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Interactions between black-legged kittiwakes and their fish prey in the North Sea. Report of the JNCC-Ørsted workshop, Edinburgh, October 2023

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Summary

The black-legged kittiwake *Rissa tridactyla* is one of the seabird species that have recently undergone severe declines in the UK. Depletion of fish prey in the North Sea, caused by climate change and/or fisheries activities, is a key pressure contributing to poor kittiwake population status. The ecological mechanisms and processes underpinning the interactions between kittiwakes and their fish prey are complex and need to be better understood in order to inform robust, evidence-based ecological measures that would improve the viability of seabird populations of conservation importance.

Ørsted have commissioned JNCC to deliver an assessment of relevant evidence, and to develop a shared understanding of key knowledge gaps and potential future research. JNCC organised a one-day face-to-face workshop in Edinburgh on 4 October 2023, bringing together experts in the fields of kittiwake ecology and behaviour, fish ecology and behaviour, fisheries science, and predator-prey interactions. A key aim of the workshop was to identify areas of research and monitoring needs that would improve understanding of kittiwake and fish prey interactions in the southern region of the North Sea, which is of direct relevance to offshore wind Hornsea Project Three.

Workshop discussions covered two main research themes, namely:

- Drivers and processes governing the availability, abundance and quality of fish prey to kittiwakes, and how these may vary across scales
- Demographic consequences of spatio-temporal changes in fish prey populations on kittiwakes, and underpinning mechanisms and processes

Engagement with experts from multiple disciplines revealed many knowledge gaps needing filling. These included:

- Linkages between fish prey behaviour and availability to surface-feeding seabirds;
- Distribution, abundance and status of clupeid populations in coastal areas;
- Distribution, abundance and behaviour of small fish prey length classes;
- Influence of hydrodynamic features, e.g. frontal systems, in predicting fish availability;
- Diet of breeding adult kittiwakes and their chicks;
- Diet of adult kittiwakes during the non-breeding season;
- Carry-over effects of kittiwake breeding season diet on overwinter condition and survival;
- Variation in fish prey energetic quality; and
- Factors driving prey selection.

Contents

1 Background to the project

The black-legged kittiwake *Rissa tridactyla* is a species of conservation concern that has suffered significant population declines in the UK (50% decline between 1986 and 2019; JNCC 2021). As for several seabird species, especially sea-surface feeding kittiwakes, marine ecosystem change and its indirect effect on fish prey populations, have been identified as a driving force of seabird population change (Mitchell *et al*. 2020). Kittiwakes also present serious risk to consenting future offshore windfarm developments in the North Sea. This is due to their sensitivity to impacts from collision with turbine blades and, to some extent, displacement from prime foraging habitats (e.g. Furness *et al*. 2013; Peschko *et al*. 2020). Legislation requires that potential impacts on protected bird populations are assessed prior to the consent of offshore windfarm development, and any adverse effects on features of Special Protection Areas (SPA) are mitigated or compensated.

With the rapid expansion of offshore wind development in UK waters, ecological compensatory measures are being increasingly considered. For example, projects recently approved in the Round 4 offshore wind plan in English and Welsh waters are required to develop compensation plans for each of the impacted protected sites. The first offshore wind farm project consented with derogation in UK waters was Hornsea Project Three (Hornsea Three), with a requirement to deliver compensation measures for impacts to the kittiwake population of the Flamborough and Filey Coast (FFC) Special Protection Area (SPA) when considered in-combination with other offshore wind farms. At that time, it was identified that increasing prey availability to breeding kittiwakes would be a significant step forward in compensating for potential ecological losses for this species. Primarily, the management of commercial fisheries was recognised by the UK's Statutory Nature Conservation Bodies (SNCBs) as a favoured compensation measure. However, a report provided during the Hornsea Three planning examination showed that this kind of compensation could only be practically possible if undertaken as a government-led approach supported by science-based evidence. Ørsted showed its willingness to fund and deliver research to provide evidence to support a government-led process. In addition to delivering research, Ørsted has constructed innovative nearshore artificial nesting structures (ANS), which provide a novel ecological compensation measure for breeding kittiwakes. In combination with the ANS, and as a part of the Development Consent Order requirements, the Hornsea Three project should deliver "details of the work within the exploration of prey availability measures that could support practical management measures to increase prey availability, and which should be undertaken alongside the artificial nest site installation" (Ørsted 2020).

To meet this requirement, Ørsted have commissioned JNCC to review and assess relevant evidence and to develop a shared understanding of evidence needs and potential future research. JNCC first undertook a desktop assessment of evidence and datasets relevant to breeding kittiwakes and their fish prey in UK waters, which could be used as a basis for informing future research on kittiwake prey interactions (Ruffino *et al*. 2023). This preliminary stocktake exercise was inspired by the recommendations made by the work conducted through the Offshore Wind Strategic Research and Monitoring Forum (OWSMRF), which identified research avenues for closing key knowledge gaps on kittiwake population dynamics and drivers of change (Ruffino *et al*. 2020).

Ruffino *et al*. (2023) presents a review of kittiwake breeding season diet and foraging range studies in the UK, current and possible future fish prey population status and distributions, as well as relevant recent research in the field. This assessment, alongside the OWSMRF review of kittiwake population dynamics and drivers of population change (Ruffino *et al*. 2020), revealed the complexity of factors influencing the nature and strength of interactions between seabird predators and their fish prey, given both current and future environmental conditions. Consultations with stakeholders highlighted several UK working groups and initiatives currently aiming to address some of these questions. Several recently funded research projects are tackling some of these knowledge gaps and are expected to deliver new evidence in the next two to four years (e.g. Ecological Consequences of Offshore Wind programme, Offshore Wind Evidence and Change programme). In parallel, UK and Scottish governments recently launched public consultations on spatial management measures for industrial sandeel fisheries in the UK waters of the North Sea, with potential implications on different components of the marine ecosystem, including seabird predators (as sandeels form a key part of the diet of breeding seabirds in the UK, including kittiwake).

Given the rapid pace at which the field of offshore wind and ecological compensation is moving in the UK, future research on kittiwake and fish prey relationships will need to be conceived in close consultation with academics and other experts. A one-day face-to-face workshop was organised in Edinburgh on 4 October 2023, to inform the scope of future research needs. The event brought together research project leads, government bodies and NGOs in order to provide updates on on-going projects and collectively identify future research needs of direct relevance to Hornsea Project Three and other future offshore wind projects in the southern North Sea, whilst ensuring the research is complementary to other existing research projects and initiatives, adds value, and is transferrable to other North Sea regions and seabird species with similar ecology and behaviour. In preparation of the workshop, a small group of experts in seabird and fish ecology and behaviour, fisheries science, and predator-prey interactions, were invited to share their thoughts and relevant knowledge in an online call on 28 August 2023. This report presents information gathered at both the workshop and pre-workshop meeting. Organisations contributing to the discussions included: Biomathematics and Statistics Scotland (BioSS), the British Trust for Ornithology (BTO), Centre of Environment Fisheries and Aquaculture Science (CEFAS), Department for Environment, Food, and Rural Affairs (DEFRA), Heriott-Watt University, MacArthur Green, Marine Directorate, NatureScot, Royal Society for the Protection of Birds (RSPB), UK Centre of Ecology and Hydrology (UKCEH), University of Aberdeen, University of St Andrews, with JNCC staff running the workshop. Some experts (Natural England) were unable to attend the workshop but subsequently provided input.

2 Context

Fish prey abundance is an important driver of the population dynamics of many seabird species, including the black-legged kittiwake. During the breeding season, kittiwakes mainly forage on small schooling fish at the sea surface, including sandeels and clupeids (e.g. sprat and young herring), whose recruitment and stock biomass in the North Sea are affected by both commercial fisheries and changes in environmental conditions (Montero-Serra *et al*. 2015, Lindegren *et al*. 2018; Régnier *et al*. 2019). Previous studies have shown a positive relationship between sandeel abundance and some components of kittiwake demography (e.g. productivity, adult survival); however effect sizes are not necessarily consistent across colonies, marine regions and years (Oro & Furness 2002; Daunt *et al*. 2008; Searle *et al*. 2023), suggesting that other factors such as availability of both main and alternative prey to surface-feeding kittiwakes (e.g. Wanless *et al.* 2018; Harris *et al*. 2022), timing of availability (Régnier *et al.* 2019; Régnier *et al*. 2024), as well as quality of prey (energetic value, see e.g. Wanless *et al.* 2018), may play a key role in modulating the effects of varying prey densities on kittiwake populations.

Better understanding of how resilient kittiwake populations are to spatial and temporal changes in the availability, abundance and quality of fish prey will help predict with more confidence how kittiwake populations may respond to changes in fisheries pressure, alongside climate change, and hence inform the design and monitoring of prey availability measures to improve the viability of kittiwake populations and other seabird species with similar ecology. This will also provide some insights as to why compensatory measures, such as artificial nesting structures, may or may not be successful at a particular location or given year, with implications for adaptive management. Addressing these questions has wider benefits, including informing the management of protected sites (SPAs), the development of seabird conservation strategies, as well as providing important ecological context to inform policy decisions.

3 Workshop aim and objectives

The overall aim of the workshop was to identify key evidence gaps and feasible research approaches that would lead to reductions in uncertainty around the mechanisms and processes underpinning kittiwake and fish prey interactions in UK waters, and which would be applicable to the southern region of the North Sea.

The workshop had three objectives:

- Share expertise and knowledge on kittiwake and prey fish species ecology and behaviour, fisheries science and predator-prey interactions;
- Provide updates on relevant on-going research projects;
- Collectively identify research ideas to improve understanding of two main Research Themes:
    - Theme One: drivers and processes governing the availability, abundance and quality of fish prey to kittiwakes, and how these may vary across scales;
    - Theme Two: demographic consequences of spatio-temporal changes in fish prey populations on kittiwakes, and underpinning mechanisms and processes.

As part of the updates on on-going research, the following presentations were provided:

- Overview of sandeel-related studies in Scottish Government (Phil Boulcott & Thomas Régnier, Marine Directorate);
- Collecting data on kittiwake prey (Paul Fernandes, Heriott-Watt University)
- UKCEH monitoring and research on the Isle of May and beyond (Francis Daunt, UKCEH);
- Linking seabird movements with available prey (PrePARED) and linking seabird demography to available prey and understanding the shifting baseline (ECOWINGS) (Kate Searle, UKCEH);
- PELAgIO: the oceanographic processes that predict fish availability and how offshore wind farms may alter foraging opportunities for marine top predators (Beth Scott, University of Aberdeen); and
- PREDICT: predicting seasonal movements of marine top predators using pelagic fish migration routes as prey availability in the North Sea (Georgina Hunt, University of Aberdeen).

Two breakout discussion sessions were held. Workshop attendees were split in two groups of mixed expertise and each breakout focused discussions on Research Themes One and Two, sequentially, as described above. An open discussion was then facilitated to identify areas for future research in the southern region of the North Sea and define an approach to prioritising.

4 Evidence needs

4.1 Drivers and processes governing the availability, abundance and quality of fish prey to kittiwakes, and how these may vary across scales

4.1.1 Defining fish prey availability to surface-feeding seabirds

It became clear early in discussions that several parameters needed to be considered when assessing the availability of prey species to surface-feeding marine predators; these include fish distribution (presence/absence), abundance (biomass available) and species/age/length composition (energetic value per individual fish), all of these are important to understand in both space and time. Species distribution models have been developed to predict the occurrence and densities of overwintering sandeels in the North Sea based on correlations with seabed habitat variables (Langton *et al*. 2021). However, the distribution of prey in the seabed may not directly translate into availability of prey at the sea surface. For surface feeding seabirds such as kittiwakes, fish prey biomass is only available when it becomes accessible at or near the surface. Fish migrate daily through the water column to track their prey and their distribution within the water column is also affected by predation risk (either by other fish species or marine predators). Importantly, another aspect to consider is time, as both biotic and oceanographic processes can bring variation in both prey accessibility and density. Therefore, a key question is what makes fish prey available, or unavailable, to foraging kittiwakes at a particular point in space and time?

4.1.2 Timing of prey availability

It was acknowledged that availability of prey to surface feeding seabirds is likely to vary at multiple temporal resolutions (e.g. daily, seasonally, and annually). In the North Sea, sandeels overwinter in the sand, with their winter seabed distribution and abundance in the North Sea predicted by Langton *et al*. (2021). The overwintering period is interrupted in December-February, when sandeels aged 1 year or older (1+ group) spawn their demersal eggs. They then emerge from the sand and remain active in the water column in spring and summer to feed. Over the early summer/early autumn period, age 1+ sandeels move back to their sandy seabed sediment, where they become unavailable to surface-feeding seabird predators. Their planktonic larvae hatch between February and April (Wright & Bailey 1996; Régnier *et al.* 2017) and are transported by the currents for up to three months before metamorphosis, marked by settlement on a sandbank (Wright & Bailey 1996; Proctor *et al.* 1998; Wright *et al*. 2019). Breeding adult kittiwakes track the availability of both sandeel age classes: in areas where sandeels represent a main prey to breeding kittiwakes, kittiwakes primarily feed on age 1+ sandeels early in the season (April-May), and then switch to young of the year sandeels (0-group) for both themselves and feeding their chicks when these juvenile sandeels become available (June–July) (Harris & Wanless 1997; Lewis *et al*. 2001).

It was commented that there are differences in the timing of sandeel age class settlement. Burying behaviour is thought to be determined by a trade-off between condition and predation risk. By being better foragers and having better body reserves than 0-group sandeels, 1+group sandeels are normally first to settle in the sand.

It was also pointed out that timing of availability of the different sandeel age classes at the sea surface can also vary between years. A recent analysis of four decades of diet data in common guillemots on the Isle of May suggests a progressive advancement of the onset of burying behaviour in older sandeels, leading guillemots to shift to alternative sprat prey earlier in the season (Harris *et al*. 2022). Changing environmental conditions, such as rising sea surface temperatures, can also affect the phenology of both sandeels and their copepod prey in a complex manner (Régnier *et al*. 2019), creating potential temporal mismatches between sandeel prey availability and marine top predator needs (Lewis *et al*. 2001; Harris *et al.* 2022; Régnier *et al*. 2024).

The importance to consider daily variation in fish prey availability was also brought forward. The work done in both the IMPRESS project (Interactions between the Marine Environment, Predators and prey: implications for Sustainable Sandeel fisheries; Scott *et al.* 2010; Cox *et al.* 2012; Embling *et al*. 2012), and CMarHab (Embling *et al.* 2013; Scott *et al.* 2013; Sharples *et al.* 2013) showed that the timing of daily tides (and presence of internal waves moving the thermocline up tens of meters to the surface at maximum speeds of the tide in areas with strong topographic features) was a mechanism that predictably makes fish more available to foraging surface seabirds, in particular sandeels and kittiwakes (Cox *et al.* 2012; Embling *et al*. 2012).

A key query among experts related to the influence of seasonality on the timing of availability of different sandeel age classes to sea surface foraging birds. Better understanding the mechanisms dictating sandeel emergence and burying behaviours was deemed critical. Similarly, the ecology of sprat and herring needs to be better understood, especially in the context of environmental change. What makes sprat and herring available to sea surface foraging seabirds, and what is the effect of seasonality? The Isle of May data indicate that clupeids are becoming more abundant in the diet of seabirds late in the breeding season, but it still remains unclear what factors explain these temporal shifts in diet. For example, are clupeids not available early in the breeding season, or are sandeels becoming less available as the season progresses?

4.1.3 Monitoring needs: resolutions, scales and gaps

A critical aspect to all conversations related to seasonal prey availability and its implications for monitoring; for example, how can we capture fine scale temporal variation in the availability of fish prey species, and age classes, near the sea surface? Coastal monitoring undertaken off Stonehaven Bay, in eastern Scotland, by the Marine Directorate provides long-term time series of ichthyoplankton (including sandeel larvae). This provides key information on sandeel and possibly clupeid hatching dates, as well as zooplankton temporal availability and seasonal temperature variations, and can be used to predict sandeel recruitment (i.e. age 0 sandeel abundance) and growth, which are informative of the period of age 0 sandeel availability to seabirds (Régnier *et al*. 2024). Although it has been shown that this information is applicable to the Firth of Forth region, further work and sampling would be needed to assess transferability to other regions. However, no proxy currently exists for predicting when 1+group sandeels may become available near the sea surface and then bury and become unavailable. ICES scientific fish surveys are a rich source of data for many commercial fish species but tend to focus on snap-shot abundance indices, rather than fine-scale temporal variation. There was agreement among experts that continuous monitoring of sandeel (and other main fish prey) behaviour was needed, which could be achieved by making use of the types of autonomous monitoring platforms and surface/underwater vehicles that are being developed and deployed as part of several on-going research projects in north-eastern Scottish waters, such as ECOWINGS, PELAgIO and PrePARED. If deployed over several months, these platforms can provide a wealth of concurrent information on different age classes of fish, plankton, and oceanographic parameters, to capture day/night and seasonal patterns (e.g. Isaksson *et al.* 2023).

Given the surface-feeding nature of kittiwakes, experts emphasised the need for fish monitoring that captures sea surface aggregations. Existing commercial and scientific fish monitoring techniques (e.g. downward facing acoustic surveys, dredging) study fish populations within the water column (ca. below 3 meters from the sea surface, below the effects of ship movements) and it is unknown whether this information can be used as a proxy of what is happening at the sea surface. This could be tested by combining different monitoring techniques that have either upward or downward facing acoustic instruments, such as mobile vehicles that can capture information from the ca. top 30 meters up to the sea surface or uncrewed surface vehicles that use downward facing echosounder to detect fish density through the water column, as deployed by project ECOWINGS. Moreover, as being used in project PELAgIO, outward facing autonomous underwater platforms placed on the seafloor for long periods of time can capture information throughout the entire water column, including the sea surface (Williamson *et al*. 2021). Furthermore, digital aerial surveys can simultaneously record seabird occurrence and numbers over vast marine areas, allowing seabird foraging behaviour and species interactions to be inferred at the scale at which predator-prey interactions occur. These aerial surveys may also be able to detect and quantify aerial extent of fish schools that are close enough to the surface to be viewed, depending on the weather and visibility (clarity) of the water. Early attempts to detect herring schools using multispectral imaging (Borstad *et al.* 1992) and other fish species using LIDAR (Light Detection and Ranging, Churnside *et al.* 2003) were noted to be quite successful. However, little has been done to develop such techniques in recent years: this may be because the platforms required to deploy them (planes) were expensive to deploy, detection was limited to surface waters, and there were uncertainties in quantification.

Altogether, these novel monitoring techniques were thought to vastly change the way marine ecosystems are monitored, by reducing some of the biases introduced by traditional fish surveys. For example, if deployed strategically, autonomous monitoring platforms could improve understanding of the distribution, abundance, and behaviour of less studied small fish length classes, which are preyed upon by kittiwakes but not typically targeted by offshore fisheries surveys. Further thinking is required as to how to robustly test the use of novel marine ecosystem monitoring instruments in relevant habitats to capture both spatial and temporal variation in biotic and oceanographic processes. Future efforts could for example seek to detect temporal (predictable) patterns of fish prey availability by deploying longer-term monitoring platforms and compare marine habitats with contrasting characteristics (e.g. levels of stratification, maximum tidal speeds, production of internal waves).

It was also highlighted that there seemed to be a mismatch between where most fish surveys are occurring and where some kittiwake fish prey are distributed. Kittiwakes forage mostly closer to shore (typically within 50 km from their breeding sites). Clupeids (sprat and young herring) can form a large part of the breeding season diet in kittiwake in some colonies and years. In the North Sea, sprat and young herring are distributed in shallow waters, including coastal UK waters and estuarine habitats, where populations are known to fluctuate seasonally. These inshore stocks are however not typically surveyed, which limits the ability to characterise their distribution and status, and evaluate effects of seasonality on, for example, fish lengths, growth rates, and consequent impacts on seabird populations that may rely on these local fish stocks during the breeding season. A key monitoring need identified in the discussions was to establish regular inshore fish surveys to capture seasonal variation in fish abundance across age classes. Further consideration of logistical challenges (e.g. accessing shallow waters), frequency of monitoring (weekly during summer or monthly throughout the year), and associated costs, would be required.

Ultimately, when collating empirical data in the marine environment, obtaining fine scale resolution data over large spatial scales was perceived as a major challenge, and therefore some considerations were given to the use of innovative modelling techniques that would allow the integration of different sources of information from existing datasets (e.g. industry data and scientific surveys) to achieve high resolution at relevant spatial scales, leading to enhanced predicted fish distribution maps.

4.1.4 Abundance versus availability

There was discussion around how to improve understanding of the influence of fish prey abundance on kittiwake demographics, and how pressures such as commercial fisheries and climate change are driving seasonal variation in prey abundance. In the North Sea, abundance and biomass of forage fish can markedly vary between regions and years, with have led to drastic consequences on the breeding success of UK breeding kittiwakes (as observed with sandeels in Shetland e.g. Poloczanska *et al.* 2004). Similarly, recent research from the ECOWINGS group led by UKCEH showed depressed kittiwake productivity at eastern Scottish colonies during the operation of a commercial sandeel fishery, and a negative association between sandeel fishing effort on kittiwake breeding success (Searle *et al.* 2013).

It was pointed out that for sandeels, high abundance may not always translate into high availability to foraging kittiwakes. Recent work from the Marine Directorate in Scotland (Régnier *et al*. 2024) suggests that during years of good growth and high recruitment, sandeels tend to disappear near the seabed early in the year, as dictated by a trade-off between condition and predation risk. This could then lead to a mismatch in timing of availability and the requirements of kittiwake predators. Further evidence from the same research group (Régnier *et al*. 2024) indicates that both sandeel abundance and the timing of sandeel availability are key determinants of kittiwake productivity on the Isle of May, with fledging success being at its highest when sandeel are abundant and there is a good temporal match between their availability and the chick-rearing period. It was therefore emphasised that both prey abundance and timing of availability should be considered, while also recognising that colonies may respond to fish prey availability and abundance differently. For example, tracking data from Flamborough and Filey Coast SPA seem to indicate that breeding kittiwakes rely on frontal systems to get their food, raising questions around how fronts are influencing the accessibility of fish biomass in the water column to sea surface predators, how that may differ between marine regions and colonies, and how any future changes in frontal dynamics due to e.g. climate change might affect prey availability. This is being investigated by the PREDICT project at the scale of the North Sea.

4.1.5 Drivers of fish population change

A number for potential important drivers of fish population change and processes were discussed, including hydrographic features, climate change, biotic interactions, and offshore infrastructures. The impact of commercial fisheries on forage fish populations were not considered in great detail as other comprehensive reviews of this topic area are already available (e.g. as part of the consultation reports to prohibit sandeel fishing in UK waters of the North Sea and Scottish waters).

4.1.5.1 Hydrographic features

Data on both fish distribution and hydrodynamic processes were identified as critical to understand why fish are where they are found in surveys. Frontal metrics (e.g. frontal gradient density, persistence, distance) can be used as proxies of the distribution of fish and their predators, and adult herrings for example have been found to associate with some frontal regions such as the Norwegian Sea (e.g. Eliasen *et al.* 2021). It was noted however that different patterns may be observed across species, seasons, and regions. The mechanisms underlying physical processes and pelagic fish dynamics are poorly known and have rarely been examined for pelagic fish (particularly adults).

While fronts generally create predictable foraging areas for fish during the summer, they are not permanent features. Storminess for example can disrupt front dynamics and break up the predictability of the location of plankton (and therefore fish) availability at the sea surface.

It was felt important to refine our understanding of the use of fronts by fish (what species, age classe, when and how), with the caveat that the data may not necessarily be available at the required resolutions and scales. Only some data products may be directly compared with the fine spatial scale of frontal system data (ca. 1.5 km); for example, HERAS fisheries acoustic data are available at a finer spatial resolution than ICES trawl survey datasets. Trawl samples are typically between 15 and 30 km apart, whereas the reported sampling units from acoustic surveys are of the order of 5 km, although the raw data is at a much finer resolution of several metres. It was also noted that frontal data cannot always be used at their finest temporal resolution, as some smoothing over multiple days occurs when preparing satellite data products, and other aspects, such as cloud cover, may limit the use of satellite data. The PREDICT project is developing Bayesian statistical tools for compiling pelagic fish datasets (fisheries independent and dependant) with fine-scale satellite data (i.e. frontal persistence and frontal gradients from NEODAAS products), and using these to assess spatio-temporal variability in fish prey availability to top predators in the North Sea.

4.1.5.2 Climate change

An apparent lack of information within the scientific community around how climate change may be impacting sea temperatures around the UK was noted. Evidence is building for the North Atlantic current slowing down, or potentially switching off (Caesar *et al*. 2021). Some models predict cooling, not warming, events in the North Sea, although the southern part of the North Sea may remain warmer. The Labrador region, where most UK breeding kittiwakes overwinter, is also predicted to become cooler. With climate change, many fish distributions are moving to either go towards the poles, or go deeper, noting however some potential variability between species and age classes (Pinsky *et al*. 2018; Baudron *et al*. 2020).

The potential impacts of climate change on North Sea fish populations have not been discussed in great length as part of this present piece of work, as a detailed review was presented in its sister report (Ruffino *et al*. 2023). In summary, current evidence suggests that potential impacts of climate change on populations of sandeels, sprat and herring would mainly manifest through changes in abundance, body size, behaviour, physiology, and trophic interactions, rather than changes in distribution. These changes have been related to, for example, both direct and indirect effects of warming of sea surface temperatures, and changes in salinity, on oceanographic processes. As there seems to remain substantial uncertainty in the predicted strength and direction of climate change impacts on North Sea fish populations, it was noted that future research should focus on validating model predictions with empirical data, such as those collected by novel platforms allowing the continuous and autonomous monitoring of marine ecosystems.

4.1.5.3 Biotic interactions

Biotic interactions, particularly the ecological interactions (e.g. predation, competition) between forage fish and other larger fish species, were identified as potentially influencing the distribution and abundance of sandeel, sprat and herring populations in the North Sea. It was believed that climate warming in the North Sea has changed the nature and strength of competitive interactions between fish species through, for example, shifting fish distributions. Some other factors include the closure of fishing activities in Marine Protected Areas, as well as scour protection around offshore wind turbines, both typically benefiting larger fish species preying on or competing with smaller fish such as sandeels (Gimpel *et al*. 2023). An ecosystem-based approach, as adopted through the end-to-end Ecopath with Ecosim modelling framework, was deemed particularly useful for testing biotic interaction hypotheses. It was recognised however that the resolution of the Ecopath with Ecosim model being developed by Natural England to advise DEFRA on fisheries management measures is currently too coarse for investigating fine scale ecological processes. There is uncertainty around the scale at which important biotic processes occur (e.g. offshore windfarm vs. sandbank vs. North Sea regions) and it was emphasised that fish survey data (e.g. ICES) may not have been used at their maximal potential. On the other hand, the development of joint species distribution models (for both seabirds and their prey) as part of the PrePARED project may allow testing of hypotheses on biotic interactions.

A discussion was had on the potential role of fish interactions in influencing the accessibility of fish prey species to foraging kittiwakes at the sea surface. For example, predation or competition may alter fish prey behaviour and consequently availability. Workshop participants queried whether there was a need to focus on multiple fish species when assessing prey availability to kittiwakes, and if so, what species should be considered.

It was stated that more research was needed on the importance of seabird interactions in either reducing or facilitating the availability of fish prey biomass to foraging kittiwakes, in the context of sharp changes in some seabird species in recent years or decades (e.g. northern gannet, common guillemot). Of particular interest is the role of competition for prey with other seabird species, benefits of synergetic feeding and density-dependence while foraging at sea.

4.1.5.4 Offshore infrastructures

Changes in several hydrodynamic features, such as sedimentation, turbulence and stratification, have been linked to the presence of offshore wind farm structures, and can cascade up to fish prey and their seabird predators. This is particularly relevant to the North Sea given potential cumulative effects of the large-scale expansion of offshore infrastructures. It was noted that although most research so far has focused on the impacts of single windfarms, it is unknown how cumulative effects of multiple structures, and associated activities such as piling, add up across a large scale. How are fish prey populations responding to these large-scale changes? Projects ECOWind-ACCELERATE, PELAgIO and PrePARED are investigating these questions. It was noted that having access to, and making use of, baseline data from before offshore windfarm construction would allow more robust evaluations of offshore wind impacts on marine ecosystems.

4.2 Demographic consequences of spatio-temporal changes in prey availability, abundance and quality on kittiwake populations, and underpinning mechanisms and processes

4.2.1 Demographic rates

When investigating the response of kittiwake populations to changes in their fish prey populations, studies have typically focused on kittiwake productivity, as this demographic parameter is often easier to monitor at colonies. However, in long-lived seabird species, population size is mainly driven by adult survival rates (i.e. in adverse conditions), adult birds would safeguard their own condition rather than offspring production. There was, therefore, a consensus among experts to focus future research on demographic rates that are influential but currently poorly understood, such as survival rates, and the main factors influencing spatio-temporal variation in these rates.

In kittiwakes, most adult mortality is believed to occur when they are at sea during the non-breeding season, potentially towards the end of the winter period. Factors influencing overwinter condition can be numerous and complex. Kittiwakes may experience different environmental and anthropogenic pressures throughout their migratory journey. Acquiring prey availability data during the non-breeding season, along their migratory corridors and stop-overs in the North Sea, as well as at their overwinter region in the North-West Atlantic, was seen as a useful first step, focusing on areas where such data may already be routinely collected, for example as part of the monitoring of Marine Protected Areas along the east coast of Canada. There may also be mortality data in the Labrador Sea region, from ring recoveries or stomach samples, which could be used as additional sources of information. It was also noted that the effect of weather conditions during the non-breeding season on the energy budgets of foraging seabirds experiencing different prey conditions should be considered, as recent tagging work showed that seabirds, including kittiwakes, can be highly responsive to wind conditions, with observed impact on at-sea distribution (e.g. project SeaTRACK; see also project SHEAR on Manx shearwaters). As these data become available, a logical next step would then be to explore temporal variation in adult survival rates (as obtained from mark-recapture studies at colonies) and disentangle the potential effects of various environmental conditions experienced by kittiwakes during the non-breeding season.

Determining the carry-over effect of breeding season diet on the winter condition of adult kittiwake was perceived as a priority. On-going research by UKCEH is seeking to improve understanding of the linkages between apparent adult survival rates in kittiwakes and sandeel abundance in the context of changes in fisheries pressure off the northeast coast of Scotland. To investigate this question further, a suggestion was made to undertake a comparative analysis of multiple UK breeding kittiwake colonies influenced by different sandeel stocks, for instance SE1, SA4 and SA7 stocks, focusing on colonies for which there is good quality data on adult survival rates. As kittiwakes from most UK breeding colonies overwinter in the Labrador region, they will likely experience similar environmental conditions and pressures at their overwintering area, therefore any overwintering effect on adult survival for a given year is expected to be homogeneous across breeding colonies. This would allow teasing apart of the relative importance of breeding season prey condition on kittiwake adult survival rates, while also accounting for other potential sources of adult mortality at colonies (e.g. HPAI if data is available). Making use of multiple years of data, from e.g. the Isle of May, would reveal temporal patterns in adult survival rates, and potentially hint at associated drivers. It was noted that studying carry-over effects from one breeding season to the next was challenging, as suitable biologging techniques and attachment methods are not yet available for kittiwakes to allow both multi-season and fine-scale tracking of at-sea movements. This is a priority for future work.

The need to acquire better estimates of kittiwake survival rates across age classes, but particularly for juveniles and immatures, became apparent. There is a lack of knowledge of how these poorly studied age classes may be affected by varying prey conditions in the North Sea. Moreover, it was noted that although there is currently much more data available on kittiwake productivity than other demographic parameters, colony monitoring effort through the Seabird Monitoring Programme in the UK has been decreasing over the past five years. If measures of breeding success are a key part of any work programmes in the future, reinstating breeding success monitoring initiatives at those key sites where monitoring effort has recently declined, is required.

4.2.2 Diet

Kittiwake breeding season diet is typically studied by analysing prey items regurgitated by chicks or adults with chicks when handling birds at colonies. Based on observations on other seabird species (e.g. European shag on the Isle of May; Wanless *et al.* 1993), it is often assumed that the food regurgitated by kittiwake adults is predominantly destinated to the chicks; therefore, diet samples collected during the chick-rearing period are considered to represent chick diet. It is unknow however whether adult kittiwakes would feed on similar prey items for both themselves and their chicks. This assumption needs testing so that we can gain confidence in adult prey composition when investigating prey impacts on adult overwintering condition and survival.

Caveats were raised on the level of confidence that conventional diet analyses could allow for identifying some prey items to species level. It is particularly true for clupeids, as sprats and herrings are difficult to differentiate in kittiwake regurgitates. Sandeels, on the other hand, are routinely identified from prey remains. Identification of prey taxa from diet samples can be done by counting the number of vertebrae, which is resource intensive and relies on the suitability of captured prey material. Breeding season diet data has been collected from seabirds with similar ecology on the Isle of May. For species that carry bill loads of fish to their chicks, such as puffin, direct observations of prey species can be made at a distance or by collecting entire fish when dropped following catching of adults at colonies. Evidence from the Isle of May suggests that there is sufficient overlap between the diet of puffins and kittiwakes to assume that chicks are fed with similar prey during the breeding season. Therefore, based on puffin dietary information, the seasonal diet shift observed in breeding kittiwakes from sandeels to clupeids later in the season seem to indicate that sprat, rather than herring, would likely be the dominant clupeid prey species. Other prey species include young gadoids, and occasionally pipefish, but these form a low proportion in the summer diet of kittiwakes at UK colonies.

It was agreed that spatial variation in breeding season diet needs to be carefully considered. The relative contribution of sandeels in the diet of breeding kittiwakes tends to decrease towards the southern part of the North Sea (compared with further north in North Sea), although the availability of regurgitate samples from colonies along the eastern English coast is very limited. Diet samples have been collected at the Flamborough and Filey Coast SPA and Lowestoft colonies but only represent a very short time window during the breeding season. Marked differences in diet have also been observed at a very local scale, showing a much higher relative contribution of clupeids in kittiwake diet at colonies (estuarine vs. marine areas) separated by ca. 30 km in south-east Scotland. Due to the limitations of conventional diet analyses for segregating between different clupeid prey species in kittiwake regurgitates, a question was raised about the quality (e.g. taxonomic resolution) of diet data available at some UK colonies, where corroborative sources of evidence (e.g. diet from species of similar ecology) may not be available.

Temporal gaps in diet studies currently limits our understanding of both seasonal and annual variation in breeding season diet. A key limitation of conventional techniques for collecting dietary data at kittiwake colonies is the potential lack of representativeness of monitoring conducted over a restricted period of the breeding season (usually a few days during the chick rearing period); sampling diet over a short time window can miss the timing of dietary shifts when they occur (Harris *et al*. 2022). Moreover, analyses of chick regurgitate samples are constrained by the resolution of diet data that this monitoring technique can achieve (regurgitates only provide a brief snapshot in time of what a chick has eaten over the past few hours) and can be biased by the incomplete picture of regurgitated prey items following digestion.

While it was thought that there was relatively good information on the diet of breeding kittiwakes for a handful of colonies, much less is known about their diet in the non-breeding season. Sources of winter diet information are either from recovery of dead birds, which may be biased, or shooting birds, which is done very infrequently. There is some anecdotal evidence of what kittiwakes might feed on during winter (e.g. krill, discards), however not much is known on the relative proportions of different types of prey in the diet. It was suggested that identifying sources of diet sample data in the Northern Atlantic region, for example from communities who may catch or shoot kittiwakes, may provide some useful information, although bearing in mind the potential challenge of relating winter diet data collected opportunistically on a small sample of birds to specific kittiwake colonies in the UK.

Alternative methods for studying kittiwake diet were proposed to increase the resolution of diet data, fill key spatial and temporal gaps, and investigate both adult and chick diet composition. This included metabarcoding techniques; samples could be collected from faeces at colonies allowing the identification of prey items to lowest taxonomic levels, including rare prey (e.g. pout, pipe fish) or prey that are not readily identifiable in digested regurgitate samples (e.g. krill). This technique would also allow increasing the temporal breadth of data collection, as samples could be collected repeatedly throughout the breeding season.

Some thoughts were also given to indirect assessments of diet through use of biochemical methods. For example, the analyses of stable isotopes and fatty acids in kittiwake plasma would provide the opportunity to investigate recent diets of both chicks and adults during the breeding season, by taking blood samples at capture. One key limitation with these methods is their inability to assess the relative contribution of different prey types in predator diet when prey have similar isotopic or fatty acid profiles. In most instances, these techniques are most useful for monitoring broad spatial and temporal changes in the diet composition of predators. They may also provide the opportunity to identify prey switching in breeding kittiwakes if repeated samples are taken over the course of the breeding season.

Suggested routes to study kittiwake winter diet included the analysis of stable isotope signatures from moulted feathers. The carbon and nitrogen isotopic composition of a regrown feather provides a chemical record of the marine area from which resources used in feather growth are derived. Moulting of primary feathers occurs sequentially in kittiwakes, starting with the smaller, inner primaries late spring, followed by the larger, outer primaries over autumn/early winter (Coulson 2011). While the inner primaries would provide material for assessing breeding season diet, sampling outer primaries may allow investigating the diet of kittiwakes during the early stages of the non-breeding season (as primary moult is assumed to be completed by the time they reach their overwintering areas; Coulson 2011), although further thinking would need to be developed to assess the feasibility of such project.

Importantly, it was noted that a combined approach to kittiwake diet analysis would reduce some of the limitations outlined above, allow for ground-truthing of findings, and therefore refine understanding of kittiwake diet at different stages of its life cycle.

4.2.3 Prey quality

Beyond a certain level of availability and abundance of prey, quality of prey comes into play when seabirds chose what to feed on and where. The question was raised about whether all fish prey species would have similar energetic content. Moreover, long-term studies on the Isle of May have shown a declining trend in sandeel size brought by adult kittiwakes to their chicks (Wanless *et al*. 2018), assumed to reflect changes in prey quality in the North Sea.

As part of the PrePARED research project, the University of St Andrews is investigating variation in fish calorific value between fish species, age, and length classes, using bomb calorimetry. It was also noted that there is likely to be natural seasonal variation in energetic quality within fish species, related to the energetic requirements of their main physiological phases (e.g. spawning season), which can therefore introduce noise in the data when linking fish quality measurements to seabird diet and/or demographic data.

It was also mentioned that typically, the energy density of sprat and herring is higher than that of sandeels (Pedersen *et al.* 2001). However, as species of sandeels are often grouped together, there is little information of the difference in energy density across the different species of sandeels.

So far, the focus has been on variation in energetic quality in relation to the oil content of the fish, and it was questioned whether protein content should also be looked at. It was noted that although protein content is relatively high in fish and unlikely to be limiting to seabirds, there may be some unknown constraints, for example, during seabird moulting with the need to draw on high protein sources to produce new feathers.

4.2.4 Prey selection and modelling of predator-prey interactions

Kittiwakes can feed on different prey species during the breeding season. Identifying the mechanisms driving variation in breeding season diet is essential to improve understanding of the demographic consequences of prey switching and assess the resilience of kittiwake populations to changes in the composition and quality of their fish prey populations. At some colonies, such as the Isle of May, there seems to be a natural shift in prey occurrence in diet towards clupeids as the season progresses; however, it remains unclear what factors dictate seasonal prey switching. It is unknown whether kittiwakes are making active choices (e.g. selecting a sandeel as opposed to a sprat or a pipe fish if all are similarly available) or are responding to prey availability (therefore lack of choice).

There was discussion on the relative influence of prey abundance on foraging decisions. For example, if preferred prey is available to foraging breeding kittiwakes but in low density, would they select an alternative prey species occurring in higher density (and therefore potentially easier to find and catch) if available? Is there a correlation between time spent foraging and prey density? Determining the prey density thresholds relevant to foraging decisions, and how prey density may affect predator searching efficiencies, prey switching behaviour and capture rates, will ultimately help parameterise predator (kittiwake) – prey (fish) models, and inform the shape of predator functional responses in relation to changes in availability and abundance of different prey types. Modelling predator-prey interactions can be data hungry, particularly in the context of generalist predators foraging on a range of prey types with varying availability, abundance, and quality. Parameterising these models with good quality empirical data is challenging due to the difficulty of observing kittiwake foraging behaviour at sea. While fine scale GPS tracking of kittiwake movements may allow inference of different behaviour states at sea (e.g. prey searching time), determining capture success rates would difficult since 3D movement loggers cannot currently be safely attached to kittiwakes, and bird-born cameras used on larger seabird species (e.g. European shags as part of the ECOWind ACCELERATE project) are not suitable. Efforts may therefore need to be directed to at-sea observations of foraging events, with the caveats that indirect proxies may be needed to infer the colony origin of the birds observed as well as what they are bringing back to their chicks, and that observers may not always be able to tell if a foraging event was successful, especially for smaller prey items.

It was suggested that future modelling of kittiwake and fish prey interactions should build on the recent advancement of food web modelling approaches by Natural England (using the Ecopath with Ecosim modelling framework), with future efforts directed to refine spatial resolution to study localised effects of changing prey availability, as well as developing non-linear functional relationships to enhance understanding of the potential for kittiwake population recovery to respond to changes in fish prey stock status. Promising insights have also been made by the University of St Andrews, modelling multi-species functional responses to describe the relationship between harbour porpoise and the availability of several fish prey species in the southern North Sea, including herring and sprat (Ransjin *et al*. 2021).

Understanding the trade-offs between the energetic costs of acquiring a particular prey type and the resulting energy gain was perceived as critical for understanding kittiwake foraging decisions, or responses to prey availability. While some prey may be less costly to catch, they may bring a low amount of energy. Furthermore, variation in foraging ranges among colonies and years is well documented in UK-breeding kittiwakes. Under the assumption that switching prey incurs a cost to foraging birds (as kittiwakes may need to re-learn or travel further), if the energetic reward of the prey is not high enough, then breeding kittiwakes may fail to meet their chicks' (and own) energetic requirements.

Recognising the challenge of testing prey selection decisions on kittiwakes, some research avenues were suggested involving the concurrent collation of datasets. For example, using long-term tracking datasets for some of the best studied colonies, it would be possible to link foraging trip characteristics to kittiwake diet and start investigating how the relative proportion of different prey types in the diet may vary with foraging locations and distances to colonies. There is some indication that kittiwakes tend to forage further offshore (greater than 50 km) in some years, but it remains unclear whether that is in response to decreases in prey (e.g. sandeels) availability. Future research needs to focus on those areas further offshore where food web dynamics are likely to be different, characterising kittiwake foraging decisions when they need to travel further to access prey (or preferred prey). In a related species, the common guillemot, previous work used energetic models to investigate the fitness consequences of different foraging ranges, prey abundance and calorific content (Langton *et al.* 2014). While the offshore distribution of migrating fish species can be predictable to a certain degree, it was reiterated that being able to accurately determine when fish prey become available to foraging kittiwakes is key to inform prey selection processes. Other potential limitations or constraints to consider when collating concurrent datasets on similar birds or colonies are the disturbance effects of tagging, handling, taking regurgitate samples, which may all impact on foraging behaviour.

5 Summary of knowledge gaps and approach to prioritising research in the southern region of the North Sea

Engagement with experts from multiple disciplines revealed many knowledge gaps needing filling to further refine our understanding of kittiwake-fish prey interactions in the North Sea. These knowledge gaps are (in no order of priority):

- What drives the emergence and settling behaviour of sandeels of different age classes, and what is the effect of seasonality on the timing of prey availability to sea surface feeding predators?
- Are water column fish surveys a good proxy of fish availability at or near surface?
- What is the distribution, abundance and status of clupeid populations or stocks in UK coastal areas of the North Sea?
- What is the distribution, abundance, and behaviour of fish prey from small length classes, typically not targeted by offshore fisheries surveys?
- How accurate are frontal metrics in predicting when and where fish prey become available to surface-feeding top predators? What fisheries datasets are most appropriate to capture dynamic associations with fronts? How will climate change impact frontal persistence and production dynamics in the future?
- What is the influence of biotic interactions (between fish species or between seabird predators) in modulating the availability of fish prey to sea surface foraging kittiwakes?
- What do kittiwake (chicks and adults) feed on during the breeding season, in what proportions, and how does this vary between colonies, marine regions, years, and over the course of the breeding season?
- What do kittiwakes feed on during the non-breeding season (while migrating and overwintering)?
- How important are carry-over effects of breeding season diet on kittiwake overwinter condition and survival?
- How are juvenile and immature kittiwakes affected by varying prey conditions in the North Sea?
- How is the energetic quality of fish prey varying between species, age classes and different times of year?
- What is the relative role of fish prey abundance, availability, and quality in driving prey selection in kittiwakes, and what are the consequences on kittiwake foraging behaviour and energy budgets?

While closing some of these knowledge gaps may be achieved by collating or re-analysing existing datasets, other questions may require new data collection, including the deployment of novel underwater monitoring techniques. The next step is to define what research would need to be prioritised in the southern region of the North Sea, whilst ensuring it is complementary to existing projects and initiatives and adds value. General principles to developing novel research projects were discussed at the end of the workshop and are summarised below.

- Build on past and on-going research projects and existing long-term monitoring initiatives across the North Sea, and capture patterns, trends in data and lessons learned.

- Consider geographic spread and select sites with contrasting fish prey conditions (e.g. different sandeel stocks) or kittiwake population status (e.g. demographic trends) to test hypotheses.
- Undertake an exercise on transferability to identify pieces of information from other locations that are most likely to transfer to the southern part of the North Sea. For example, how much information from the Isle of May would be applicable to other colonies? Consider differences in colony size (density effect) and trends in demographic rates (resilience) between colonies, and how these parameters may affect the nature of the relationship between kittiwakes and their prey (e.g. how different kittiwake populations may respond to changes in their prey populations).
- Determine which aspects need local data and which can be taken from elsewhere. This will help determine what types of new data may need to be collected, or reanalysed in different spatial/temporal scales etc.
- For the types of information that could be transferred from well-studied colonies such as the Isle of May or the Stonehaven coastal monitoring station, build on existing knowledge to refine approach at new monitoring locations (e.g. determine minimum monitoring effort requirements, constraints, and limitations).
- What are the most critical spatial and temporal gaps in the available data? If better understanding of breeding season diet is a priority for future work, efforts should be directed to colonies in eastern English waters, where dietary information is currently lacking. Similarly, collecting GPS tracking data from unstudied locations in this area would fill an important gap, as currently only kittiwakes from FFC SPA have been GPS tracked to study their breeding foraging ranges. Another important gap is the seasonal variation in fish prey distribution in coastal areas.
- Consider the trade-off between investing in techniques that might require some high short-term investment (e.g. DNA barcoding, AUVs, artificial intelligence diet image processing), but would have longer term value added to existing monitoring programmes and longer-term cost savings.
- Consider the prioritisation of long-term monitoring, at both existing and currently un-monitored sites. An example of site where long-term monitoring could be prioritised is the Lowestoft colony, where nests are easily accessible, the site is registered as a Recapture For Adult Survival study with the BTO, however ringing effort is likely to decline in the near future.
- Maximise the collection of concurrent datasets, on both seabirds and their fish prey, including their ecology, behaviour and physiology.
- Seek important datasets, and approach relevant organisations to identify potential constrains with acquiring information (e.g. data ownership and rights - particularly relevant to fish datasets).
- Account for timescales of projects, and their cost-benefit ratio. While modelling of ecological processes can produce outputs quickly, they can be associated with large uncertainty, while the collection of empirical data in the field may help to ground-truth model validations but would be achieved in the longer run.

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