulmars have a clear affinity towards trawler vessels, the major perpetrator of discarding in the study region (Atlas of Demersal Discarding, Anon. 2011). With discard rates presumably decreasing, it would be expected that fulmars may shift their fishing effort either towards natural prey, or towards other fishing gears with available by-products. This may lead to increased associations with longline and purse seine vessels, where fulmars can depredate bait or assimilated prey, though this in turn may cause increased rates of bycatch from fulmars getting caught in these gears (Dunn & Steel 2001).

Including fishing effort as a covariate in foraging habitat preference analysis may be useful for a range of species that take discards, target similar prey species to fisheries, or even actively avoid vessels. More generally, including anthropogenic factors in habitat models can improve our understanding of species distribution and behaviour across a range of taxa. For example, Russell et al. (2014) showed that windfarms can influence the foraging behaviour of seals by creating artificial reefs and excluding fisheries, both thought to lead to increased abundance of prey. Similarly, Lieber et al.

(2019) showed how a persistent artificial wake created by a wave power harvester created a foraging hotspot for surface-feeding seabirds through persistent mixing of the water column. Human industry is shaping the habits and habitats of species, and this study highlights the value of considering such anthropogenic factors when investigating species' ecology.

3.5 Appendices

Trip metrics compared across breeding stages and areas

Table S1: Differences in trip metrics between fulmars at different breeding stages. *Data is taken from a subset of complete tracks used to quantify vessel associations.

Breeding Stage	**Incubation**	**Early Chick Rearing**
Max Distance to Colony (km)	215 ± 382	134 ± 147
Total Distance Covered (km)	1996 ± 3017	703 ± 797
Duration (hours)	58.8 ± 72.1	23.2 ± 19.0
Proportion in ARS (%)	24.7 ± 16.5	30.3 ± 20.6
*Proportion in Vessel-Associated ARS (%) **	8.2 ± 7.8	11.1 ± 15.8

Table S2: Differences in trip metrics between fulmars in different major geographic areas. *Data is taken from a subset of complete tracks used to quantify vessel associations.

Area	**Celtic Sea**	**Scotland**
Max Distance to Colony (km)	129 ± 182	153 ± 219
Total Distance Covered (km)	1201 ± 1356	896 ± 1605
Duration (hours)	40.4 ± 41.5	27.9 ± 37.1
Proportion in ARS (%)	25.1 ± 17.6	32.6 ± 21.4
*Proportion in Vessel-Associated ARS (%) **	14.4 ± 15.6	6.6 ± 13.8

Maximum distance travelled and proportion of time spent in ARS are similar between the two major geographical areas, which suggests that foraging strategies are consistent between groups. Duration and total distance covered tend to be higher in incubating fulmars, possibly due to relaxed time constraints compared to when they provision chicks. More ARS in association with fishing vessels is detected in Celtic Sea fulmars. These data are largely more recent than the chick rearing and Scottish data, and this difference may stem from the improved quality and availability of VMS data for recent years.

7-state HMM parameters

Table S3: Behaviours inferred by the 7 states of the HMM.

State	Description of inferred behaviour
St1	Resting on water
St2	ARS on outward leg of the foraging trip
St3	Transit on outward leg of the foraging trip
St4	ARS in association with a fishing vessel
St5	Transit in association with a fishing vessel
St6	ARS on return leg of foraging trip
St7	Transit on return leg of foraging trip

Table S4: Starting parameters of step length, turning angle and distance to vessel for the 7-state HMM, this example based on a colony with a 3-minute interpolated track point interval. Step length parameters are scale and shape on the Weibull scale. Turning angle parameters are mean and concentration of a wrapped Cauchy distribution. Distance to vessel parameters are location and scale of a log normal distribution.

Starting parameters	St1	St2 & St6	St3 & St7	St4	St5
Step	1, 0	1, 0.1	5.3, 1.6	1, 0.1	5.3, 1.6
Angle	0, 0	0, 0	0, 1	0, 0	0, 1
Vessel Distance	1, 0.1	1, 0.1	1, 0.1	7, 0.7	7, 0.7

St1 has a low step length and low angle concentration to hopefully reflect a state that represents when the fulmar is resting on the water. St2, St4 and St6 have moderate step lengths and low angle concentration in order to reflect tortuous bursts during ARS and foraging. St3, St5 and St7 have large step lengths and moderately concentrated angles to represent direct uninterrupted movement thought to reflect commuting sections of tracks, travelling between the colony and foraging grounds. St4 and St5 are given parameters reflecting a shorter distance to the nearest vessel on the log normal scale than the other states in order to infer transit and ARS in association with a vessel (appendices, tables S3 & S4).

3-state HMM starting parameters and emission distributions

Table S5: Starting parameters of step length and turning angle for fitting of the 3-state HMM. Step parameters are mean and standard deviation of a Gaussian distribution. Angle parameters are mean and concentration of a Von Mises distribution.

Starting parameters	**State 1 - Rest**	**State 2 - ARS**	**State 3 - Transit**
Step	500, 600	3900, 900	6900, 1300
Angle	0, 0.1	0, 0.1	0, 1

State 1 has a low step length and low angle concentration to hopefully reflect a state that represents when the fulmar is resting on the water. State 2 has moderate step lengths and low angle concentration in order to reflect tortuous bursts during ARS and foraging. State 3 has large step lengths and moderately concentrated angles to represent direct uninterrupted movement thought to reflect commuting sections of tracks, travelling between the colony and foraging grounds.

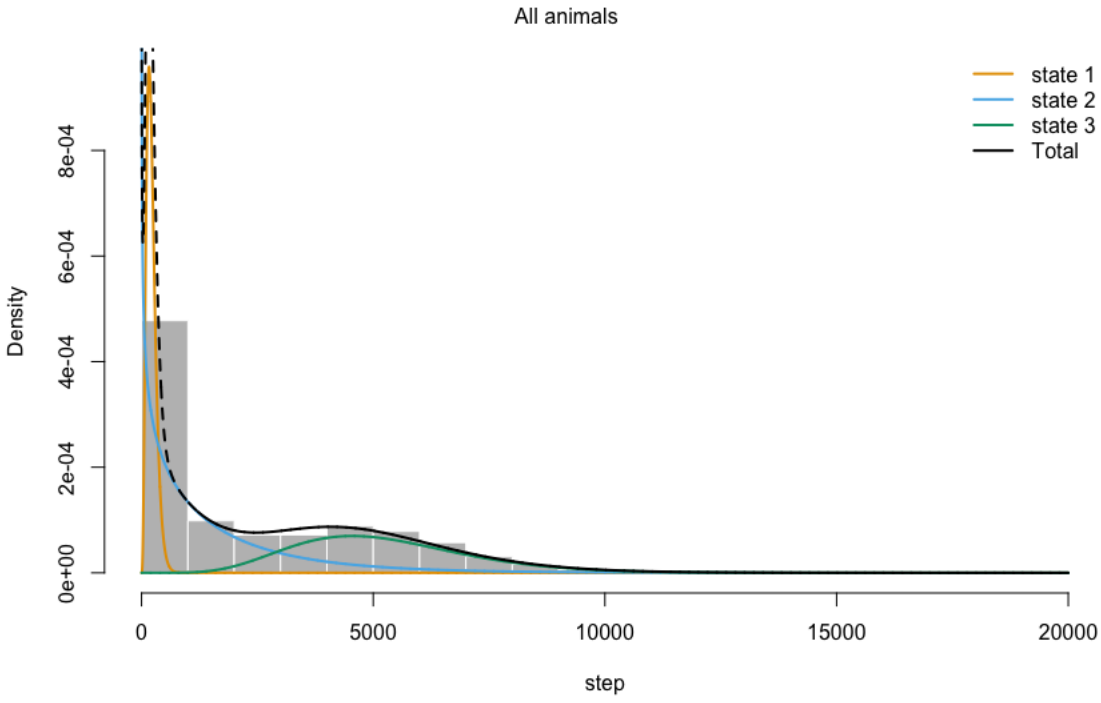


Figure S1: Emission distribution of step length variable for the 3-state HMM. Step is measured in metres, states estimated are assumed to represent rest (1), ARS (2) and transit (3).

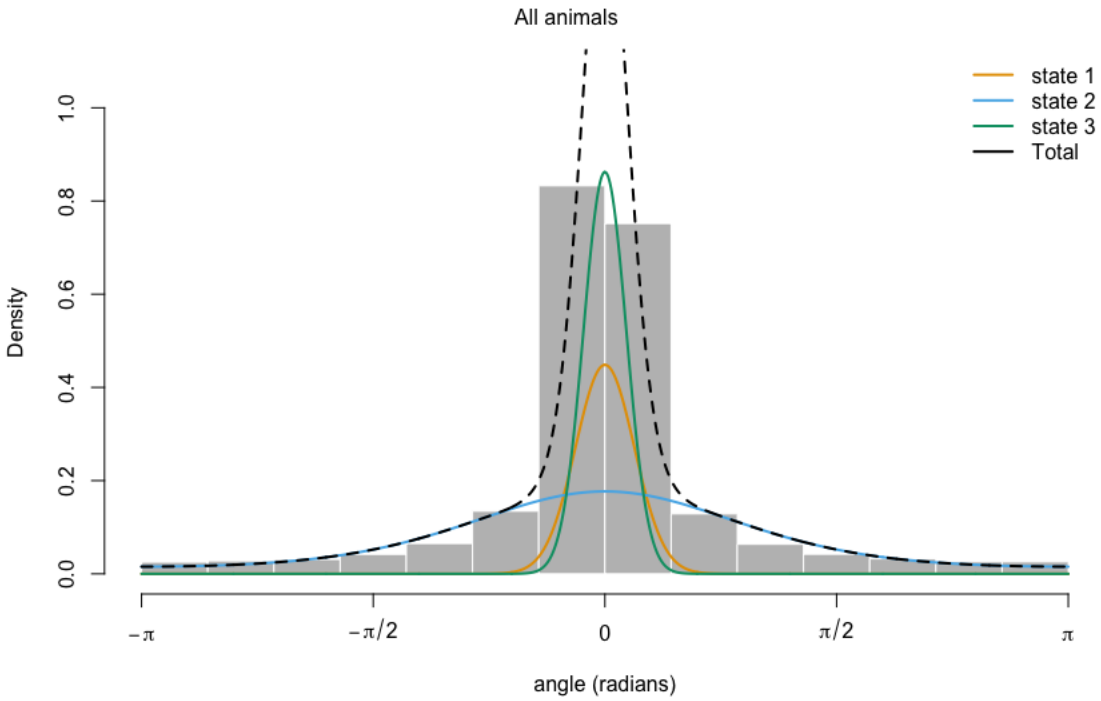


Figure S2: Emission distribution of turning angle variable for the 3-state HMM. States represented are the same as in figure S1.

Box Cox derived transformation factors

Table S6: Box-Cox derived transformation factors

Variable	**Transformation factor**
Fishing effort	0.217
Chlorophyll-a concentration	-0.359
SST	None
Depth	-0.169
Seabed roughness	-0.170
Distance to coast	0.262
Stratification index	None

Fishing effort consistency across months and years

Fishing effort was transformed by square root to reduce positive skew, then Pearson's correlation analysis was performed using the *raster* package.

Table S7: Pearson correlation coefficients comparing fishing effort across the 4 months of fulmars' breeding season. Monthly raster layers were averages across all data available, 2012-2018.

Month	**May**	**June**	**July**	**August**
May	1	0.86	0.80	0.76
June	-	1	0.90	0.83
July	-	-	1	0.89
August	-	-	-	1

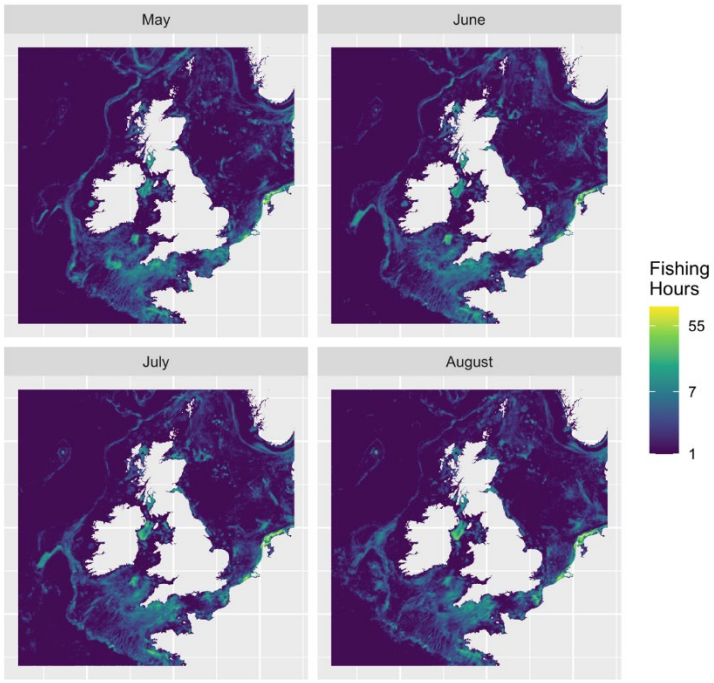


Figure S3: Long term fishing effort by month, 2012-2018

Summer monthly fishing hours across data available (2012-2018) appear reasonably consistent, though effort spreads over abyssal waters slightly more in July and August (figure S3). Consecutive months are more highly correlated than those with a gap between (table S7).

Table S8: Pearson correlation coefficients comparing fishing effort across the 7 years of available data, 2012-2018. Yearly raster layers were averaged across May to August, the fulmar breeding season.

Year	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**
2012	1	0.50	0.49	0.46	0.48	0.45	0.43
2013	-	1	0.82	0.78	0.77	0.76	0.74
2014	-	-	1	0.82	0.80	0.79	0.76
2015	-	-	-	1	0.86	0.84	0.79
2016	-	-	-	-	1	0.86	0.81
2017	-	-	-	-	-	1	0.86

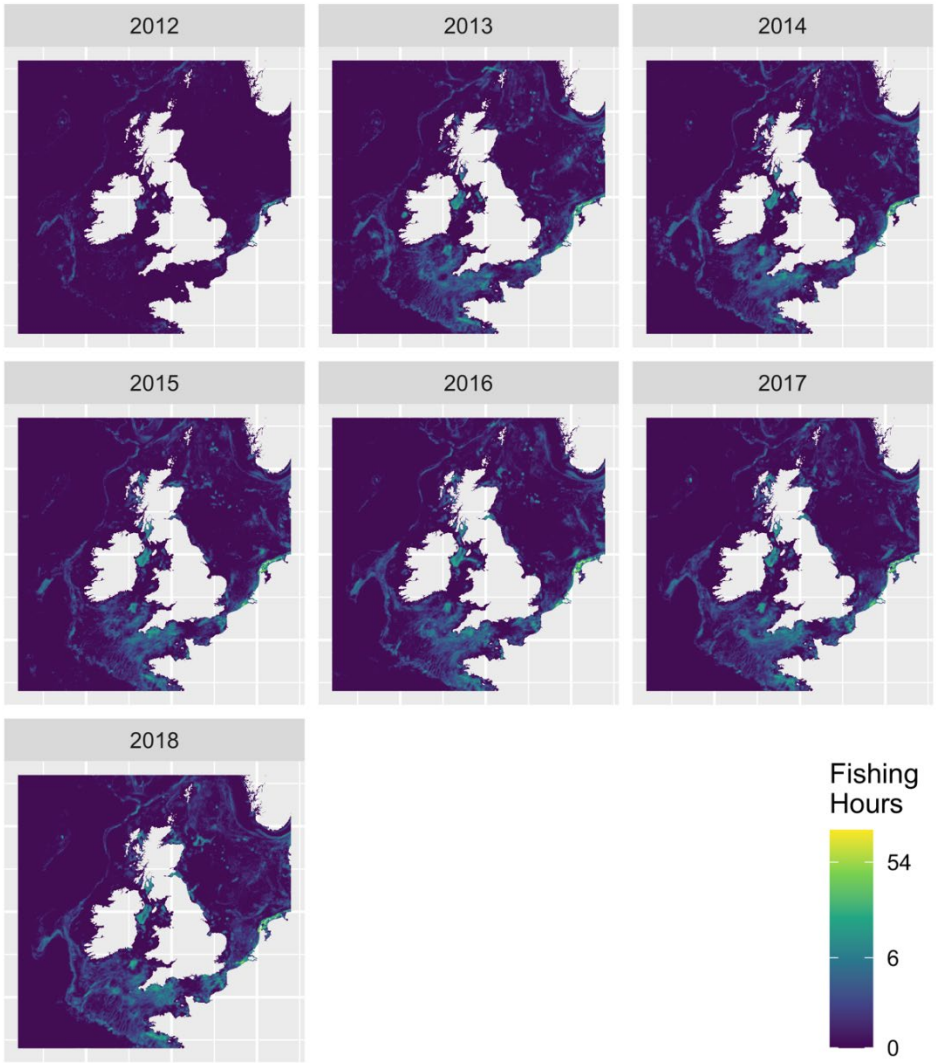


Figure S4: Summer fishing hours (May to August) for each year of available data.

Overall summer fishing effort generally increases year after year (figure S4), though this may be due to greater coverage of fishing vessels monitored rather than a reflection of reality. The correlation between consecutive years increases over time, bolstering this argument. Values for 2012 are much lower than for other years, again probably due to lower monitoring effort, and this is reflected in the correlation coefficients for this year (table S8).

Model using fishing efforts specific to gear type

Table S9: Model coefficients for model that uses fishing effort split by major gear type. Trawler and gillnet fishing effort were the only fishing effort covariates retained of the 6 gear types tested.

Variable	**EDF**	**χ2**	**p-value**
Trawler Fishing Effort	2.7	176.5	<0.001
Gillnet Fishing Effort	0.7	3.9	0.043
Sea-Surface Temperature	0.9	26.6	0.002
Stratification	1.0	41.4	<0.001
Chlorophyl-a	0.8	20.8	<0.001
Seabed Roughness	0.9	13.7	<0.001

Abstract

Fisheries waste is used by many seabirds as a supplementary source of food, but interacting with fishing vessels to obtain this resource puts birds at risk of entanglement in fishing gears. As a result, bycatch is one of the leading contributors to seabird declines worldwide, and this risk may increase over time as birds increasingly associate fishing vessels with food. Light level geolocators mounted on seabirds can detect light emitted from vessels at night. We used a 16-year time series of geolocator data from 296 Northern fulmars (*Fulmarus glacialis*) breeding at temperate and arctic colonies to investigate trends of nocturnal vessel interactions in this scavenging pelagic seabird. Rates of seabird-vessel encounters increased over time across the North Atlantic, despite a reduction in fleet sizes and fisheries waste over the same period. Males were more likely to attend fishing vessels, and higher encounter rates were correlated with lower time spent foraging and a geographically restricted overwintering distribution. Differences in attendance at vessels among individuals was highly consistent across years. Our results may signal an increased reliance on fishery-associated food sources and greater risk of bycatch, potentially due to declines in natural prey availability. Our findings highlight the need to better understand the consequences of vessel interactions, and their potential role in population declines.

4.1 Introduction

Many seabird species interact with fishing vessels in order to scavenge bait, offal, or discards (Bicknell et al. 2013). Vessels provide a conspicuous visual cue above the water (Votier et al. 2013, Michel et al. 2022), and may also provide olfactory or auditory cues to attract scavengers. The distribution of commercial fisheries has been shown to affect the behaviour and distribution of scavenging seabirds, as birds direct foraging effort towards areas where vessels are active (de la Cruz et al. 2022, Chapter 3). Individual-level consistency in the proportion of fisheries waste in the diet of some species suggests that vessels can provide a consistently available food source (Votier et al. 2010, Giménez et al. 2021). On the other hand, intense fisheries can drastically reduce the amount of natural prey species available to seabirds (Wanless et al. 2018). The availability of fisheries waste may compensate in some ways for reductions in natural prey, though this artificial resource may not always sufficiently substitute natural diet (Grémillet et al. 2008) and may be more energetically costly than foraging on natural prey (Cianchetti-Benedetti et al. 2017).

Close proximity to vessels to scavenge waste and bait greatly increases seabirds' risk of being bycaught in fishing gears (Carneiro et al. 2022). Bycatch is one of the leading contributors to seabird population declines worldwide, affecting as many as 100 species (Dias et al. 2019). Bycatch can occur through entanglement with nets as seabirds attempt to take fish in or around the net (Bærum et al. 2019, Chritensen-Dalsgaard et al. 2022), or snagging on longline hooks when attempting to depredate bait or the catch (Brothers 1991). How the at-sea distribution of seabirds overlaps with commercial fisheries directly influences that species' bycatch risk (Clay et al. 2019).

Biotelemetry and remote sensing can be used to identify and monitor seabird-fisheries interactions. Larger fishing vessels are obliged to carry transponders that regularly relay their location to relevant authorities, with these data collated to map the global footprint of fisheries (Kroodsma et al. 2018). Fine-scale seabird tracking data can be related to vessel locations to establish distance to the nearest vessel, and how this may impact the likelihood of an interaction (Bodey et al. 2014, Pirotta et al. 2018, Orben et al. 2021). Seabird-borne devices that are sensitive to radar can detect

vessels directly, which is useful in areas where a high proportion of interactions involve vessels not reporting location, either due to falling below the size threshold that legally obliges them to do so, or because they are operating illegally (Weimerskirch et al. 2017). Cameras attached to seabirds can similarly detect vessel interactions more directly (Votier et al. 2013, Tremblay et al. 2014), also lend insights into how they interact with both the vessel itself and other scavenging seabirds (Michel et al. 2022). Light level geolocators can be used to detect nocturnal vessel interactions by identifying anomalous light spikes at night, when far out at sea and away from other potential sources of light (Krüger et al. 2017). The advantage of this method is that the technology involved is relatively cheap and simple, and unlike other tag types can collect data over entire annual cycles. Such devices have been deployed on thousands of seabirds since they were first developed, in order to identify distributions during the non-breeding season.

The northern fulmar (*Fulmarus glacialis*) is a seabird species known to scavenge fisheries by-products (Ojowski et al. 2001) and has formed the basis for several studies on seabird-fisheries interactions, both through direct observation (e.g. Camphuysen & Garthe 1997) and using biotelemetry (e.g. Pirotta et al. 2018, Chapter 3). Fulmars underwent a southwards expansion in the 19th and 20th century, establishing breeding colonies in the UK, Ireland, and the north coast of mainland Europe (Burg et al. 2003), with this spread often attributed to the intensification of fisheries in these areas (Fisher 1952). However, fulmars are now the most commonly bycaught seabird in North Atlantic fisheries (Fangel et al. 2015, Hedd et al. 2016), and are currently experiencing declines across their Atlantic range (Cordes et al. 2015, Mallory et al. 2020), resulting in them being listed as endangered in Europe (Birdlife International 2015).

We aim to examine long-term spatial and temporal trends of nocturnal fulmar fisheries interactions, using established methods to identify vessel encounters (Dupuis et al. 2021) from an extensive geolocator dataset. We will used fine-scale data from previous work to establish whether daytime and nocturnal vessel association rates are comparable. Factors that may influence encounter rates, including sex, time of year, range, and individual repeatability, will also be tested, as

well as the correlation between vessel attendance and migration effort and activity budgets. Together, these analyses will provide important information on which factors influence vessel attendance, how this is changing over time, and what this means for bycatch risk of this species.

4.2 Methods

4.2.1 Deployment and recovery of geolocator devices

All fulmar capture, handling, and tag attachment were conducted under appropriate region-specific licences. Breeding adult fulmars were captured at the nest by hand, hand net, or noose pole and handling time was kept to a minimum. GLS devices were deployed and recovered on 296 breeding adult fulmars from 2006 to 2022 in four colonies across the Northeast Atlantic (Table 2). Recoveries were often > 1 year after deployment, providing a total of 737 years of data from 296 individuals (Table 2). Geolocators were attached to a coloured plastic ring fitted around the tarsus, with total deployment weight (devices plus leg ring and cable tie attachment) always < 1% body mass. Several types of geolocator were used and were grouped into 3 classes for subsequent analyses based on functionality following Dupuis et al. (2021), as the immersion sampling rate and light sampling units vary between models, which may impact encounter detection or behavioural classification. Individuals were sexed where possible (n = 183), either genetically or using morphological measurements (van Franeker & ter Braak 1993).

Table 1: Study colonies, number of individuals successfully tagged at each, and years for which data were available.

Colony	**Years**	**Individuals**	**Years of tag data**
Eynhallow, Scotland	2006-2022	150	389
Little Saltee, Ireland	2010-2012, 2019-2022	38	62
Skjalfandi, Iceland	2014-2021	54	163
Jan Mayen, Norway	2014-2021	54	123
Total	2006-2022	296	737

4.2.2 Processing of locations

Light level data from different geolocator types were standardised and scaled from 0 to 1 (appendices, figure S1). Using a threshold method (Lisovski et al. 2019), transitions between day and night (twilight events) were identified, allowing the calculation of latitudes (using the length of day and night) and longitudes (based on the time of midday and midnight). Unrealistic twilights, due to shading or encounters with anthropogenic light sources, were filtered out using a moving-window smoothing function. Using a probabilistic algorithm, a location was estimated 600 times for each inter-twilight period (Merkel et al. 2016). To mitigate against unrealistic location estimation, the most likely location of these 600 was selected based on constraints established using additional data from the geolocators' temperature and immersion sensors, combined with satellite-derived estimates of sea-surface temperature, estimated range, and maximum flight speed of the species (Merkel et al. 2016). All data analyses were conducted using R version 4.1.2 (R Core Team, 2022).

4.2.3 Nocturnal vessel encounters

Nocturnal vessel encounters were identified using the same principal as Dupuis et al. (2021), identifying anomalously high values in raw light data during the night (light spikes). Expected solar angle (αs) of each raw light datapoint was calculated based on time, date, and nearest estimated location using the *oce* package (Kelley & Richards 2020). Datapoints without a successful location estimate within 4 days of their timestamp were excluded to avoid excessive inaccuracy when calculating αs. Two thresholds were used to define light spikes, depending on αs. For αs between 9 and 12 degrees below the horizon, standardised light levels were classified as light spikes when above 0.2. For αs greater than 12 degrees below the horizon, this threshold was reduced to 0.02. Natural light readings for both tags are 0 for a αs greater than 6 degrees below the horizon (appendices, figure S2), so these threshold values were conservative to avoid false classification of light spikes. To further reduce the likelihood of false positives, light spikes that were not preceded and followed by a period of darkness lasting at least one fix interval were excluded. So were those without any time immersed in saltwater in the preceding or following 20 minutes.

Light spikes were then grouped into encounters, clusters of light spikes with no more than 40 minutes separating them. This threshold was identified following methods described by Dupuis et al. (2021). Each encounter was given a unique identifier. Number of encounters per calendar date, proportion of nocturnal fixes (αs < -9) per calendar date, and number of encounters per year tagged (July 1st to June 30th of the subsequent year) were then calculated. GPS tracking data and associated vessel monitoring data from a previous study (Darby et al. 2021) were used to compare time in association with vessels during the day versus at night. This suggested that vessel encounters at night were likely to be reasonably representative of vessel attendance overall overall (figure 1).

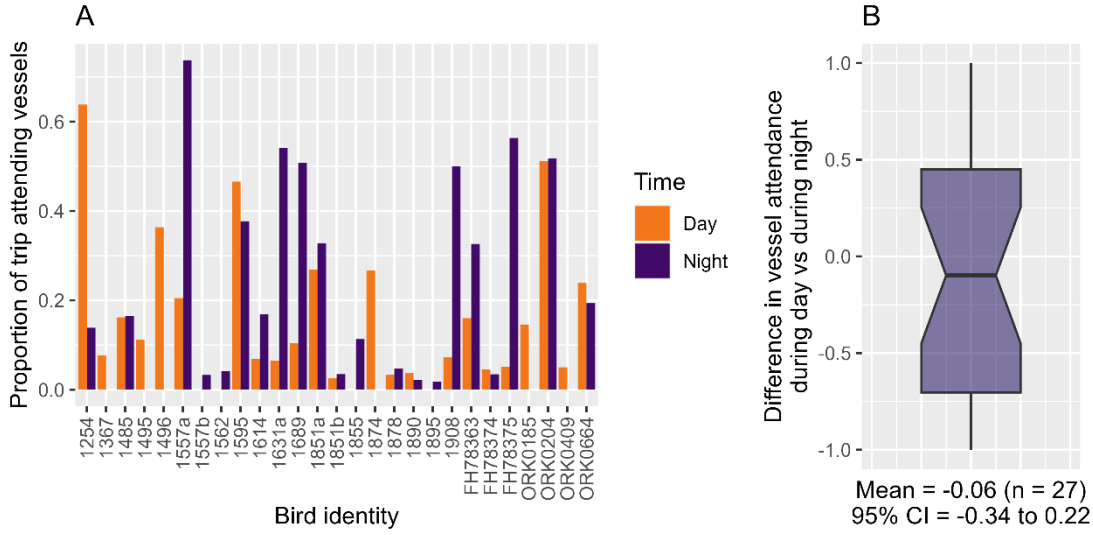


Figure 1: Comparison of diurnal versus nocturnal vessel attendance using concurrent fulmar and vessel tracking data from Darby et al. (2021). Left: A shows the proportion of vessel attendance during the day (solar angle > -9) and during the night (solar angle < -9) for 27 breeding fulmars from Scottish and Irish colonies that attended vessels during foraging trips. Right: B shows the distribution of differences between proportion of time spent associating with vessels during the day and during the night, with 0 meaning no difference, positive values representing more nocturnal vessel attendance, and negative values representing more daytime attendance.

4.2.4 Distribution and behaviour data

Home ranges were calculated for each bird for each non-breeding season tagged (September 1st to April 30th the following year), using the *adehabitatHR* package (Calenge 2006) to calculate the 90% utilisation distribution (UD) of location estimates. Prior to UD estimation, locations were reprojected to azimuthal

equidistant projection centred on each colony. The breeding season was excluded when estimating home range because distributions will be central-place constrained, and light sensors on geolocators are often obscured when the bird is sitting on the nest, limiting the proportion of usable twilight data at this time of year. Behaviour of the bird was calculated based on activity data from the geolocator immersion data following established methods (Mattern et al. 2015). Loggers recorded the proportion of time spent immersed in saltwater per 10-minute interval. If the logger was immersed for ≥ 95% of this interval, the bird was assumed to be sitting on the water. If the logger was immersed for ≤ 5% of the interval, the bird was assumed to either be in sustained flight or sitting on the nest. Anything between these two values was labelled as mixed behaviour, and most likely represents foraging, when the bird is flying for short periods of time between landing on the water surface to feed (e.g. Rayner et al. 2012). The proportion of time per day spent over the entire non-breeding season (September 1st to April 30th the following year) engaged in mixed behaviour was calculated.

4.2.5 Fisheries data

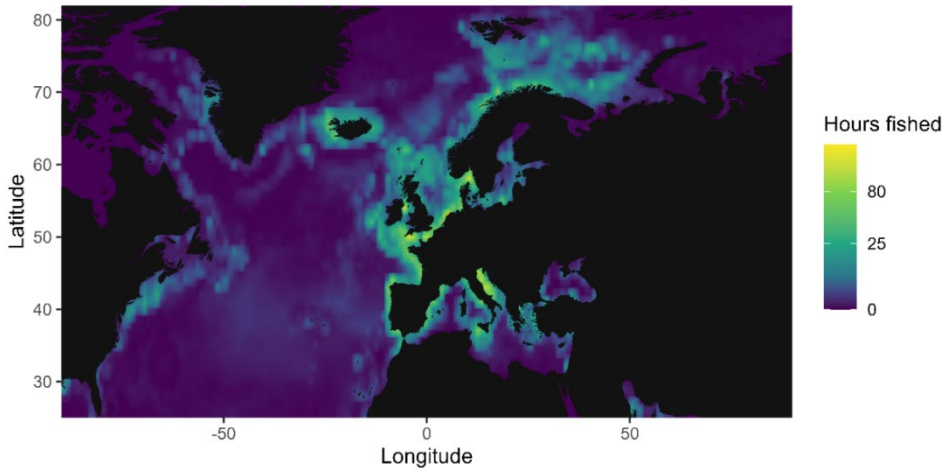


Figure 2: Distribution of fishing effort across the North Atlantic. Data shown are hours fished per km² from 2012 to 2020, aggregated to 1 x 1° spatial resolution.

The spatial distribution of fishing effort was calculated over the range of the fulmar tracks. Fisheries data were sourced from Global Fishing Watch's collated Automatic Identification System dataset (Kroodsma et al. 2018). These data were available from 2012 to 2020, with increasing coverage over time. Because the data quality varies

between years, and the timeseries does sufficiently cover the fulmar GLS data used in this study, the entire dataset was aggregated to a single spatial layer at 1 x 1° resolution to provide a metric for *persistent* fishing effort (figure 2). Values in each grid cell were calculated as hours fished per km^2, accounting for latitudinal differences in grid cell size. These values were then appended to all fulmar track points.

4.2.6 Modelling of vessel encounters

Vessel encounters per night were modelled using generalised additive mixed-effects models (GAMMs) against spatial and temporal covariates using the *mgcv* package (Wood 2008). Two models were run, one with encounters per night as the response with a negative binomial error structure, and another with presence/absence of encounter in each night (0 or 1) as the response with a binomial error structure. The suitability of each model structure was tested with simulated residuals using the *DHARMa* package (Hartig 2022) and the binomial error structure was selected as the better fit. Fishing effort was included as a linear fixed effect. Proportion of nocturnal fixes per day ($\alpha s < -9$) was also included as a spline, as this will affect the likelihood of detecting encounters, while Julian day was included as a cyclic cubic spline to explore variation throughout the annual cycle. Bird identity was included as a random effect to capture inter-individual variation in vessel attraction (Darby et al. 2021). Logger type was included as a fixed effect to account for differences in light sensitivity not captured by the light-level standardisation process. The interaction between the linear effect of breeding year (July 1^{st} to June 30^{th} of the subsequent year) and colony was included as a covariate to assess trends of vessel encounters over time across the four study colonies. Sex was included as a factor, also retaining birds of unknown sex to avoid reducing the sample size. Serial autocorrelation was tested for in both model structures using an autocorrelation function plot, and a first-order autoregressive error structure was applied. Model predictive power was tested by calculating the area under the receiver-operator curve (AUC) using the *ROCR* package (Sing et al. 2005).

4.2.7 Repeatability of vessel encounters

The individual repeatability of vessel encounters was modelled using the *rptR* package (Stoffel et al. 2017), with encounters per year per individual as the response variable with a Poisson error structure. Individual identity was included as the random effect and grouping variable for repeatability estimation. Other covariates included mean fishing effort, sex, colony, year, 90% UD area, number of days recorded by the logger that year (minimum 150), and logger type. The *lme4* package (Bates et al. 2015) was initially used to fit and select a generalised linear mixed-effect model (GLMM) prior to fitting the repeatability estimation model. Two models were initially compared, one with year and colony included as an interaction, and one with each included separately, then the fit of each compared using AIC. The latter was chosen, and then the best fitting combination of covariates within this model was selected using the *dredge* function in the *MuMIn* package (Barton 2020), again using AIC as the selection metric. Variance inflation factors were checked for retained variables to check for collinearity. The final model was then fitted using *rptR*.

4.2.8 Modelling of behaviour

A GLMM was used to identify spatial and temporal trends in non-breeding season behaviour over time. Proportion of time spent in "mixed" behaviour was used as the response variable. 90% UD area was included as a proxy for migration effort. Number of encounters per year was included as a proxy for vessel attendance, taken as the square root to account for positive skew. Other covariates included were an interactive term between year and colony, sex, days for which locations were available, and logger type. Individual identity was included as a random effect.

4.3 Results

4.3.1 Processing of locations

Fulmar tracks from all four study colonies covered vast areas of the North Atlantic (figure 3). Densities were highest near study colonies, though hotspots were also evident south of Greenland and in the Barents Sea.

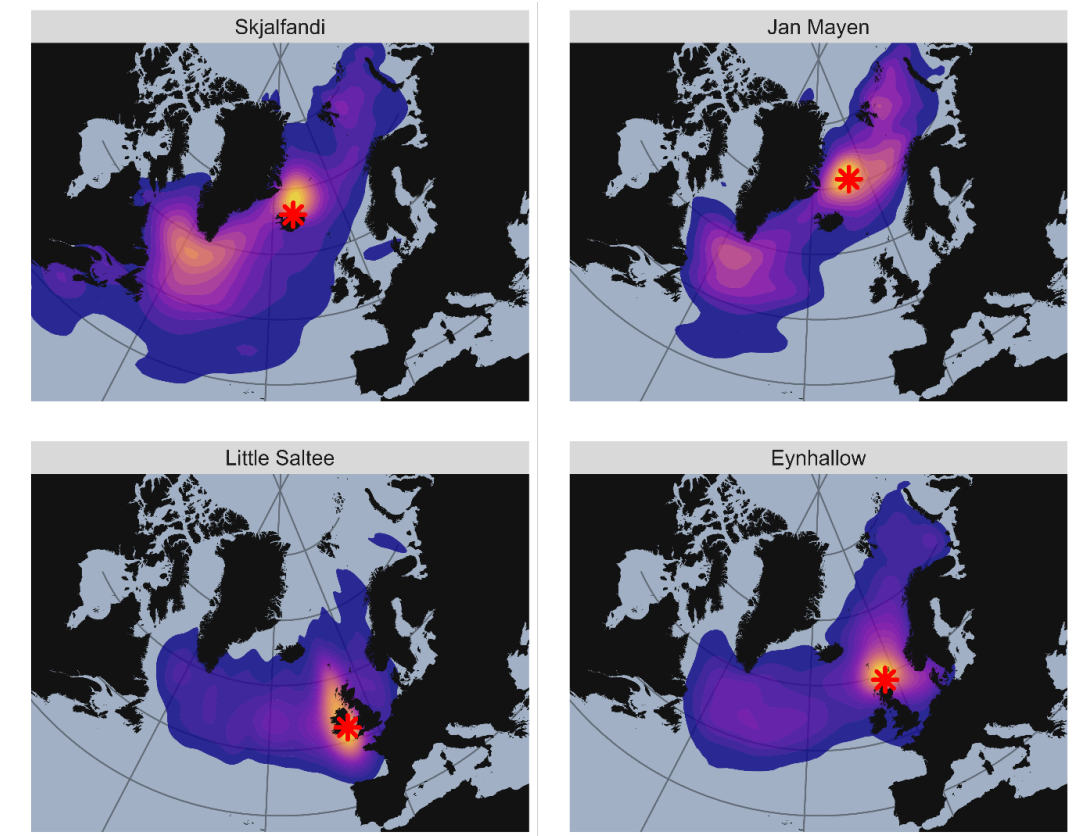


Figure 3: Fulmar location denisties from the 4 study colonies, Skjalfandi, Iceland (n = 54), Jan Mayen, Norway (n = 54), Little Saltee, Ireland (n = 38), and Eynhallow, Scotland (n = 150). Study colonies are denoted by red star symbols. Pre-breeding and breeding season (March through August) locations were excluded when calculating densities, as locations at this time are heavily clustered around the breeding colonies.

4.3.2 Modelling of vessel encounters

12,689 encounters were detected by identifying light spikes in over 180,000 nocturnal periods (αs < -9), i.e. one encounter per ~ 15 nights of data. All initially included variables were retained in the final binomial GAMM, predicting the presence/absence of encounters per night (table 2). Model AUC was 80.5%, indicating good predictive power.

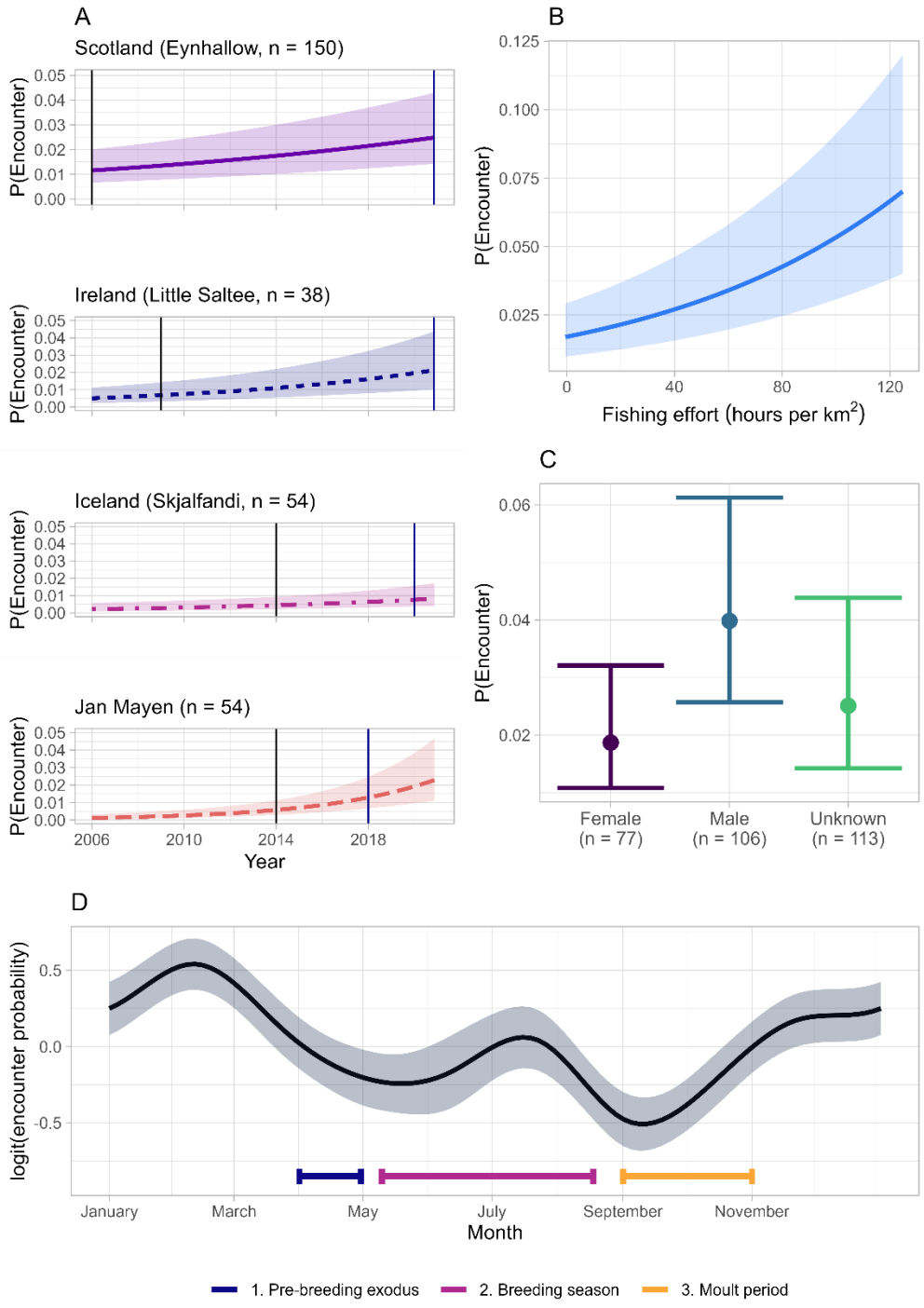


Figure 4: Model covariates for the binomial GAMM explaining probability of vessel encounter per night (P(Encounter) on the y-axis of each subplot). Shaded areas around each trend line and error bars for the factorial effects of sex represent 95% confidence intervals. Black and blue vertical lines in A show the beginning and end of the available time series per colony respectively. Timing of pre-laying exodus, breeding, and post-breeding moult are annotated by error bars below the plot describing the effect of time of year (D), though these timings are coarse and can vary slightly by both individual, colony, and breeding success. Note that the y-axis scales vary between panels A-D to represent different effect sizes more clearly, and because the effect in D is on the logit scale.

Encounters were more likely to be detected in areas of intense fisheries (figure 4B), and when nights were longer. Fulmars from Eynhallow were significantly more likely to encounter vessels than in the other three colonies. Fulmars from all colonies showed a significant positive correlation between year and likelihood of encounter (figure 4A). Males were more than twice as likely to encounter a vessel than females (figure 4C). Logger type did not significantly affect the likelihood of encounters. Time of year was also an important predictor. Encounters were less likely in April and May, during the pre-breeding exodus, and September, during the post-breeding moult (figure 4D).

Table 2: GAMM model terms explaining the presence/absence of vessel encounters per night. Covariates included as splines are denoted as s(covariate). Terms are reported with either degrees of freedom (df) or estimated degrees of freedom (edf) depending on whether they are included as spline or parametric terms.

Model term	**df/edf**	**Chi-squared value**	**p-value**
s(julian day)	7.4	695.4	<0.001
s(n nocturnal fixes)	8.5	511.7	<0.001
fishing effort	1	152.4	<0.001
sex	2	23.0	<0.001
logger type	2	3.0	0.23
colony	3	39.6	<0.001
colony:year	4	92.5	<0.001
bird identity (random effect)	260.3	4683.9	<0.001

4.3.3 Repeatability of vessel encounters

Individual fulmars were highly repeatable (86% ± 1.9% SE) in terms of number of encounters per year. Like the previous model, the GLMM component of this model again indicated a progressive increase in encounters per year, with a similar trend apparent across the four study colonies (figure 5). Number of encounters per non-breeding season varied between colonies irrespective of year. This model also suggested that total area covered during the non-breeding season was negatively correlated with the number of encounters during that same period (figure 6A),

though this may simply be a product of higher fishing vessel presence concentrated around fulmar colonies (figure 6B).

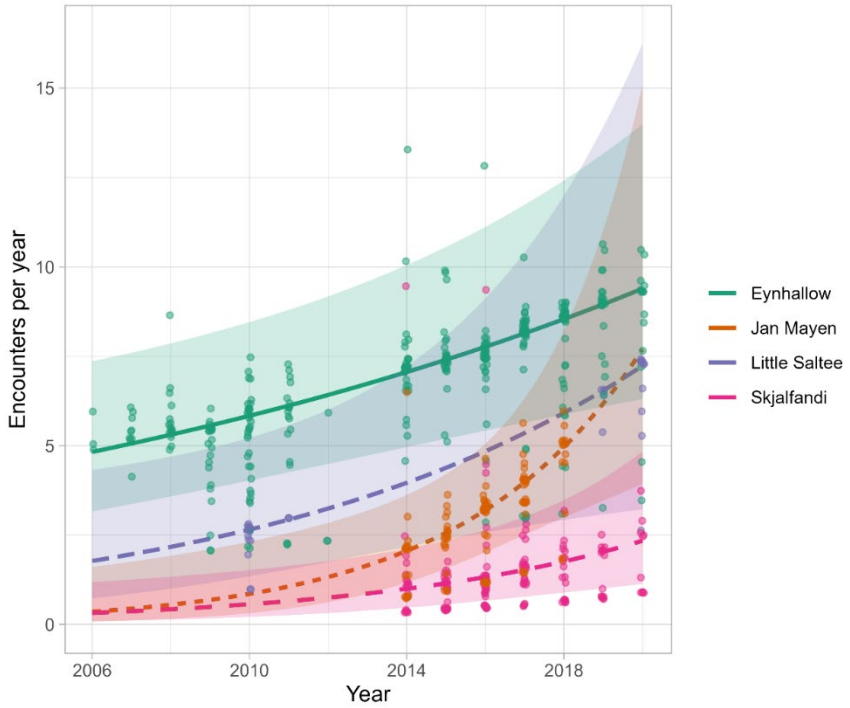


Figure 5: Interaction between colony and year when explaining encounters per non-breeding season in the repeatability model. Plotted points are partial residuals and shaded areas around linear effects are the 95% confidence intervals. Note that trend lines extend beyond available data in earlier years for Jan Mayen, Little Saltee, and Skjalfandi.

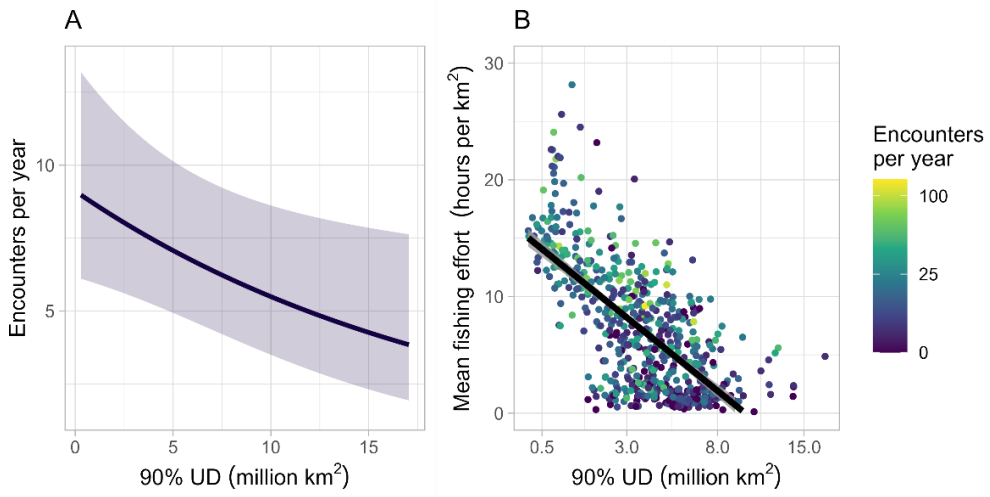


Figure 6: Left (A): Correlation between encounters per year and 90% UD area during the non-breeding season. The shaded area represents the 95% confidence interval. Right (B): Relationship between 90% UD area and mean fishing effort of non-breeding season locations for the same period. 90% UD area is square root transformed, with the original values displayed on the x axis. The black line represents the simple linear relationship between these two variables (R^2 = 46%).

4.3.4 Modelling of behaviour

Table 3: Model terms retained by the GLMM explaining the proportion of mixed behaviour per year. Terms are reported with F-value, degrees of freedom (df) and p-values.

Model term	F-value	df	p-value
colony	25.0	3	<0.001
sex	43.9	2	<0.001
encounters	32.8	1	<0.001
logger type	395.8	1	<0.001

Time spent in mixed behaviour was significantly negatively correlated with number of encounters per year (figure 7). Also significant were the effects of colony, sex, and type of logger (table 3). Fulmars from Skjalfandi and Jan Mayen spent a greater proportion of time in mixed behaviour, as did females. Migratech loggers were likely to record a lower proportion of mixed behaviour, possibly due to their coarser immersion sampling interval. There was no significant correlation between year or 90% UD area and proportion of mixed behaviour, and these variables were removed by the model selection process. This GLMM had a marginal R^2 of 55%, indicating good model fit.

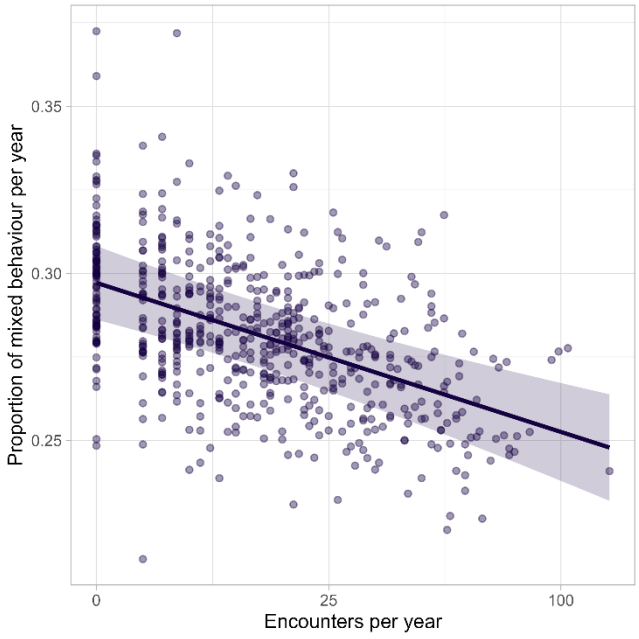


Figure 7: Partial effects plot of the correlation between number of encounters and proportion of time engaged in mixed behaviour. Points are partial residuals.

4.4 Discussion

This study indicates that fulmars from colonies across the Northeast Atlantic are increasingly encountering vessels at night. This either reflects increased vessel attendance at all times of day or a switch towards more nocturnal foraging to exploit this conspicuous food source, both possibly suggesting an increased reliance on fisheries food subsidies. Fleet sizes, gross fleet tonnage, total catch, and discard rates of many North Atlantic fisheries have dropped or remained static over the same period (stats.oecd.org, Eurostat 2019, appendices, figures S3 & S4), so availability of fisheries waste or increased cues from vessels are unlikely to explain this increase. Widespread changes in fisher behaviour (e.g. setting lines or nets at night) would explain increasing nocturnal encounters without necessarily signalling a diel increase, and while night setting is encouraged for some bycatch-prone fisheries (Løkkeborg 2011), it is rarely practiced. Using anomalous light-spikes recorded by geolocators to identify nocturnal encounters with fishing vessels, significant predictors of encounter rates included distribution, colony, time of year, and sex, with males more likely to encounter vessels. We predicted and observed a spatial relationship between vessel encounter rates and fishing intensity (Dupuis et al. 2021). As has been shown in other scavenging seabird species, such as northern gannets (*Morus bassanus*) (Patrick et al. 2015), attendance of vessels is highly repeatable on an individual basis.

Fulmars in more recently established colonies (Eynhallow and Little Saltee), had higher encounter rates than the long-established colonies in Skjalfandi and Jan Mayen. Fulmars' recent colonisation at the southern edge of their range has historically been attributed to increasing availability of fisheries waste (Fisher 1952). This may suggest that fisheries waste can subsidise the natural diet of fulmars (Phillips et al. 1999, Darby et al. 2021), with subsidies likely providing only a fraction of fulmars' food (Camphuysen & Garthe 1997). However, the consistent availability of this extra resource may increase the viability of colonies outside the historic range of this species. Regionally varying fishing practices are further likely to influence the likelihood of seabirds attending vessels (Soriano-Redondo 2016). Fulmars from Skjalfandi in Iceland had the lowest vessel encounter rates, which may be related to Iceland's ban on discarding non-target catch coupled with high pelagic fish biomass.

A similar result was found in breeding northern gannets from Icelandic colonies interacting less with fishing vessels compared to gannets from elsewhere (Clark et al. 2020). Though fulmars scavenge offal and bait from hooks as well as discards (Brothers 1991, Camphuysen & Garthe 1997), similar processes may result in the reduced fishing vessel attendance of Icelandic fulmars. Norway also imposes a long-standing discard ban (Gullestad et al. 2015), which in combination with the relatively low fishing pressure around Jan Mayen, may help to explain the reduced encounter rates of fulmars from this colony. Similarly, European Union fisheries are subject to a landings obligation (ec.europa.eu/fisheries/cfp/) which prevents the discarding of undersized commercial fish species, but still allows the discarding of non-commercial species. This may explain the higher vessel attendance around Saltee and Eynhallow, where less species-targeted demersal trawlers are likely to discard a greater proportion of unwanted non-commercial species, and are the primary gear type targeted by breeding fulmars in the UK and Ireland (Darby et al. 2021).

Fulmars from all colonies had increasing nocturnal vessel encounter rates over time. Vessel waste may form a necessary supplement for reduced availability of natural prey (Grémillet et al. 2008), and it's possible that fulmars are becoming increasingly reliant on vessels to supply a greater proportion of their food intake. Fulmars are relatively generalist feeders, consuming a wide range of prey (Phillips et al. 1999), a trait shared by many fisheries waste scavengers (Bicknell et al. 2013). They are thought to primarily feed at the sea surface, with the limited data available showing that they can dive to at least 2.6 metres (Garthe & Furness 2001). An increase in vessel attendance that is not explained by an increased availability of vessels or waste may reflect reductions in natural prey abundance at, or just below, the water surface within their range. Progressively fewer discards from vessels may also mean that fulmars may require more attempts or time in attendance to scavenge sufficient food, though this may apply only in areas with recent discard reductions.

Fulmars were significantly less likely to encounter vessels in the immediate post-breeding period, which is likely to correspond with the timing of their feather moult (Grissot et al. 2020). Many seabirds' flight efficiency is decreased by higher wing loading during moult (Cherel et al. 2016), so perhaps following fishing vessels is less

energetically viable at this stage. Changes in diet have been recorded during the moult of other bird species (e.g. Anderson et al. 2000), so changes in the nutritional requirements may also partially explain reduced encounter rates at this time of year. Dietary shifts may also explain reduced encounter rates prior to summer, as fulmars stockpile energy and specific nutrients in advance of egg-laying and incubation (Mallory et al. 2008).

The energetic cost-benefit of scavenging on fisheries waste versus targeting prey naturally is largely unknown. It has been proposed that seabirds targeting vessels can suffer from the reduced nutritional content of waste compared to natural prey (Grémillet et al. 2008). High encounter rates were correlated with non-breeding distribution, with fulmars travelling further generally interacting with fewer vessels. However, the cause and effect of this relationship is difficult to qualify. Fulmars travelling further generally spend more time in the high seas where fishing effort is reduced compared to areas closer to the coast. We also provide the first evidence that fulmars interacting with vessels spend less time foraging overall, suggesting that subsidising diet with fisheries waste is time-efficient. Further fine-scale data on energetic expenditure during natural foraging and scavenging, from accelerometers for example (Elliott et al. 2013), would be required to infer energetic differences between discards foraging and natural foraging.

4.5 Conclusion

The increase in fulmars' nocturnal vessel attendance over time may increase bycatch risk for this already heavily bycaught species, despite the lack of a corresponding increase in the number of vessels or availability of discards over the same period. This may suggest a reduction in the availability of fulmars' natural prey and an increased reliance on vessel waste. Fulmars are highly mobile generalist surface feeders, so a reduction in their natural prey could reflect a reduction in available biomass more generally in the upper water column in pelagic habitats in the North Atlantic.

4.6 Appendices

Logger light adjustment

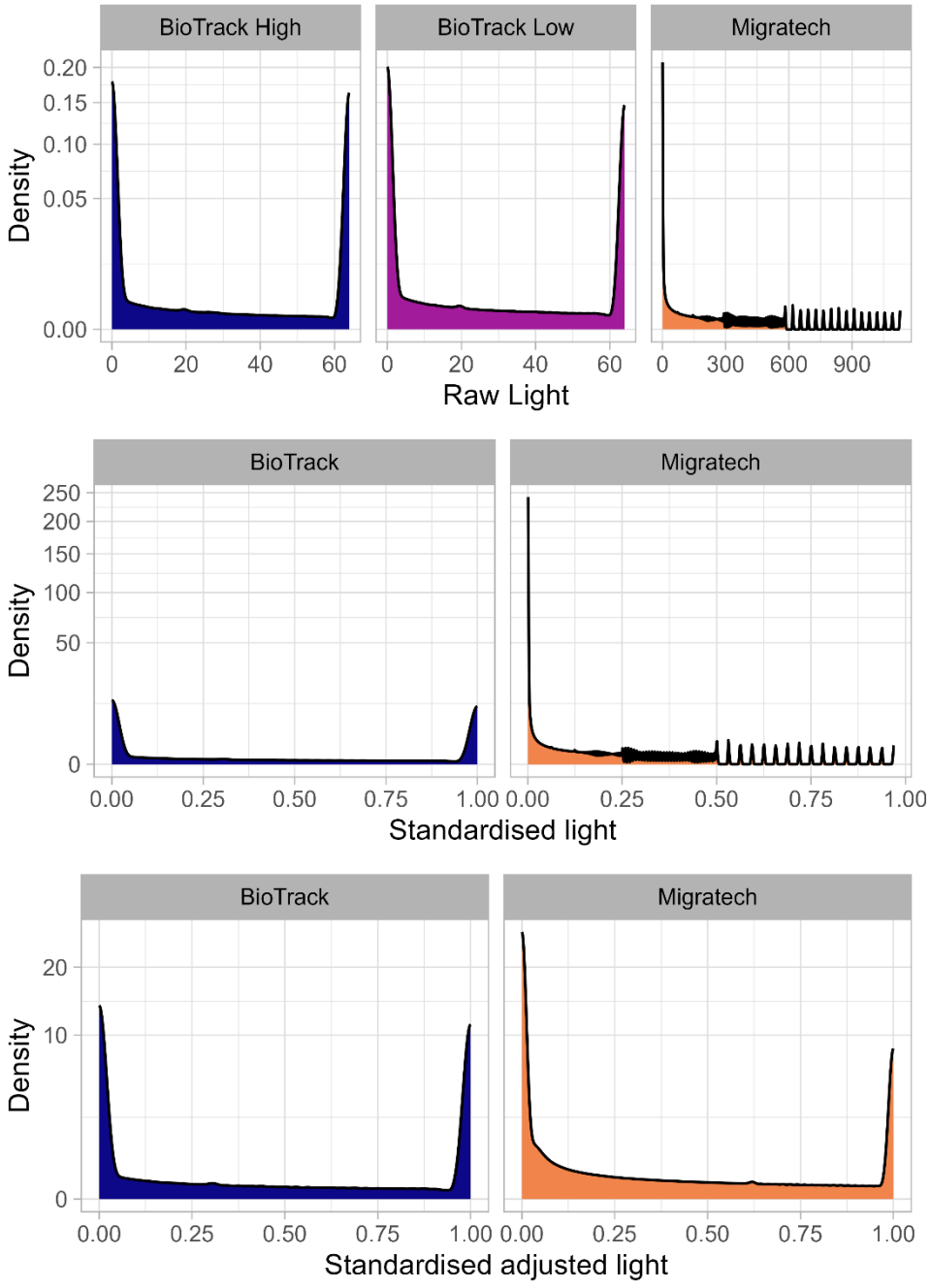


Figure S1: Light standardisation process across tag types, classified according to Dupuis et al. (2021). The top row displays raw light readings from all tags. BioTrack Low and Biotrack High were equivalent, so were grouped together. In the middle row, all light readings were scaled from 0 to 1 to examine differences in densities between the two major tag types. Migratech light readings were then further scaled by limiting standardised reading to 0.1, i.e. reducing any values > 0.1 to 0.1. All values were the returned to a 0 – 1 scale by multiplying by 10. The distributions of readings from both tag types are now approximately similar and are displayed on the bottom row.

Defining thresholds for encounter detection

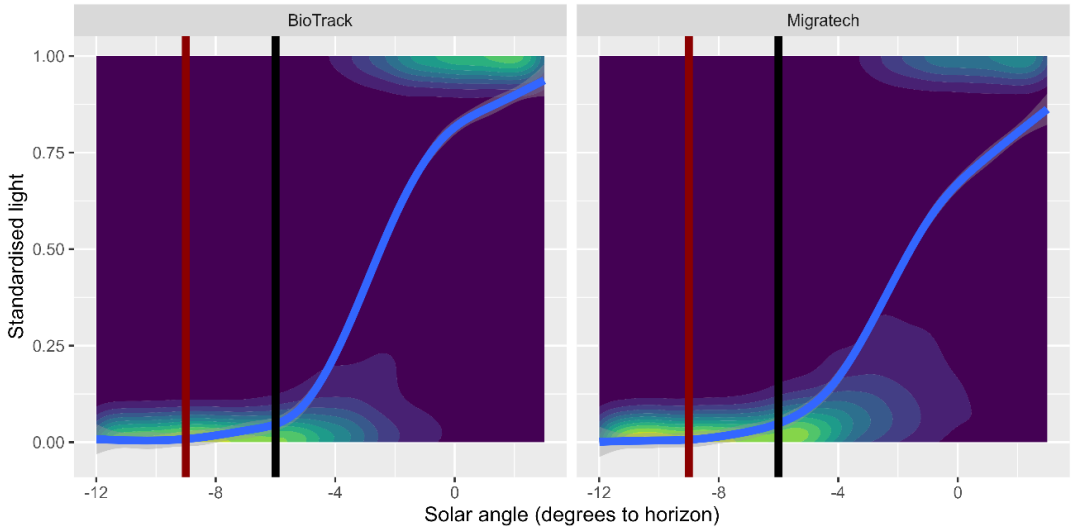


Figure S2: Density of standardised light readings from both logger types. Light readings are taken as a randomised subset of 10,000 data points from fulmars from Skljalfandi, Iceland. Fulmars from this colony had the fewest anomalous nocturnal light spikes. Solar angle at civil dawn/dusk (-6 degrees) is indicated by the vertical black line, below which most light readings are 0. The blue line represents the cubic spline relationship between solar angle and standardised light. This crosses the x-axis at a solar angle of ~ -9 degrees, as indicated by the vertical red line. This forms the upper threshold used for identifying nocturnal light spikes, as it is highly unlikely that any higher light readings at these solar angles represent natural light.

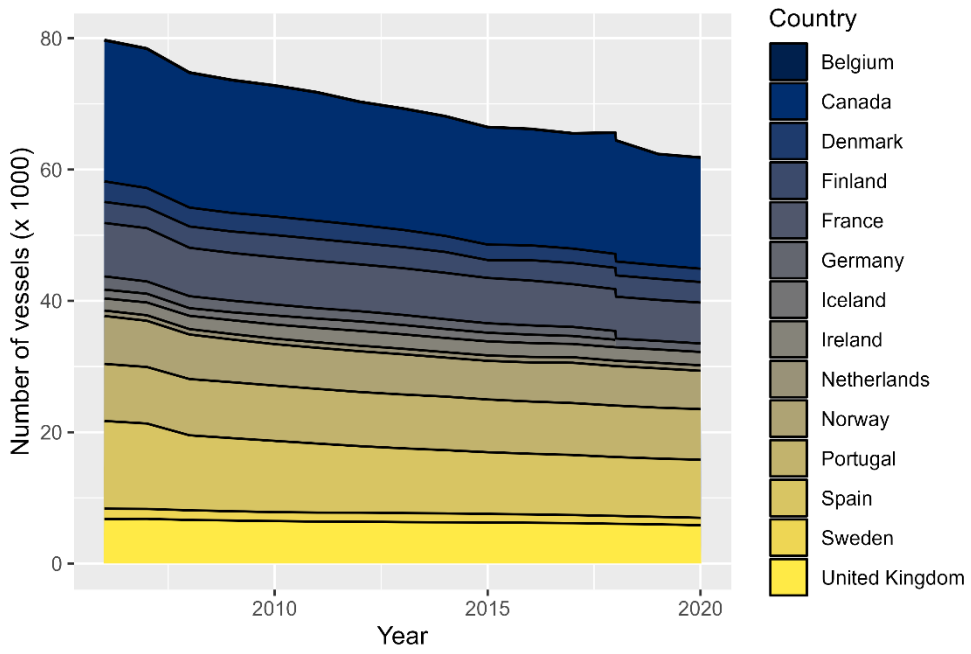


Figure S3: The sum of vessels per fleet in many of the fisheries operating across the study area. Sourced from OECD database.

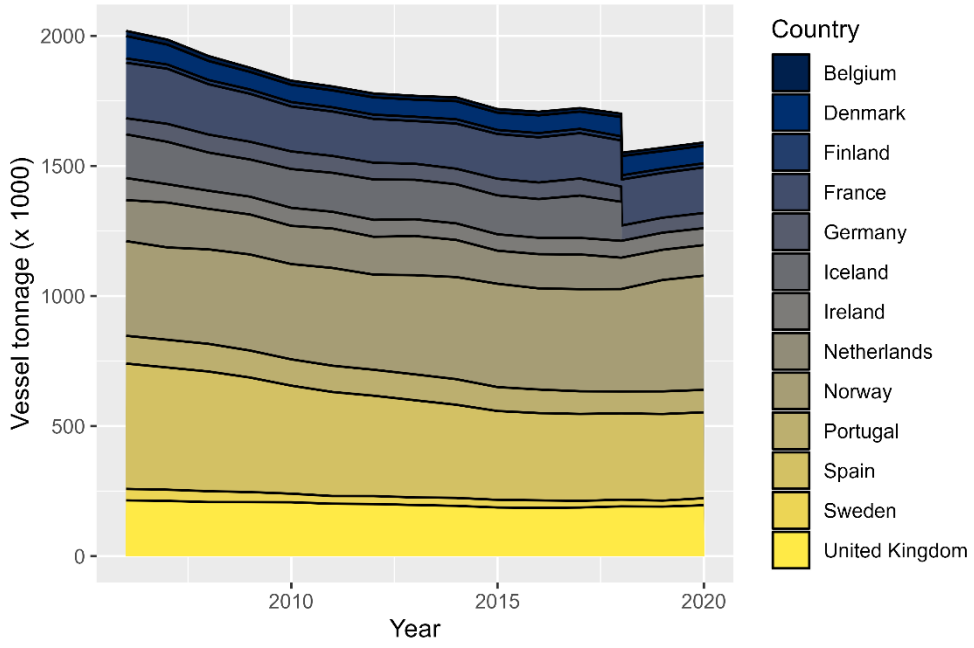
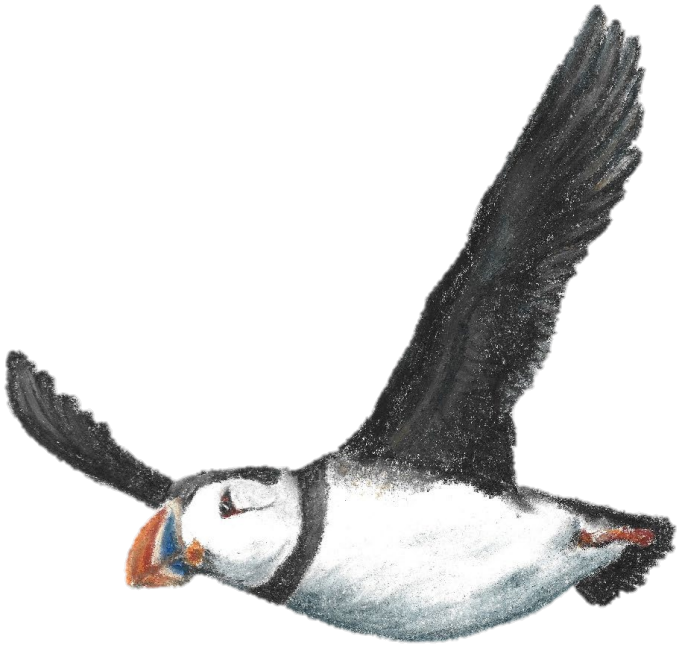


Figure S4: The gross tonnage of many of the fishing fleets operating in the study area. Sourced from OECD database.

CHAPTER 5: NEW BIOLOGGING APPROACH REVEALS UNIQUE FLIGHTLESS MOULT STRATEGIES OF ATLANTIC PUFFINS



Published as: Darby JH, Harris MP, Wanless S, Quinn JL, Bråthen VS, Fayet AL, Clairbaux M, Hart T, Guilford T, Freeman R, Jessopp MJ (2022) A new biologging approach reveals unique flightless molt strategies of Atlantic puffins. *Ecology and Evolution 12*: e9579.

Abstract

Animal-borne telemetry devices provide essential insights into the life-history strategies of far-ranging species and allow us to understand how they interact with their environment. Many species in the seabird family *Alcidae* undergo a synchronous moult of all primary flight feathers during the non-breeding season, making them flightless and more susceptible to environmental stressors, including severe storms and prey shortages. However, the timing and location of moult remains largely unknown, with most information coming from studies on birds killed by storms or shot by hunters for food. Using light-level geolocators with saltwater immersion loggers, we develop a method for determining flightless periods in the context of the annual cycle. Four Atlantic puffins (*Fratercula arctica*) were equipped with geolocator/immersion loggers on each leg to attempt to overcome issues of leg-tucking in plumage while sitting on the water, which confounds the interpretation of logger data. Light level and saltwater immersion time-series data were combined to correct for this issue. This approach was adapted and applied to 40 puffins equipped with the standard practice deployments of geolocators on one leg only. Flightless periods consistent with moult were identified in the dual-equipped birds, whereas moult identification in single-equipped birds was less effective and definitive and should be treated with caution. Within the dual-equipped sample, we present evidence for two flightless moult periods per non-breeding season in two puffins that undertook more extensive migrations (> 2000km) and were flightless for up to 77 days in a single non-breeding season. A biannual flight feather moult is highly unusual among non-passerine birds, and may be unique to birds that undergo catastrophic moult, i.e. become flightless when moulting. Though our conclusions are based on a small sample, we have established a freely available methodological framework for future investigation of the moult patterns of this and other seabird species.

5.1 Introduction

Biologging and telemetry studies have greatly advanced our knowledge of the behaviour and distribution of far-ranging animal species (e.g. Jouventin & Weimerskirch 1990, Kooyman 1966). They have also provided insights into their behaviour, especially when direct observation is impossible or impractical (e.g. Wilson et al. 1991, Michel et al. 2022), which is often the case for the many marine species that spend prolonged periods at sea far from land (e.g. Weimerskirch et al. 2006, Doyle et al. 2015, Bennison et al. 2019, Brooke 2018). Using telemetry, the behaviour of far-ranging species can be defined at a relatively fine temporal scale, such as diel patterns of movement (Seyer et al. 2021), and over longer time series to describe life-history strategies, such as migration (Amélineau et al. 2021) or periodic moult (Grissot et al. 2020). By looking at the behaviour of an animal in relation to its spatial and temporal distribution, it is possible to identify key areas of conservation concern, and identify drivers of declines (Frederiksen et al. 2012, Fayet et al. 2021).

Many of the world's seabirds are threatened and declining (Dias et al. 2019, Paleczny et al. 2015), creating a pressing need to better understand vulnerable stages of their annual cycle. Seabirds tend to be highly susceptible to the impacts of climate change, including sea temperature rise and shifts in prey distribution and abundance (Durant et al. 2003, Sandvik et al. 2005), as well as extreme weather events (Clairbaux et al. 2021), with large wrecks recorded following severe winter storms at sea (Harris et al. 2014, Morley et al. 2017, Anker-Nilssen et al. 2018). Larger members of the seabird family *Alcidae* (hereafter alcids) moult all their primary flight feathers simultaneously (Peery et al. 2008) leading to a protracted flightless period, placing them at greater risk from such dynamic stressors. Alcids are often the most common species washed ashore in storm wrecks in the northern hemisphere (Morley et al. 2017). Obligatory flightless moult places birds at greater risk from storm events, since they are unable to fly to avoid the storm track. Being flightless also potentially reduces alcids' ability to escape from marine predators (Ulman et al. 2015), and increases their vulnerability to surface pollutants, because of the increased time spent on the water surface and the inability to escape expansive films of harmful substances such as petroleum oil (Robertson et al. 2012).

The Atlantic puffin (*Fratercula arctica*), hereafter puffin, is an alcid species that has undergone rapid population declines across most of its European breeding range during the 2000s (Harris & Wanless 2011), leading to its classification as Endangered in Europe by the European Red List Assessment in 2015 (BirdLife International, 2015). Because puffins become flightless during moult (Gaston & Jones 1998, Harris et al. 2014), they must carefully time and locate their moult to coincide with sufficient food availability, which can be patchily distributed at sea (Fauchald 2009, Jessopp et al. 2013). Clairbaux et al. (2021) calculated the fasting endurance of puffins as 6.5 (±2.5) days in mid-autumn, and 4.6 (±0.6) days in winter. Local depletion of food during moult puts puffins at risk of starvation. Anker-Nilssen et al. (2018) found that most puffins washed ashore in a post-storm wreck in southwest Norway in early 2016 were in the late stage of primary moult, and almost all individuals were emaciated. Moult may have prevented them from escaping the storm when they were flightless, during which they clearly struggled to find food. Similar to other diving seabirds, puffins' feeding strategy and functional dive depth may vary depending on environmental conditions (Darby et al. 2022), which would help to explain their highly varied diet (Baillie & Jones 2004), especially during the winter, when adverse weather conditions are most likely to impact their foraging behaviour (Falk et al. 1992, Harris et al. 2015).

The duration, timing, and location of moult in puffins are major gaps in our knowledge of this species, because moult occurs during the non-breeding season when birds are at sea, often far away from their colonies (Fayet et al. 2017). Harris et al. (2014, 2022) assessed moult stage based on feather development in a large sample of puffins either washed ashore during storm wrecks or shot by hunters for food. These studies found that moult of all primary flight feathers occurred at any time from September to March, with peaks in October and March. This variable timing contrasts with other alcids, whose moult typically occurs shortly after the breeding season (Gaston & Jones 1998, Peery et al. 2008). Identifying the flightless period of puffins using biologging studies has also proven difficult. Leg-mounted saltwater immersion loggers are commonly used to classify seabird behaviour during the non-breeding season. Reduced time spent flying, during flight feather moult for instance, is usually reflected by an elevated proportion of time the leg and logger are

wet (Grissot et al. 2020). Puffins, like other alcids, repeatedly tuck their legs into the plumage when on the water (Harris et al. 2010, Linnebjerg et al. 2014, I. Sempere, Oceanário de Lisboa, pers. comms, figure 1), confounding simple behaviour classification using these loggers.

This study uses light-level geolocators with integrated saltwater immersion switches deployed on puffins to identify patterns of behaviour thought to be consistent with flightless moult. By combining data from four individuals with a geolocator on each leg (dual-equipped birds), we developed a behavioural classification method using raw light and saltwater immersion data. We show that we can use results from dual-equipped birds to quantify and correct for behaviours that would confound traditional methods, and enable us to identify flightless periods assumed to represent moult. We then adapt and validate this method for single-equipped birds, for which there are far more data. This approach may help us to identify overwintering strategies and areas of conservation concern for puffins and other alcids, whose highly restricted mobility during flightless moult may exacerbate the negative impacts of environmental threats (Ausems et al. 2021).

5.2 Methods

5.2.1 Deployment and recovery of geolocator devices

Geolocators (seven BAS Mk18-L, and one Mk14) were deployed on both legs of four adult puffins during the 2010 summer breeding season on Skomer Island, Wales (51.737N, 5.297W). Single geolocators (31 Biotrack (2012)/Lotek (2020) Mk4083 and 12 BAS Mk18 (2010)) were deployed on 40 adult puffins during the breeding season in 2010, 2012 and 2020 on Skellig Michael, Ireland (51.771N, 10.539W). Birds at both colonies were captured during chick-rearing either using purse nets at burrow entrances or by hand from the burrow, weighed and fitted with geolocators before being released back to their burrow. Capture and handling times were kept to a minimum. Geolocators were attached to a coloured plastic ring fitted around the tarsus, with total deployment weight (devices plus leg ring and cable tie attachment) always < 2% body mass, under 5g for dual-equipped loggers, and under 3g for single-equipped loggers. Device effects were carefully monitored, especially for the dual-

equipped individuals, as this method is unorthodox and may impact birds to a greater degree than single tags. According to the light data recorded by the tags, dual-equipped birds continued to return to their burrows, presumably to provision chicks, after the tags were attached. All 4 returned to the colony the following year, with 3 confirmed as breeding, and one not confirmed only due to the inaccessibility of its nest chamber. The overwintering areas for the dual-equipped birds were representative of the areas used by birds with single tags equipped (Fayet et al. 2016).

The attached geolocators measured light every minute in 6-bit units from 0 (light is below civil twilight, sun > ~ 6 degrees below the horizon) to 64 (sun is well above the horizon) and saved the maximum light level sampled in 5-minute intervals, or 10-minute intervals for the single Mk14 logger used. Saltwater immersion data were sampled every 3 seconds as binary units of 0 (dry) or 1 (wet) and the number of wet samples in 10-minute intervals were saved as values between 0 (all dry) or 200 (all wet). Devices were recovered from birds during the subsequent breeding seasons. All work was carried out under licence from the British Trust for Ornithology (CO/6143, C/5311), with work in Ireland further licenced by the National Parks and Wildlife Service (06/2020, C41/2020, 26/2010, C051/2011, C116/2012, C039/2013, 11/2013). Attachment of dual-equipped geolocators was granted ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel, with ethical approval for handling and tagging in Ireland also approved by the University College Cork Animal Ethics Committee. All analyses were performed using R version 4.1.2 (R Core Team, 2022).

5.2.2 Location data

Positions were obtained from light-level data using a threshold method following established procedures (Lisovski et al. 2019). Twilight events were identified when raw light-level crossed a threshold of 1 which separates day from night. From these twilight events, latitude can be calculated using the length of day and night, and longitudes based on the time of noon and midnight. Twilight events were validated using the *twilightEdit* function from the *TwGeos* package (Lisovski et al. 2016), which utilises a moving-window approach to recognising improbable twilight events by

comparing twilight times across multiple days. This function either adjusts or deletes individual anomalous twilights, due to prolonged leg tucking for instance, depending on their incongruity within the time-series. Sun angle calibration for calculating latitudes was performed using the Hills-Ekstrom algorithm for identifying the most likely solar zenith based on multiple runs of latitude prediction. This was implemented using the *SGAT* package (Sumner et al. 2009). Around equinox events, the precision of latitude estimates drops considerably as the difference in daylength gets less distinct across the latitudinal gradient. Latitudes were therefore smoothed using locally-weighted smoothing (LOESS) for a 2-month period around the equinox in autumn (22 Aug – 23 Oct) and spring (19 Feb – 22 Apr), then smoothed again using linearly interpolation for a subsequence of dates closer to the equinoxes (1 Sep – 13 Oct, 1 Mar – 12 Apr). Areas of apparent residency were identified over the non-breeding season (August to March) using Lavielle segmentation, following methods from Amelineau et al. (2021), and mean distance to the colony of each area of residency was calculated. Migratory effort was described as the distance to the furthest point of residency from the colony.

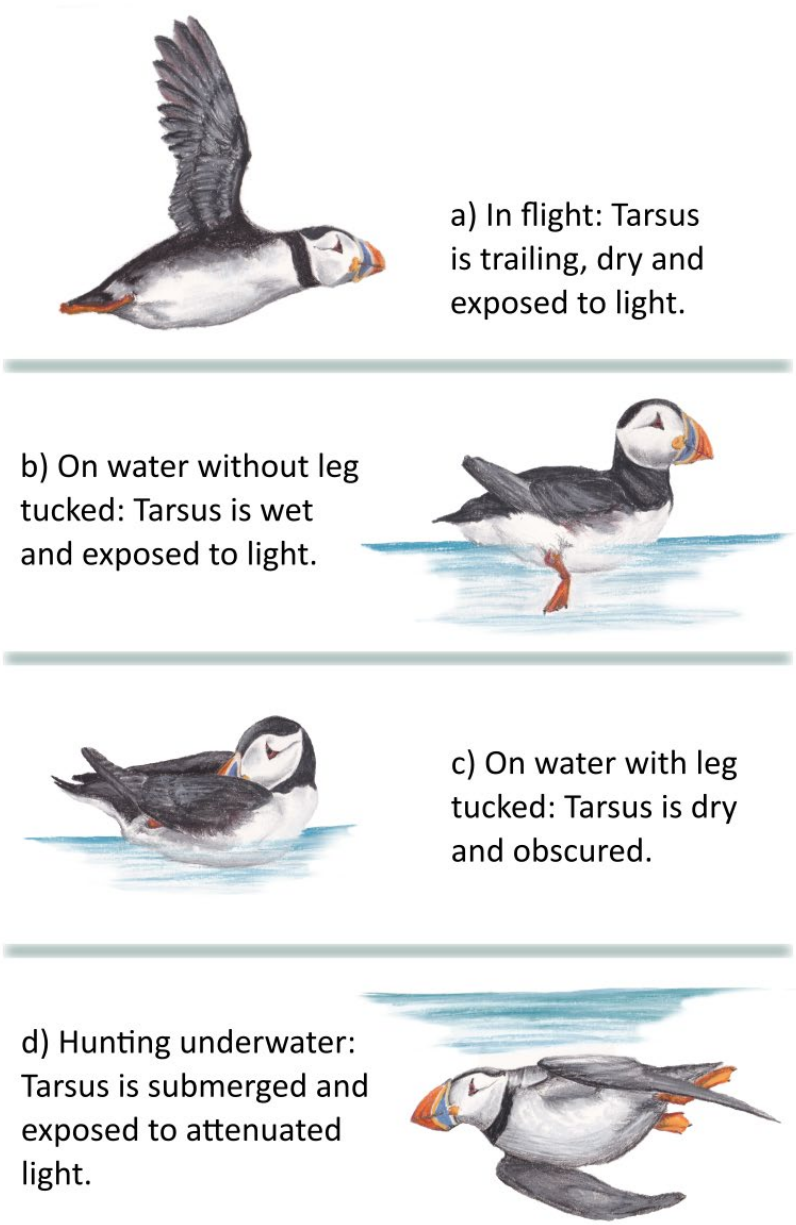


Figure 10: Different puffin at-sea behaviours and the position of the tarsus during each. Loggers were mounted on the tarsus of study individuals. Puffins trail their tarsus in flight (a), which leaves the geolocator exposed to light and dry. Puffins sitting on the surface of the water may lower one or both legs for paddling and balance (b), which leaves the tarsus submerged and exposed to light. Puffins inactive on the water may also tuck one leg into their plumage (c), obscuring the tarsus from daylight and keeping it dry. Puffins hunting for prey underwater will have their tarsus submerged and exposed to light levels attenuated by water (d), though this is unlikely to reduce actual light readings, which are taken as a maximum over 5- or 10- minute intervals.

5.2.3 Accounting for leg-tucking behaviour

Puffins tend to tuck their legs into their plumage while resting on the water, usually just one at a time, but sometimes both (appendices, figure S1, pers. obs.), leaving the

logger dry despite the puffin being on the water surface (figure 1). This means it can be difficult to distinguish between flight and rest from a geolocator immersion signal alone (Fayet et al. 2016). We developed a new method that identified and accounted for leg-tucking using concurrent light signals. Raw light readings were scaled from 0 to 1. We calculated the expected solar angle for each data point (angle between the sun and the horizon), based on time, date, and location, using the *oce* package (Kelley & Richards 2020). We then modelled the scaled geolocator light reading against solar angle in a generalised additive model (GAM) using the *gam* function of the *mgcv* package (Wood 2011) over a subset of 100,000 light data points. Using this model, we predicted expected light readings for all data points based on solar angle at the time and position of the fix. If light readings were anomalously low, > 2x standard deviation below the predicted value, it was assumed that the bird was exposed to higher light levels but was leg-tucking for the duration of that fix interval, obscuring the logger. Fixes either side of a light-informed tucking event were also classified as tucking, given that when puffins initially tuck or untuck their legs, maximum light levels in that fix would not be anomalously low, but the proportion of time the tag spent immersed would still underestimate the time the puffin spent on the water.

These lower-than-expected light fixes were classified as tucking, and were appended to concurrent immersion data using a time series merge implemented using the *xts* package (Ryan & Ulrich 2020) to account for missing or delayed points in either data stream. The immersion data points associated with these fixes were adjusted to 100% wet, to reflect that they were assumed to be resting on water despite the logger reading fully or partially dry. This correction could only be applied to data occurring during daylight hours (solar angle > -6 degrees) and not during the hours of darkness.

5.2.4 Combining data from dual-equipped loggers

Immersion data from both leg tags were combined for each dual-equipped puffin, again using a time series merge implemented using the *xts* package. This time series merge accounts for both missing data points and differences in start times between paired loggers, merging the data from one logger to the nearest possible timestamp in the other logger's data stream. Proportions of time spent wet were compared

pairwise for each fix interval and the higher value retained in a single data stream. This meant that even if one leg recorded dry and the other recorded wet for the same time interval, the "wet fix" was preferentially retained. If one leg was submerged, then the puffin must have been resting on the water, and the "dry fix" was an instance of leg-tucking not captured by methods described in the previous section. This method may slightly overestimate time immersed. However, any time spent immersed at all can't represent directed sustained flight, so this should not have an impact on our results. The time series merge we used also accounted for differences in light recording intervals for the one individual (EL60648) with different logger types. The data stream with the shorter recording interval was used as the basis for the time series merge, and the coarser resolution data from the other logger used to correct the closest data points timewise. This mismatch may impact the efficacy of the correction, though no issues were evident when comparing results between this individual and the others.

5.2.5 Identifying moult periods in dual-equipped birds

We then assumed the corrected proportion of time spent dry per day was time in flight ($prop_{flight}$) and calculated the 5-day rolling average of this ($prop_{flight\text{-}5}$), centred on a focal day, and calculated using data from 2 days before to 2 days after. This rolling average was used to smooth noise in the data, which was likely caused by leg tucking that our corrections could not detect, and to facilitate identification of moult periods. Only sections of days with a predicted solar angle of > -3 degrees were used to calculate this proportion, as some anomalous sustained dry periods were retained in nocturnal data points. Though these periods could in fact be due to sustained flight occurring at night, it is more likely due to puffins tucking both legs at once (Robertson et al. 2012, pers. obs.), or visits to the nest burrow approaching the breeding season. The tucking correction applied earlier will not have captured this on either leg's logger, as the expected light level at lower solar angles (< -6 degrees) is zero.

An inferred flightless period was identified as a persistently low set of values of $prop_{flight\text{-}5}$, identified using an incrementing threshold. This threshold value was iteratively increased from 0 by 0.0002 increments until a minimum sequence of 30 consecutive days were defined as below this threshold. Days with $prop_{flight\text{-}5}$ below

this threshold value were defined as flightless. This 30-day minimum sequence of flightless days required to constitute moult was defined according to previous estimates of this species (Harris et al. 2014) and observations of puffins in an aquarium setting (D. Dial, National Aquarium USA, pers. comms). A maximum threshold value of 1% $prop_{flight\text{-}5}$ was applied to restrict the likelihood of falsely identifying moult during periods of reduced flight, during which the puffin was not obligatorily flightless but rather had reduced flying time, likely due to remaining resident in an area of favourable feeding or weather conditions. This meant that the 5-day rolling average of corrected flight, or $prop_{flight\text{-}5}$, had to remain below 1% for a period to be considered as moult. Moult was therefore defined as a continuous period of at least 30 days, during which little to no flight (< 1% of daylight hours) was inferred to have occurred by the processed immersion data. The same process was repeated, omitting any initially identified moult, to explore the possibility of a second flightless moult.

5.2.6 Testing single leg data in dual-equipped birds

A similar moult identification method was attempted using data from each dual-equipped logger in isolation. As before, the proportion of time spent wet was corrected for tucking behaviour using raw light signals. Any points with a solar angle below -3 degrees were omitted for this analysis, to ensure that leg-tucking was sufficiently captured using light data. $Prop_{flight}$ and $prop_{flight\text{-}5}$ were again calculated, and the same incrementing threshold method was used to identify putative moult periods of minimum 30 days duration. A maximum threshold value of 1% $prop_{flight\text{-}5}$ was again applied to restrict the likelihood of falsely identifying moult from noisy immersion time series. Independently derived inferred moult periods were compared to combined data from dual-equipped loggers. Based on limited but good agreement (see results), the process was then applied to the geolocator data collected from 40 individuals equipped with single loggers from Skellig Michael, Ireland.

5.2.7 Observations from captive puffins

Several aquaria house puffins as part of displays. Aquarists from 4 of these facilities provided observations about moulting habits of these puffins in an aquarium setting to contextualise results and check whether our conclusions were physiologically viable. We spoke to aquarists from Tierpark Bern, Switzerland, the National Aquarium, USA, Oceanário de Lisboa, Portugal, and Biodôme de Montréal, Canada. All mentioned variation in moulting behaviour. Meret Huwiler of Tierpark Bern described how juvenile puffins moult their primaries twice in one year. Older age classes have a single primary moult, the timing of which advances as they age, from midwinter to early autumn. Debra Dial of the National Aquarium described variation in timing of moult between wild-caught and captive-reared individuals initially, and highlighted how age, lighting and the birds' condition can all affect the timing and duration of moult, with the latter estimated as 45-50 days. Ana Ferreira and Irene Sempere of Oceanário de Lisboa described how appetite increases prior to moult, and that puffins do not rest or tuck their legs any more or less during moult than at other stages. All 4 facilities were able to confirm that puffins tucked their legs into their plumage. Further relevant observations are referenced as personal communications throughout the text.

5.3 Results

5.3.1 Accounting for leg-tucking behaviour

Leg tucking was identified using raw light and immersion data streams from loggers from both single- and dual-equipped birds. Clear differences in raw immersion data can be seen from each leg of a single puffin, largely down to leg-tucking (figure 2A & 2B). Though we capture and account for much of the daylight leg-tucking using concurrent light data from the same logger (figure 2C), differences between corrected immersion time series from each leg suggests that not all leg-tucking is accounted for in this method (figure 2D & 2E, table 1). The proportion of time spent dry per day is reduced by > 50% when concurrent light levels are used to correct for leg-tucking, and this corrected proportion is further reduced by > 50% when data from two tags are combined (table 1). Data from both legs are therefore likely necessary to accurately identify flightless periods, i.e. primary feather moult (figure

2F). Using the dual-equipped loggers, we calculated that puffins spent 21.7% (SD = 20.1) of daylight hours (solar angle > -3) tucking either or both legs, 10 times greater than the time spent in flight per day (1.9%, SD = 5.8). Puffins spent less than 1% of daylight hours in flight for 75% of days during the non-breeding period. Although the small sample size precluded detailed analysis, the proportion of time spent leg-tucking also varied with individual, time of year, and leg (appendices, figure S1).

Table 9: Time spent dry according to raw immersion signal (no adjustment), immersion data corrected for leg-tucking using concurrent light data only (Light adjustment), and immersion data corrected using corresponding data from another logger on the same bird (Dual tag). Behaviours presented are time pent dry per day, time spent dry per non-breeding season per individual (NBS), and proportion of data points which were recorded as being >95% dry per NBS. Values are means ± standard deviation. All values are calculated as proportions of daylight hours (solar angle > -3).

	No adjustment	***Light adjustment***	***Dual tag***
Time spent dry / day	11.8 ± 14.4%	5.3 ± 8.5%	1.9 ± 5.8%
Time spent dry / NBS	11.8 ± 5.1%	5.3 ± 1.9%	1.9 ± 0.8%
> 95% dry fixes / NBS	6.6 ± 3.78%	1.6 ± 1.0%	0.8 ± 0.6%

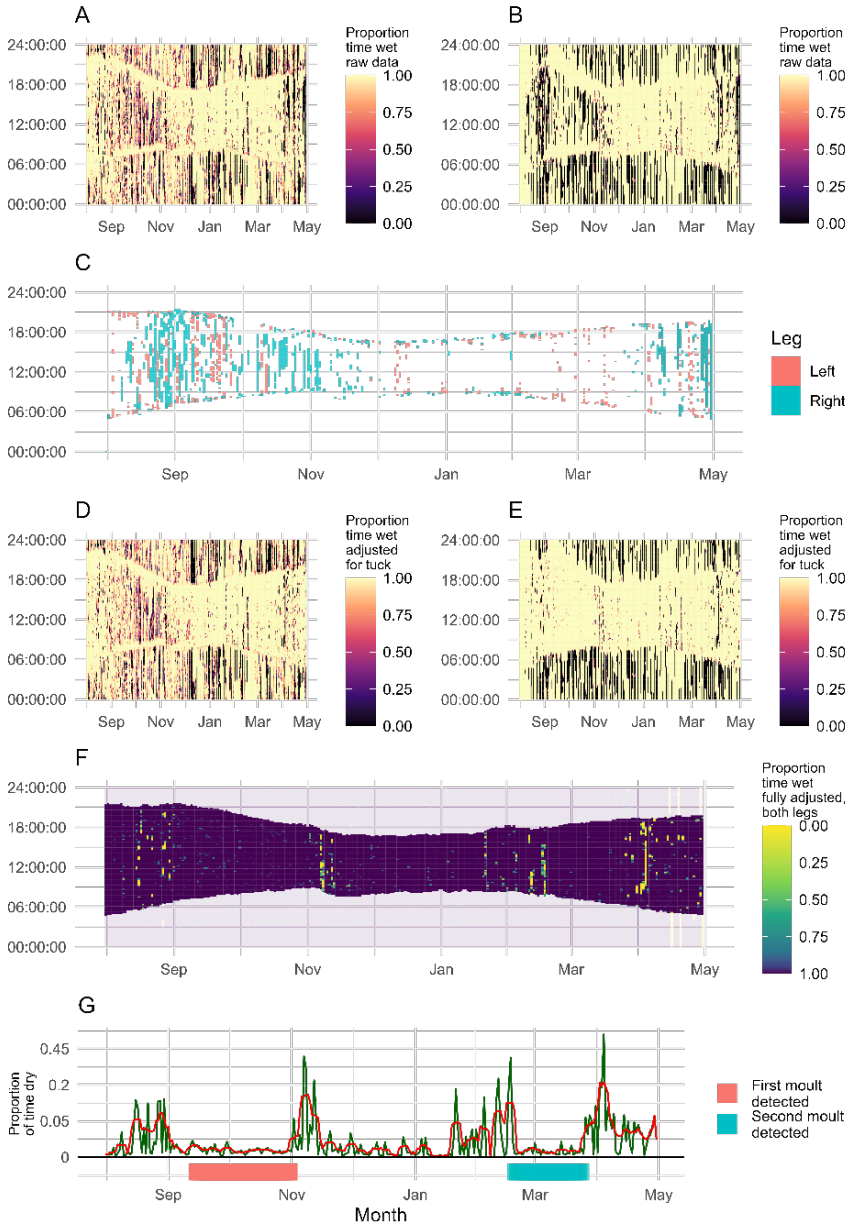


Figure 2: Geolocator data process for a dual-equipped puffin (EJ47625) prior to moult identification, accounting for leg-tucking using raw light signals, and combining data from loggers on each leg. The x-axis represents calendar date, and in A to F, the y-axis represents time in Universal Time Zone. A and B are the raw saltwater immersion signals from the puffin's left and right leg respectively. C highlights the data points inferred as leg-tucking using the raw light signals. D and E show the immersion data corrected for leg-tucking events shown in C, again for the puffin's left and right leg-mounted loggers, respectively. F shows the combined minimum of D and E, which represents the most accurate estimate of flight activity, given the data available. In F, data with a predicted solar angle of less than -3 are made semi-transparent to highlight the time series retained for moult detection. Consistent 0 values at night in F during April probably represent time spent in the burrow, i.e. neither leg wet. G represents a time series of $prop_{flight}$ (green) and $prop_{flight\text{-}5}$ (red). The red bar underneath the plot represents moult inferred on the first iteration of the moult identifiation process, the blue bar represents a potential second flightless moult identified by the second iteration. The y-axis of G is square root transformed to facilitate the visualisation of positively skewed data, with the actual untransformed values displayed.

5.3.2 Identifying moult periods from dual deployment birds

Table 10: Flightless moult periods identified in the four dual-equipped individuals. 1st moult refers to the earliest moult inferred by the moult identification process, and 2nd moult is any later moult identified as occurring later in the non-breeding season. A range of results are presented for each puffin, as results vary depending on which logger's time-series (left or right leg) is used as the basis for the combination of data.

ID	1st moult start	1st moult duration	2nd moult start	2nd moult duration
EJ47625	7th - 16th Sep	36 - 45 days	20th Feb	32 days
EL60569	1st - 9th Sep	54 - 63 days	-	-
EL60573	17th - 19th Sep	33 - 35 days	9th - 14th Feb	32 - 37 days
EL60648	19th – 21st Sep	44 - 46 days	-	-

Each dual-equipped puffin had a moult period inferred to begin in September, while two had a second inferred moult period beginning in mid-February (table 2 & figure 3). There was some variation in the duration of moult, from 32 to 63 days. During inferred moult periods, the percentage of time spent dry according to raw immersion signals was 12.8%, while it was reduced to 3.9% when adjusted for leg tucking using data from a single leg. When data streams from both legs were corrected for tucking and combined, the proportion of time spent dry during inferred moult was 0.1%, compared to 2.5% for the rest of the non-breeding season. There was no marked increase in percentage of time spent leg tucking when undergoing moult (appendices, figure S2), consistent with observations of captive puffins (M. Huwiler, Tierpark Bern, pers. comm).

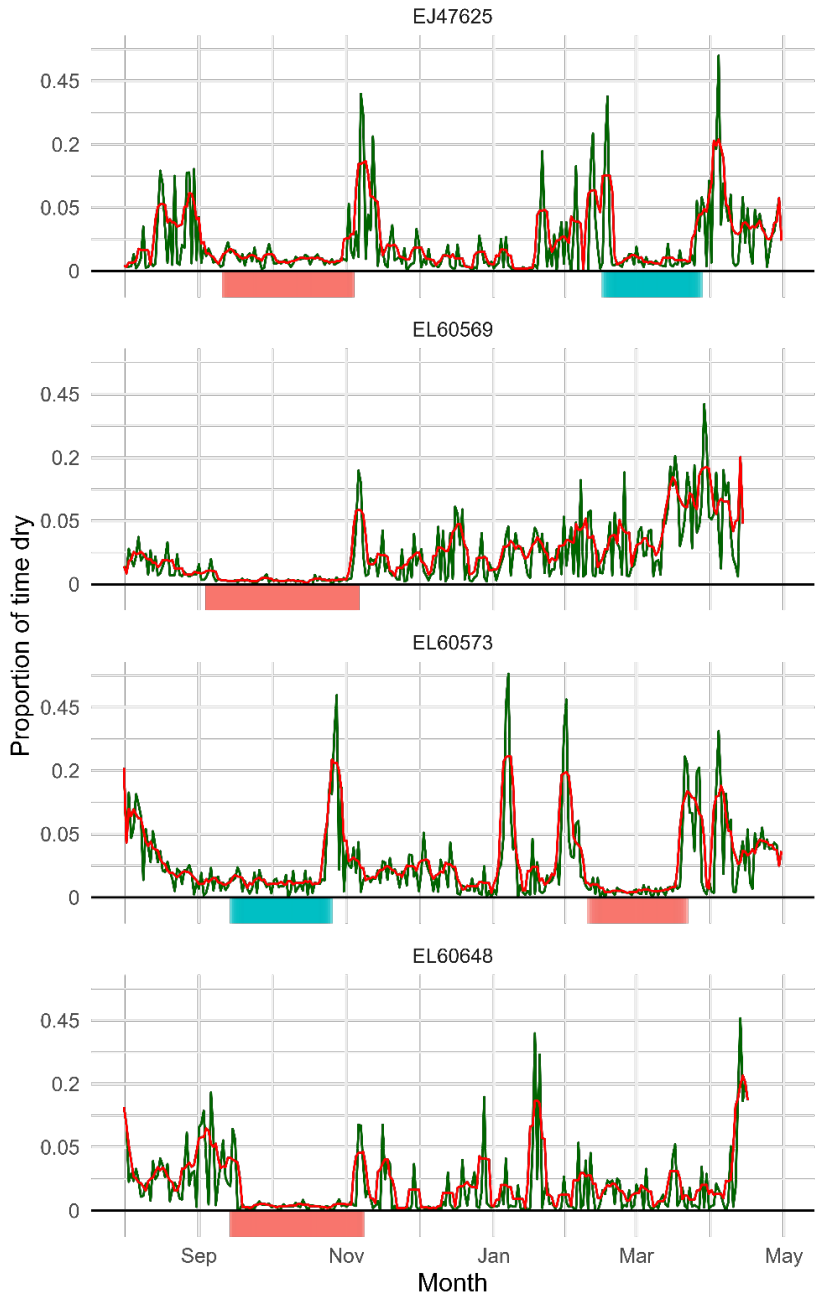


Figure 3: Inferred timing of flightless moult in four dual-equipped puffins. Immersion data were combined between two geolocators for each puffin. The green line represents time spent dry per day ($prop_{flight}$) and the red line is the 5-day rolling average of this ($prop_{flight\text{-}5}$). The y-axis is square root transformed, with the actual untransformed values displayed. The red bar underneath each plot represents moult inferred on the first iteration of the moult identifiation process, the blue bar represents a potential second flightless moult identified by the second iteration.

All moult periods occurred close to equinox periods, when the latitudinal accuracy of light level geolocation is greatly reduced. The average position of inferred moult was used to graphically represent moult location (figure 4), given that puffins are unlikely

to move extensively when flightless, and most of the variation in location during moult is almost certainly due to error in location estimates. Both individuals with two inferred moult periods had more extensive migrations than those with one (table 3), with the autumn flightless moult occurring when they were furthest from their colony and the spring moult when much closer to the colony (figure 4).

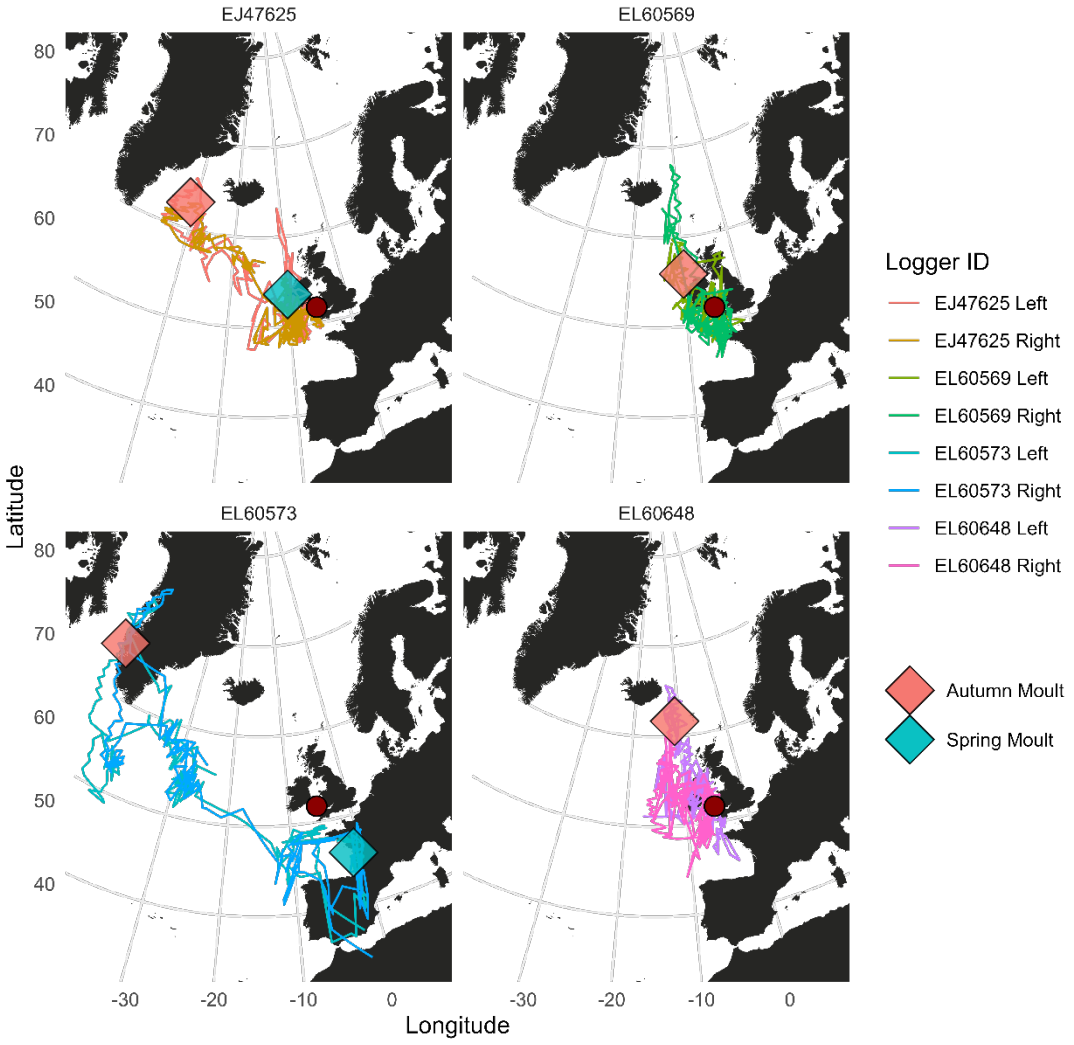


Figure 4: Puffin tracks and associated moult periods. Each plot represents one individual and their mean moult locations, with a track derived from each logger. Geolocator positioning accuracy is reduced around the equinoxes, negatively affecting the latitudinal accuracy of moult locations, which were all inferred to occur around the equinoxes. The red dot corresponds to the colony location, Skomer, Wales. Note that portions of the track apparently crossing land are products of the inaccuracy of geolocator location estimates around the equinoxes, and associated smoothing.

Table 11: Metrics for each dual-equipped bird relating to migratory effort and moult periods. Residencies were described using Lavielle segmentation of net-squared displacement from the colony. Number of inferred moult periods and time spent in inferred moult altogether are also shown.

Bird ID	Most distant residency (dist / time)	Inferred moults	Total time in moult
EJ47625	2054km / 49 days	2	77 days
EL60569	728km / 41 days	1	63 days
EL60573	3040km /42 days	2	72 days
EL60648	1250km / 39 days	1	46 days

5.3.3 Identifying moult using single leg data

Using single logger data streams, only 1 moult period could be successfully identified from the 4 dual-equipped individuals, on the left leg of puffin EJ47625. The dates of this, 16th September to 30th October, exactly matched the moult period identified using data from both loggers. The percentage of time spent dry in this moult period was 0.4%. No second inferred moult period was detected on the second iteration of the moult identification method, even though this process identified a second moult period for this bird when data from both loggers were combined.

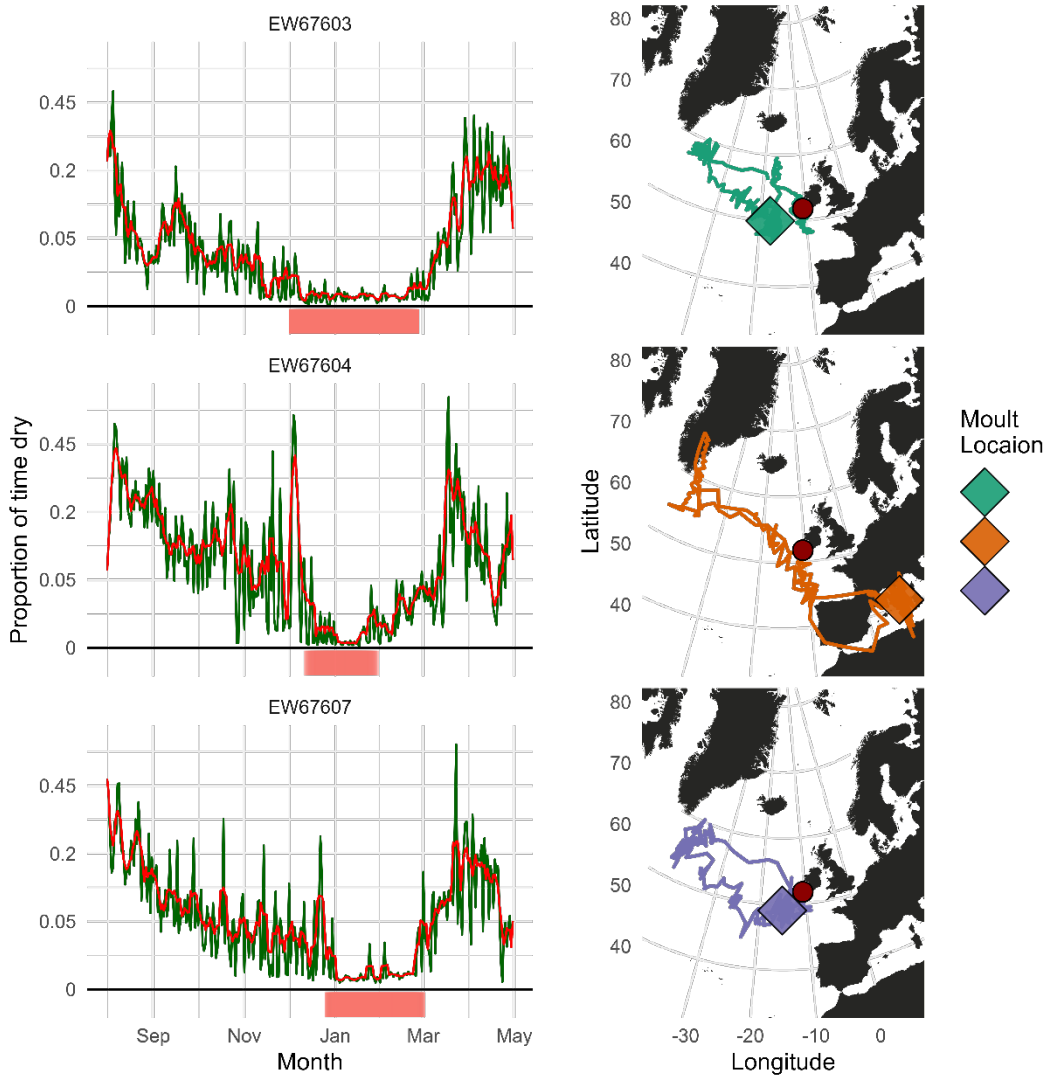


Figure 5: Timing and location of inferred moult of Skellig Michael puffins. On the left, the proportion of time spent dry per day is graphed over the non-breeding season. The green line represents time spent dry per day ($prop_{flight}$) and the red line is the 5-day rolling average of this ($prop_{flight\text{-}5}$). The y-axis is square root transformed, with the actual untransformed values displayed. The red bar underneath each plot represents putative moult inferred by the moult identification process. On the right, the corresponding inferred moult location is shown by a diamond shape, overlaid on the migratory path of the individual. The red dot represents Skellig Michael, their breeding colony. Note that portions of the track apparently crossing land are products of the inaccuracy of geolocator location estimates around the equinoxes, and associated smoothing.

Of the 40 single-equipped individuals from Skellig Michael, inferred moult periods were only apparent in 3 individuals. Periods of sufficiently reduced flight consistent with moult were not detected by our method in any of the other individuals (appendices, figure S4). These moult periods were 35, 52 and 72 days in duration and occurred in midwinter, starting in December or January, and took place either beyond the Irish Atlantic shelf margin (n = 2) or in the Mediterranean Sea (n = 1)

(figure 5 & appendices, table S1). Puffins from Skellig Michael showed reduced leg-tucking activity around midwinter, especially for puffins tagged in 2020, which corresponds with the moult periods inferred for this group (appendices, figure S3). This suggests that moult is more easily identifiable at this time of year due to an apparent reduction in leg-tucking behaviour, so the temporal distribution of moult inferred here is likely biased towards this period. These 3 individuals all moved approximately 2000 km from the colony to their furthest point of residency (appendices, table S2), comparable to one of the Skomer birds that was inferred to have completed two moults.

5.4 Discussion

5.4.1 Methodology

To identify moult in puffins, we have developed a new method combining multiple data streams from geolocator loggers to identify year-round behaviours of seabirds more accurately. While this seems to work reasonably well for dual-equipped individuals, it also highlights some shortcomings of using standard single-deployment geolocators to identify fine-scale behaviours. Halpin et al. (2021) show how species' behaviour can unpredictably influence location estimates using light-level geolocators. Leg-tucking in alcids presents a similar problem for the interpretation of behaviours from saltwater immersion loggers on the same devices (Fayet et al. 2017, Linnebjerg et al. 2014). We provide a method to partially correct for this behavioural classification issue using concurrent light and immersion data. The limitations of this partial correction are reflected in the low success rate of moult inference in single-logger birds. Because puffins and some other alcids spend very little time in flight even when not undergoing moult (see results, Dunn et al. 2020), flightless moult is impossible to identify without relatively accurate behavioural data, and the few individuals for which moult periods were detected using a single logger are likely biased towards times of the year when leg tucking behaviour is less prevalent. Despite these limitations, our methods provide new insights into the behaviour and life-history traits of a threatened species, and improve our knowledge of the timing and location of a highly vulnerable period in the puffin's annual cycle.

Over the last 10 – 15 years, hundreds of alcids have been tagged with a single geolocator throughout their biogeographic range (Fayet et al. 2017, Reiertsen et al. 2021), but our method does not have the power to identify moult in a sufficient proportion of individuals to robustly investigate population-wide patterns. More complex methods, for instance using machine learning to identify flightless stopovers (Guilford et al. 2009), usually require large amounts of pre-assigned training data to confidently infer behaviour, but may even then be liable to misclassification due to individual- or colony-level differences in behaviour (Bennison et al. 2018). Finer resolution data, such as from accelerometers, would allow us to identify flight with much more confidence (e.g. Patterson et al. 2019). GPS loggers would record far more accurate locations, potentially allowing us to identify imposed residency due to flightless moult. To date, none of these alternative devices are small or efficient enough for year-round deployment on puffins.

Geolocators that record temperature can also be used to help correct for leg-tucking (Elliot & Gaston 2014, Dunn et al. 2020), though like the light-based corrections used in this study, temperature-based corrections do not fully capture all instances of leg-tucking. A ventrally mounted immersion switch would provide a truer representation of flight/non-flight behaviour. Despite being light enough for long-term deployment, current techniques to mount these devices long term on the body instead of on a leg-ring have been shown to negatively impact the bird's performance (Lameris et al. 2018). For now, dual-equipped geolocators are probably the most viable method to investigate the flightless moult of puffins and other alcids. As technology improves and devices become smaller, the combined weight of two loggers will have less impact on an animal. Detecting moult in alcids is still contingent on behaviour differing at this stage compared to the rest of the non-breeding season, but results from this study would suggest that is in fact the case.

Stable isotope analysis of feathers sampled during the breeding season may be used to coarsely gauge the location of the most recent primary moult (e.g. St. John Glew et al. 2018) and to validate geolocator based findings, as the tip of the feather will have similar isotopic properties to the oceanic area in which it was formed even if it is sampled several months later. To complement this, a relatively accurate

geolocator-informed moult timing and location tells us where and when flight feathers were formed, allowing us to analyse the trophic position of food consumed during feather formation using stable isotope analysis (St. John Glew et al. 2019). A better understanding of the timing and location of moult may also provide information on the prevalence of toxic chemicals in marine food webs where feathers are being developed by looking at chemical composition of these feathers (Fort et al. 2016).

5.4.2 Biological findings

We have shown that the flightless moult strategy of breeding puffins varies markedly between individuals, and possibly colonies, despite usually being a fixed life-history trait within migratory bird species (Barta et al. 2008). We also found evidence that some individuals may undergo flightless moult twice in a non-breeding season, with this strategy possibly tied to more extensive migrations, though this relationship is based on a very small sample size. Puffins spend very little time in flight in the non-breeding season altogether, so caution is advised when interpreting these prolonged periods of little to no flight as being obligatory due to flight feather moult. However, the duration and timing of these flightless periods are consistent with previous estimates of moult in this species, and if this is the case, our results provide the first evidence for two flightless moult periods per year in a wild volant bird species (Beltran et al. 2018).

The exploration-refinement hypothesis (Guilford et al. 2011) suggests development over time of a fixed migration strategy that exploits predictable prey availability in space and time, leading to inter-individual variation (e.g. Harris et al. 2015). More extensive migration may allow puffins to exploit reliable food resources (Jessopp et al. 2013), especially during moult when their diving abilities are likely compromised (Bridge 2004).

Prolonged flight during migratory phases may lead to accelerated feather wear and reduced flight efficiency for a bird with an already high wing-loading (Navarro & González-Solís, 2007, Greenewalt 1975), whose burrow nesting habits probably cause flight feather wear during the breeding season. Increased energy requirements for long-distance migrants also necessitate increased foraging effort and dive rates

(Fayet et al. 2016), potentially causing further wear in wing feathers. For several reasons, puffins may require two moults in one non-breeding season to maintain flight feather condition and retain flight efficiency (Barta et al. 2008). It may be that one or both moults are incomplete, allowing the puffins to remain partially volant. Small alcids in the genus *Aethia* forego synchronous moult, instead staging the replacement of primary flight feathers, allowing them to continue flying throughout moult (e.g. Bond et al. 2013). Some storm-wrecked puffins have shown evidence of a similar partial primary moult (M. Harris, unpublished data), though this has only been observed in a vanishingly small proportion of a very large sample of recovered birds, so is likely an anomaly or due to poor health. Biannual synchronous flightless moults have been observed in captive juvenile puffins (Swennen 1977, M. Huwiler, Tierpark Bern, pers. comm.), and while it is uncertain how these observations relate to wild breeding adults (Thompson & Kitaysky 2004), it does highlight that this strategy is physiologically possible. In contrast, the two Skomer individuals that stayed closer to the colony (< 1500km) during the non-breeding season clearly underwent a single flightless moult in autumn, not long after the summer breeding season. Flight feather moult is energetically demanding (Guillemette et al. 2007) and reduces foraging efficiency (Bridge 2004), so there are potential advantages in strategies that forego a second flight feather moult where possible. A trade-off likely exists between the energy required to undergo long-distance migration to highly productive areas, potentially necessitating two flightless moults, versus reduced migration effort and a single flightless moult in an area where feeding conditions may be poorer. Moult strategy in puffins could be dichotomous (biannual versus annual moult) associated with high versus low energy intake and expenditure, reflected in the activity budgets of long- and short-distance migrants (Fayet et al. 2017).

Previous studies, based on birds recovered dead rather than those from birds equipped with loggers that survived the non-breeding season, described an early/late bimodal distribution of puffin moult timings in the North Sea and around the Faroes Islands, with peaks in October and March (Harris et al. 2014). This timing largely agrees with our findings from Skomer individuals. It may be that dead birds identified as moulting in March were going through a second moult. Harris et al.

(2022) found that almost all birds found wrecked on the East coast of Britain after storms in November and December 2021, had already undergone primary moult, which may reinforce the idea that primary moult in February/March may be a second occurrence. However, many more suitable tracking data, e.g. from dual-equipped puffins, would be required to suggest this with any confidence.

The inferred moult of three Skellig Michael individuals occurred once, from December to February, with no evidence that this followed an earlier post-breeding flightless moult, although again, this is based on a small sample where moult could be resolved from single logger data streams. Similar moult timings were observed by Anker-Nilssen et al. (2018), who reported that most puffins found following storm wrecks on the coast of Norway in February/March 2016, likely originating from colonies on the East coast of the UK, were in the latter stages of moult and had only recently become volant. Birds found dead are more likely to have been wintering relatively close to land, and so may not provide an unbiased sample of the wider population (Fayet et al. 2017). It is also possible that storms disproportionately affect moulting puffins that cannot fly to escape storm tracks, with reduced foraging efficiency during moult further compromised by storm conditions (Clairbaux et al. 2021). This does not seem to universally be the case, with a high proportion of moulting birds found in one wreck on the Norwegian coast (Anker-Nilssen et al. 2018) and a low proportion in another in the Bay of Biscay (Morley et al. 2017), despite both wrecks occurring at a similar time of year.

5.4.3 Conclusions

While limited to a small sample size, the results of this study markedly advance our understanding of a vulnerable period in the non-breeding season of a threatened species. We raise the intriguing possibility that puffins have a unique biannual flightless moult, leaving them flightless for 60-80 days over the course of a single non-breeding season, accounting for 20-30% of that total period. This highly unusual strategy may be tied to migration effort, though this is speculative due to our limited sample size. However, we have established a freely available workflow to further analyse dual-equipped seabirds to improve behaviour classification using geolocators. We hope this will promote further research on the flightless moult of

puffins and other alcids. At this stage in their annual cycle, they are particularly vulnerable to negative impacts from reduced prey availability, surface pollution and increased storm prevalence.

5.5 Appendices

Variation in tucking behaviour

Two puffins (EJ47625 & EL60569) spent considerably more time tucking their right leg than their left, especially before midwinter, whereas the other two tucked both legs a similar amount throughout the year. One puffin (EL60658) also spent much less of its time tucking than the other three (figure S1).

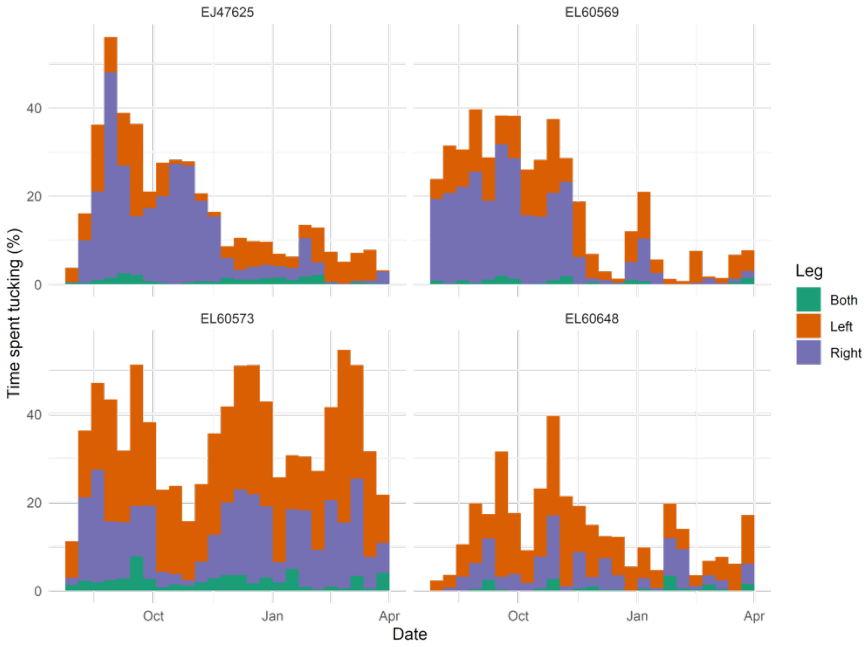


Figure S1: Percentage of daylight time spent leg-tucking, informed by raw light data and predictions. Tucking events are grouped by leg. Each of the 4 plots represent a different individual.

Tucking while moulting

No increase in amount of time spent tucking was observed during inferred moult in the dual tagged birds (figure S2). We had hypothesised that puffins may spend more time tucking during moult, due to prolonged time spent resting while flightless, but this does not appear to be the case. Further information from captive puffins reinforces that tucking behaviour doesn't become more frequent during moult (M. Huwiler 2022, TierPark Bern, pers. comms.), and in contrast, their appetite increases at the onset of moult (D. Dial 2022, National Aquarium USA, pers. comms.), which may result in less time spent leg-tucking in the wild.

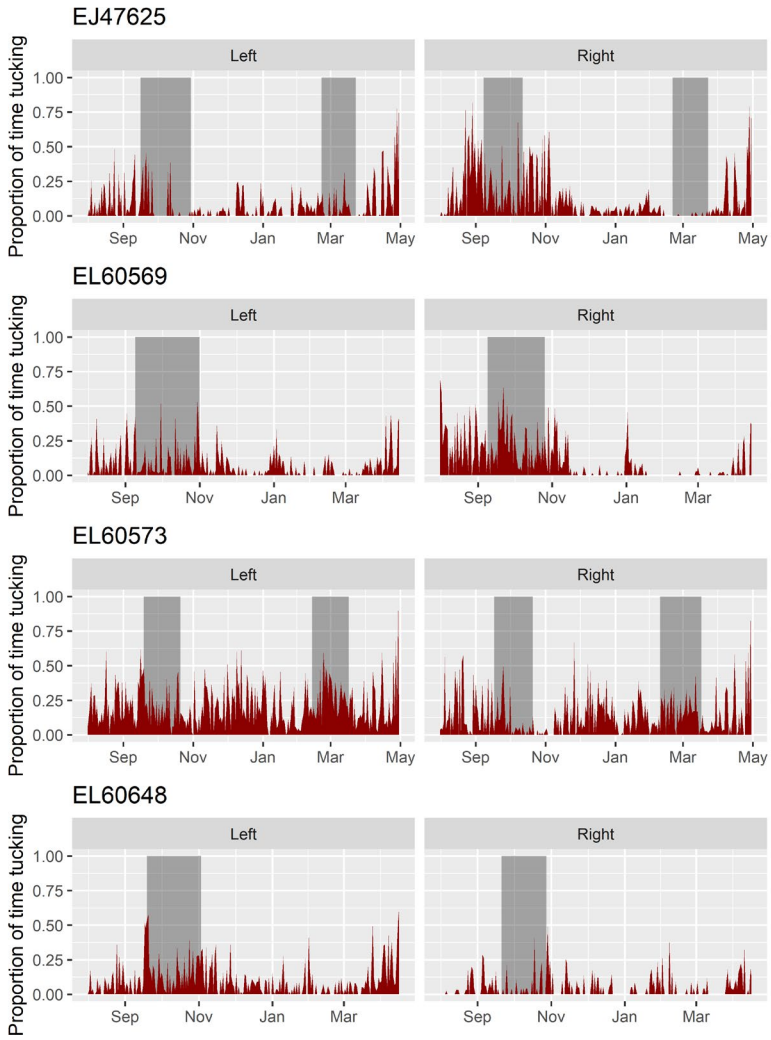


Figure S2: Graph showing the amount of time each dual-tagged puffin spent tucking each leg per day over the non-breeding season (dark red), with moult periods overlaid (grey shading).

Tucking behaviour of Skellig Michael puffins

Tucking behaviour was much more prevalent in autumn than in winter in Skellig Michael puffins (figure S3). The peak in "tucking" behaviour around the end of April/start of May possibly corresponds to the first visits to the study colony and burrow nests, where the light-logger will be obscured underground during daylight hours. The reduced leg-tucking activity around midwinter, especially for puffins tagged in 2020, corresponds with the moult periods inferred for this group. This suggests that moult is more easily identifiable at this time of year due to an apparent reduction in leg-tucking behaviour, so the temporal distribution of moult inferred here is likely biased towards this period.

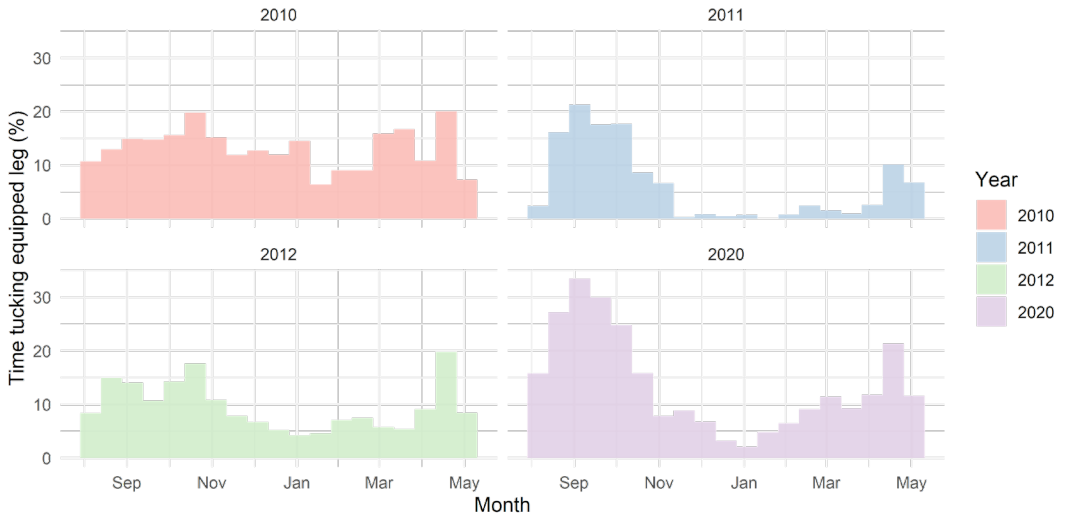


Figure S3: Percentage of time spent leg-tucking per daylight interval (solar angle > -3), informed by raw light data and GAM predictions. Tucking events are grouped by year and pooled across all Skellig Michael study individuals. Year refers the non-breeding season beginning August of that year and ending in May of the next.

Moult metrics for Skellig Michael puffins

Table S1: Date, duration, and coarse location of inferred moult of Skellig Michael puffins.

ID	Moult start	Moult duration	Location
EW67603	9th Dec	72 days	Atlantic
EW67604	19th Dec	35 days	Mediterranean
EW67607	2nd Jan	52 days	Atlantic

Migration metrics for Skellig Michael puffins

Table S2: Distance and time spent at the furthest residency along the migratory track. Periods of residency are inferred by Lavielle segmentation. See methods in the main text for further details.

ID	Most distant residency (dist / time)
EW67603	1820km / 92 days
EW67604	2073km / 71 days
EW67607	1900km / 104 days

Failed moult identification for Skellig Michael puffins

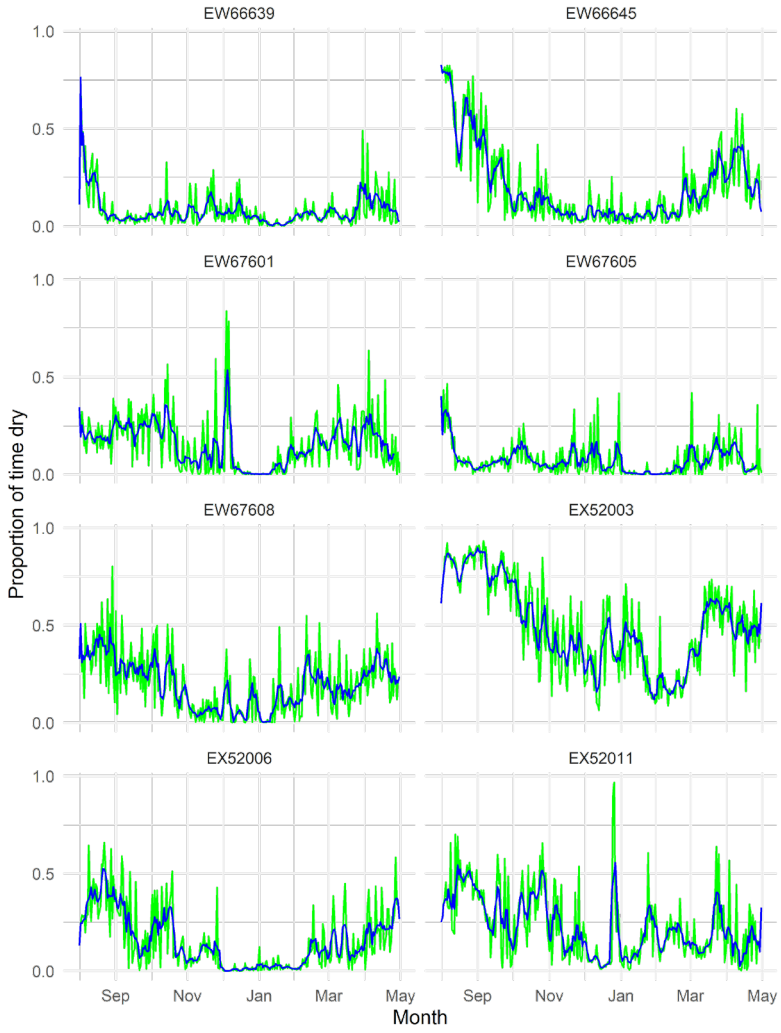


Figure S4: Time series showing the proportion of flight for day (green line) and 5-day rolling average of this (blue line) of 8 Skellig Michael puffins after tucking correction. Our moult identification did not infer moult periods in any of these time series.

Figure S4 shows time series from single-equipped geolocators from 8 puffins for which no moult was inferred by our method. Though periods of reduced flight are visually apparent in certain cases (see EW67601, EW67605), they did not meet the criteria for classification as moult by our method. This is due to the rolling average of time spent dry not remaining below 1% per day for a sufficient period. According to the results from dual-equipped data, these periods may represent periods of residency during which the puffin did not fly extensively but was not obligatorily flightless. Tucking is shown to be less prevalent during these periods, which mostly occur in midwinter (figure S3). Shorter daylengths at this time may necessitate increased foraging effort in puffins for the limited daylit time available, reducing time available for leg-tucking/resting.

CHAPTER 6: DISCUSSION

6.1 Main thesis findings

"As soon as transmitter and satellite technology allow, there will surely be interesting findings to be harvested by tracking shearwaters beyond the horizon" (Brooke 1991). Our understanding of the at-sea behaviour and distribution of pelagic seabirds is constantly developing through biologging studies. This thesis provides four examples of using biologging to interpret fine-scale behaviours and their relationship with drivers of broad-scale distribution. Seabird movement and distributions are often modelled using proxies for oceanographic conditions and productivity (Tremblay et al. 2009, Cox et al. 2016, Kane et al. 2020, Waggitt et al. 2020). However, the predictive power of these proxies is often poor, as they are often several steps removed from true drivers of distribution, such as prey availability or detectable cues of the presence of prey. In this thesis, novel combinations of environmental and biologging data are used to provide biologically relevant descriptors and predictors of fine-scale behaviour, such as fishing vessel presence and underwater visibility, which provide insights into the drivers of broader scale distribution. Stressors and conditions in the marine environment are described using remote sensing data, from satellite, forecast modelling, fishing vessel monitoring systems, or using the biologging devices themselves. The impacts of this proximate environmental information on seabird ecology are investigated using a range of telemetry devices and analytical techniques. Though each chapter focused on a single study species, the principals and methods developed can be applied to other seabird species, or even other taxa.

In chapter 2, the foraging behaviour of a diving seabird, the Manx shearwater, is described as a response to underwater visibility. How light availability affects the diving behaviour of seabirds has been touched on using time of day, or solar angle alone (Wilson et al. 1993, Shoji et al. 2016). In this instance, underwater visibility is described more completely using a combination of solar angle, modelled forecasts of cloud cover, and satellite-derived measures of water turbidity. This compound metric of underwater visibility was shown to constrain dive depth, frequency, and location for this visual hunter. In chapter 3, primary productivity near the water surface was

also described using satellite imagery, using chlorophyll-a concentration as a proxy. This was shown to influence the distribution of foraging in a predominantly surface-feeding seabird, the northern fulmar, even though the prey of this species is several trophic levels removed from primary producers (Phillips et al. 1999). However, this species is a known scavenger of fisheries waste, and when the distribution of commercial fisheries was used to explain their foraging distribution, it far outperformed any metrics available for natural food availability. Human activity influences almost every oceanic habitat (Halpern et al. 2008), and this chapter provides impetus to consider anthropogenic factors when investigating drivers of seabird distribution in other systems.

For some seabird species, migration strategies may vary drastically between individuals (Fayet et al. 2016). This thesis explores how individuals' migration strategies affect their vulnerability to certain stressors at sea. Loggers were deployed on seabirds year-round, recording maximum light level and the proportion of time immersed in saltwater in 10-minute intervals. Light time-series can be used to roughly gauge location up to twice per day (e.g. Phillips et al. 2004). Light levels can also be used to detect nocturnal vessel interactions of scavenging seabirds over the annual cycle (Krüger et al. 2017, Dupuis et al. 2021). In chapter 4, fulmars, our model scavenger species, were shown to be individually repeatable in the amount of time they spend around vessels, at least at night. Further to this, the time spent at vessels correlated with distance travelled in the non-breeding season, with those staying closer to the colony likely to encounter vessels more frequently. The cause-and-effect of this relationship is difficult to interpret, but in any case, it shows that fulmars with different migration strategies vary in their level of vessel interaction, meaning that their risk of bycatch also varies (Soriano-Redondo et al. 2016).

Staying on the topic of migration, this thesis also addresses how different migration and life-history strategies may influence seabird vulnerability to storms and reduced prey availability. Immersion data from geolocators can be used to identify different behaviours of seabirds at sea (Mattern et al. 2015). If we examine the distribution of these behaviours relative to the full annual cycle, long term trends can tell us about important features such as feather moult (Cherel et al. 2016) or migratory phases

(Guilford et al. 2009). However, data from these loggers can be confounded by idiosyncratic behaviours of seabirds (Halpin et al. 2021), as is the case for the puffin. To get around related issues, light and immersion levels were combined in chapter 5 from loggers mounted on each leg of puffins to better understand their year-round behaviour. Better estimates of behaviour were used to tease apart the timing and location of feather moult, during which puffins become flightless (Harris et al. 2014), and so more vulnerable to the adverse impacts of extreme weather, reduced local prey availability, and surface pollutants.

Another theme throughout this thesis is the use of varying spatial and temporal scales of data to describe different aspects of seabird movement and behaviour. This ranges from dive depth data recorded every 2 seconds, at a resolution of 1cm, right up to location estimates up to twice per day at a resolution in the magnitude of hundreds of kilometres. The behaviours that are defined rely massively on both the type and resolution of data recorded by biologging devices, and environmental data quality is similarly very important when associating behavioural responses with environmental cues. For instance, proximate conditions and associated responses are best described at fine scales, such as the impact of wind on flight (Elliott et al. 2014) and the influence of water clarity on diving visual hunters. However, certain stimuli are detected and responded to over much larger spatial scales, such as avoiding dangerous sections of storm systems (Lempidakis et al. 2022) or directing towards fishing vessels (Bodey et al. 2014). Interpreting life history strategies of seabirds is possible at much coarser scales again, with migration strategies evident on an ocean-basin scale (Frederiksen et al. 2012). Within this thesis, new methods are developed to handle data at varying scales for different tasks, progressing both our understanding of seabird ecology as well as how to study it.

6.2 Future state of oceanic habitats

Climate change, commercial fisheries, and shifting prey availability are all stressors that have implications for seabird populations (Dias et al. 2019). All are dynamic, associated negative impacts are highly unlikely to abate in the coming decades, and in many cases will intensify. Climate change is likely to move the climatic envelopes of many seabird species towards the poles as air and sea temperatures generally

increase (Clairbaux et al. 2021). It is also increasing the frequency and intensity of winter storms in many of the ocean's productive areas (IPCC 2014), with associated conditions often lethal for seabirds (Morley et al. 2017). Increased seabed shear stress and sediment resuspension due to changing weather conditions are also reducing underwater visibility of enormous areas of productive shelf seas (Wilson & Heath 2019). Similarly, changing temperature and nutrient availability are changing the frequency and intensity of planktonic blooms, with the potential to greatly decrease underwater visibility over massive areas (Signorini & McClain 2009). Shifting optical properties of the ocean and inclement weather associated with storms may restrict the foraging capabilities of seabirds.

Our understanding of the total productivity of the world's fisheries is partly dependent on the reliability and coverage of reported catches, despite these often containing conspicuous data gaps and innconsistencies (Pauly & Zeller 2016). However, several metrics would suggest that the global fisheries catch is declining since the mid-1990s, with vessels generally having to cover greater distances per unit catch, and as a result now cover 90% of the world's oceans (Tickler et al. 2018). Despite this massive distribution, fleets are generally decreasing in size, both in terms of overall vessels and gross weight (stats.oecd.org, Eurostat 2019), reflecting the reduced catch available and the increased effort required to achieve it. The quantities of waste that fisheries produce should also reduce over time as more jurisdictions ban discarding unwanted catch (e.g., ec.europa.eu/fisheries/cfp/).

Seabirds are highly individual in their foraging behaviour, and members of the same species will vary in the degree to which they attend vessels to scavenge waste (Votier et al. 2010). The drivers of this variety may be down to individual differentiation of foraging strategy within the same environment (Patrick et al. 2015), or due to local availability of resources (Clark et al. 2020). Understanding this variability is key to forecasting how populations will react to shifting fisheries distributions, practices, and the availability of associated food. Many scavenging species may have to seek new sources of food as fisheries waste becomes scarcer (Bicknell et al. 2013). Reduced fleet sizes could reduce the overlap between seabirds and potentially harmful fishing gears, or simply increase the distance that vessel-attending seabirds

must travel to attain a meal (Cianchetti-Benedetti et al. 2017). However, a push towards sustainable fisheries may reduce the fishing pressure on already depleted fish populations, including important prey species for many seabirds (Wanless et al. 2018). Fisheries waste is thought to be a poor substitute for natural prey (Gremillet et al. 2008), and increased availability of natural prey may reduce seabirds' reliance on vessel waste.

6.3 Technological advances

There is plenty that biologging still has to teach us about seabirds. Devices are ever improving in terms of size, efficiency, power requirements, and functionality. We are only recently learning about the at-sea movements of the smallest seabirds through tagging efforts (Rotger et al. 2020), as GPS tags weighing less than 1g are now available. As such tags develop further in terms of size and functionality, we will also begin to understand the fine-scale at-sea behaviour of these diminutive species. Location data are being accumulated for more species, colonies, and individuals, as well as over more protracted time series. There is a great diversity in the way seabirds occupy and exploit their marine environment, even within species (Fayet et al. 2017, Wakefield et al. 2013), which is only clear when sufficient data are available. Fortunately, this is now increasingly the case, with large collaborative efforts, such as the SEATRACK program or the BirdLife Seabird Tracking Database, collating comparable data on the ocean basin scale and allowing for comparisons between multiple species or colonies (e.g. Amélineau et al. 2021, Reiertsen et al. 2021, Clairbaux et al. 2021). Such collaborative efforts, including the SEATRACK program, were integral to chapters of this thesis.

Further to the amount of tracking data currently being collected, equally or more important are the improvements in quality, both in terms of precision and resolution. As mentioned, light-level geolocators have been used to describe the year-round movement of seabirds, with locations estimated twice daily based on inter-twilight intervals. These data suffer low accuracy, often in the order of hundreds of kilometres (Phillips et al. 2004), as well as being confounded by periods of equinox and behavioural idiosyncrasies of the birds themselves (Halpin et al. 2021), which are issues encountered and discussed in detail in chapters 4 and 5 of this thesis. Bulky

tags that transmit relatively accurate locations via satellite have been attached to larger species longer term (e.g. Péron & Grémillet 2013), though the size and attachment method may be prohibitive for smaller species (Lameris et al. 2018). The costs of both the tags and the satellite transmission of data also prevent mass deployment of loggers.

Manufacturers are being tasked with designing small and affordable GPS-based substitutes for geolocators, which would improve the spatial resolution of location estimates from hundreds of kilometres down to just a few metres. This would be a game-changing development in the study of long-term at-sea behaviour and distribution of seabirds, counteracting many of the shortfalls of light-level geolocators, such as low accuracy during equinoxes during the migration period of many seabirds. Prototypes of these devices are currently being trialled, and we may see studies appearing using these accurate data in the near future. The question of when puffins moult their flight feathers, for example, could be far easier to answer with more accurate location data, as their mobility is highly restricted at this time, which should be reflected by short distances between daily relocations.

On shorter timescales, loggers can reveal exceptional detail about behaviour. Triaxial accelerometers recording 10s of times per second have the potential to teach us about fine scale interactions with environment and associated energetic costs through analysis of forces acting on individuals, especially when combined with location data (Collins et al. 2020). This is a useful tool for investigating energetic consequences of change in oceanic habitats, such as changing wind regimes, obstacles that divert from foraging grounds, and foraging on fisheries waste versus natural foraging. Understanding energetic expenditure and how this may change with time is key to understanding seabird survival and reproductive output (Dunn et al. 2020, Regular et al. 2014).

Stressors that induce energetic consequences and reduce fitness may have lasting effects (e.g. Steenweg et al. 2022). Effects from multiple stressors encountered over time will therefore accumulate, and this must be considered when quantifying the impacts of at-sea activities on seabirds (Busch et al. 2013, Bailey et al. 2014). Agent-based modelling has been implemented as a solution to understanding these

cumulative impacts (e.g. Warwick-Evans et al. 2018). These models incorporate the likelihood of encountering a stressor, the negative impact of that stressor, and the recovery time from that negative impact. Simulations are run, and the cumulative effects of multiple stressors over time on multiple simulated "agents" (in our case, seabirds) is then estimated. For these models to resemble and represent natural systems, prior knowledge of both the species and their environment is essential, as well as an understanding of how they interact. This technique is becoming a commonly used tool for identifying cumulative impacts of offshore windfarms (Warwick-Evans et al. 2018) and oil pollution (Madsen et al. 2022). However, it also has potential to identify the combined effects of other potentially non-lethal stressors, including inclement weather, plankton blooms, habitat disturbance, and changes in food availability. As biologging techniques continually improve, both in terms of technology and data available, and methods of interpretation such as those developed in this thesis, agent-based models can be used to tease apart specific causes of decline.

6.4 Relevance and recommendations

Throughout this thesis, analyses of both biologging and environmental data are developed in new ways towards understanding seabird ecology. These include innovative applications of environmental data, such as the first use of fishing effort or underwater visibility as covariates in seabird habitat use models. Novel or emerging analyses of biologging data are also used to improve behavioural interpretation. This includes identifying nocturnal seabird vessel encounters from light-level loggers in chapter 4, or pairing light-level and immersion data from geolocators to improve long term behavioural classification of seabirds in chapter 5. Further to what has been developed within this thesis, these chapters also provide the basis for future research and applications for new biologging methods.

In chapter 2, the impact of underwater visibility on the foraging behaviour of seabirds is understood solely in terms of movement. However, other types of data streams may provide better information about the proximate surroundings and responses of study species. Bird-borne cameras, for instance, can give us a first-hand view of cues that seabirds use to find food (Michel et al. 2022) and to what extent these cues occur

above or below the water (Tremblay et al. 2014). Video may also reveal the rate of successful food capture during foraging and scavenging. Bird-borne cameras are becoming lighter and have recently been successfully deployed on Scopoli's shearwaters (*Calonectris diomedea*, Michel et al. 2022). Though such cameras are still too cumbersome for Manx shearwaters, other seabird species with comparable foraging methods are likely to be affected similarly by environmental conditions and may provide alternative model species for studying the impacts of oceanic turbidity. Otherwise, light level loggers weigh less than cameras as they require less battery power and could sample the light conditions necessary to attempt prey capture. Such direct measurements of environmental conditions can be paired with fine-scale movement data from accelerometers, which would allow us to identify prey-capture attempts within dives, rather than relying on metrics describing the whole dive. The energetics of prey capture in different conditions could then be measured, and cumulative energetic consequences of foraging in turbid water could be quantified.

Chapters 3 and 4 focus on how vessels alter the broad-scale movement patterns of a heavily bycaught seabird species, the northern fulmar. Fisheries in the North Atlantic are generally decreasing in fleet size and total catch (stats.oecd.org, Eurostat 2019), but still fulmars from many colonies are increasingly attending vessels over the last decade. Fulmars from Ireland and the UK were shown to attend trawlers far more than other types of fishing vessel. However, the European Union's Common Fisheries Policy includes a ban on discarding of non-marketable catch fully implemented by 2019 (ec.europa.eu/fisheries/cfp/), which likely has implications for many of the seabirds that scavenge on fisheries waste (Borges 2021, Bicknell et al. 2013). The reduced level of discarded fish from trawlers available may even lead many seabirds to scavenge alternative fisheries by-products, such as bait from longline hooks (Seriano-Redondo et al. 2016). Longlines are generally much more prone to seabird bycatch than trawl type gears and are responsible for the bycatch of huge numbers of seabirds each year (Anderson et al. 2011).

Several means of bycatch mitigation have been suggested for various fishing gears (Løkkeborg 2011). Night setting is advised for some longline fisheries where bycatch is an issue, though this thesis shows that fulmars extensively forage and scavenge on

fisheries waste at night, which means this method is not likely to be very effective. Switching off vessel lights while setting at night supposedly improves the efficacy of this method, though fishers are often reluctant to do so, and enforcing this method would be next to impossible (ICES 2010). Other strategies include weighting longlines so that they sink faster or deploying bird scaring (tori) lines alongside longlines, though these are not very effective at reducing bycatch of many seabird species in the Mediterranean (Cortés & González-Solís 2018). The motivation for fishing vessels to implement these mitigation measures is often lacking, as they can be restrictive and incur additional costs. Scarcely any external monitoring occurs on these vessels, so levels of bycatch are difficult to estimate (ICES 2010).

A data-driven approach to bycatch mitigation should be employed to ensure that governing bodies legislate effective measures. Chapter 3 provides a framework for how to identify seabird/fishing vessel interactions, which can be used to develop a better understanding of seabird bycatch risk and the energetic consequences of scavenging fisheries waste. Bycatch mitigation measures often focus on limiting the time that fishing gears are available at the surface of the water (Rouxel et al. 2022). Fulmars are suspected to only forage at or near the water surface (Garthe & Furness 2001, Hobson & Welch 1992), so such methods that sink dangerous gears out of reach should theoretically work well. However, preconceptions about foraging modes of seabirds are often overturned, and maximum dive depths and foraging ranges are often underestimated until sufficient data are collected (e.g. Guilford et al. 2022, Wischnewski et al. 2019). Methods developed in chapter 3 can be used in combination with more detailed biologging data from bycatch-prone seabirds to tell us about their diving behaviour while foraging and scavenging on fisheries waste. This in turn would be critical to deciding how to reduce the risk of bycatch considerably by ensuring that dangerous gears are set out of reach of diving seabirds. It would also help us to forecast the consequences of changing fisheries practices on the energetic budgets of this species.

Chapter 5 of this thesis differs from the others, as it relates the behaviour of a seabird to intrinsic factors, in this case moult strategy, rather than environmental conditions. Tying moult distribution to environmental conditions was the original intention of

this work, but was not feasible because of limitations of effective sample size, due to shortcomings of the developed methods to identify behaviours accurately in the majority of cases. With a more representative sample size, as well as more accurate location estimates from long term GPS deployment, the timing and location of moult in puffins could be examined in more detail, to see if it coincides with locally enhanced food abundance or reduced risk of encountering winter storms. Puffins display a variety of migration strategies, which are shown to correlate with demography and productivity (Fayet et al. 2017). A greater understanding of moult strategies of puffins from colonies across their range would give additional context to this relationship. Puffins are susceptible to the impacts of adverse weather and winter storms (Morley et al. 2017, Anker-Nilssen et al. 2018), which they would struggle to escape when flightless.

While this chapter highlights the shortcomings of conventional tracking data for studying long term behaviours of puffins and related species, it also provides a methodological framework and suggestions for improving such analyses. It shows how geolocators mounted on each leg of a study individual can be used in tandem to greatly improve behavioural classification. This involves attaching extra weight to study individuals, which may have fitness consequences (Cleasby et al. 2021). However, the small sample of birds (n = 4) equipped with two tags in this study had similar overwintering strategies, reproductive success, and behaviours compared to birds with single tags from the same area (Fayet et al. 2016). As biologging technology advances, geolocators will continue to become lighter without losing functionality, which in turn will likely reduce negative impacts of attachment. Additionally, as other types of devices become smaller and more suitable to year-round deployment, we may forgo geolocators in favour of loggers that record finer resolution movement data to answer the same questions with more confidence.

6.5 Conclusions

Biotelemetry is critical to understanding the behaviour and distribution of far-ranging seabirds. The use of such technology for studying seabirds has shed light on so many unknown and misunderstood aspects of their ecology, and will continue to do so as long as technology and methods develop. Given the precarious state of many seabird

populations, these studies are a necessary tool to understanding seabirds' responses to changing oceanic habitats, drivers of population change, and how to mitigate against them using conservation measures. This thesis uses biotelemetry to provide insights into the at-sea ecology of three pelagic seabirds, though the insights gained can be applied to many more. The Manx shearwater provides a model diving species, to show how cloudier waters may constrain foraging behaviour of visual hunters. The northern fulmar provides a model scavenging species, to show how seabird distribution and behaviour can be changed by the presence and use of fishing vessels to provide an extra source of food. The Atlantic puffin provides a model species that undergoes flightless moult, a stage of the annual cycle during which storms and prey shortages may have a greater impact on reproduction and survival. Studies of seabirds' relationships with their environment provide vital context necessary for understanding seabird population health and working towards effective conservation strategies. With biologging tools at our disposal, we are better able to forecast how seabirds will respond to their changing oceanic habitats.

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