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Towards better understanding black-legged kittiwake and fish prey interactions

An assessment of scientific evidence to inform future research needs in the North Sea

Report to Ørsted

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Please note:
This report has been revised (September 2023) to replace Figure 1 with a corrected version.

Summary

The black-legged kittiwake (*Rissa tridactyla*) is a species of conservation concern that has suffered significant population declines in the UK. Given on-going pressures acting on a number of fish prey species in the North Sea, improving understanding of kittiwake-fish interactions is key to predict how UK kittiwake populations may respond, and be resilient, to spatio-temporal changes in fish availability. This report presents an assessment of kittiwake breeding season diet and foraging range studies in the UK, current and possible future availability of three main fish prey species (sandeels, herring and sprat), as well as relevant recent research in the field. The review of scientific evidence was then used to identify key data and knowledge gaps and draw recommendations for future research that would significantly increase our understanding of kittiwake-fish prey interactions, and the sustainability of these in the future.

The review of diet studies has highlighted gaps in study coverage across UK kittiwake colonies, including the southern North Sea and western British Isles. Temporal gaps are also apparent, with a great proportion of the diet samples collected so far being 15 years old or older. On-going changes in fish prey community composition due to climate change and fisheries pressure mean that the diet datasets available may not be representative of current prey availability to breeding kittiwakes. A key limitation of conventional kittiwake diet analyses is the lack of standardised protocols and quantification of biomass ingested, which has resulted in sparse datasets and a possibly biased picture of the relative importance of different prey species.

Although kittiwakes have been the focus of a large number of GPS tracking studies in the UK, less is known about their foraging distributions during the breeding season in the Irish and Celtic Seas, where environmental conditions differ from the North Sea. The review has also revealed marked differences in foraging distances and distributions across years and sites, as well as between periods of the breeding season and sections of a SPA site. This indicates that repeated tracking studies across spatial and temporal scales is essential to fully capture variability and understand the role of both extrinsic and intrinsic factors in driving at-sea usage.

The current stock status and distributions of main kittiwake fish prey (sandeels, sprat, herring) are relatively well assessed at a regional scale. However, fish datasets in their raw form are not necessarily available at the spatial and temporal resolution that is needed to assess prey availability to adult foraging kittiwakes during the most energetically demanding period of their breeding cycle. Advances in statistical modelling that allow the integration of multiple sources of information will help refine the spatial and temporal dynamics of fish prey distributions.

The present review of evidence seemed to indicate that adult populations of sandeels, herring and sprat in the North Sea may be more likely to respond to increases in temperatures through reduction in body size, recruitment and reproductive investment, changes in trophic interactions and trophic mismatches, than shifting their distribution. These secondary impacts can however affect population abundances, quality of fish prey and availability of prey to surface-feeding predators. Overall, predicting the effects of changes in environmental conditions on fish populations and their predators remains complex and several evidence gaps make full appreciation of the mechanisms and strength of environmental change impacts challenging, especially for sprat populations.

Research is ongoing to tackle some of these knowledge gaps, through for example the development of innovative at-sea monitoring techniques, the combination of multiple sources of evidence to refine predictions of the spatial and temporal dynamics of fish prey

populations, and the coupling of state-of-the art modelling with empirical evidence gathering at the spatial and temporal scales that matter for predator-prey dynamics.

This assessment is intended to provide Ørsted with the scientific evidence needed for identifying future research that would address ecological questions relevant to Hornsea Project Three and their kittiwake compensatory measure plans, whist ensuring the research is complimentary to other existing projects and adds value.

Documentation supporting this report can be found on the report entry:

Annex 1: Supplementary Material Table S1: MERP Diet Studies References

Annex 2: Supplementary Material Table S2: Summary of recently completed/on-going UK research projects relevant to kittiwake-fish prey interactions

Contents

1 Background

The expansion of offshore wind energy has been identified as a key component in meeting UK Government's target of reducing greenhouse gas emissions by 2030 and achieving Net Zero by 2050. However, there are a number of significant concerns about the potential impacts of offshore wind farms (OWF) on the marine environment. Populations of marine birds, in particular, are known to be sensitive to the impacts of collision, displacement and barrier effects from OWF (e.g. Masden *et al.* 2009; Furness *et al.* 2013; Searle *et al.* 2014). Legislation requires that potential impacts on protected bird populations are assessed prior to the consent of OWF development, and any adverse effects are mitigated or compensated.

As marine birds use both the terrestrial (breeding) and marine (foraging) environments, they face a multitude of pressures, often interacting in a complex manner. In this context, understanding the main drivers of population change and their mechanisms of operation will help predict with more confidence the relative impact of OWFs alongside other pressures, and design effective options for managing pressures.

Prey availability is an important driver of the population dynamics of many seabird species. In the UK, small schooling fish make up the bulk of seabird breeding season diet; these species include sandeels, sprat and herring, whose abundance and biomass in the North Sea are affected by both commercial fisheries and warming of sea surface temperature (e.g. Montero-Serra *et al.* 2015; Lindegren *et al*. 2018). Better understanding how spatio-temporal variation in fish prey availability affects seabird populations will help predict with more confidence how these populations may respond to changes in fisheries pressure, in combination with climate change, and hence identify ecological compensatory measures to improve population viability. This will also provide some insights as to why compensatory measures, such as artificial nesting platforms, may or may not be successful at a particular location or given year. Moreover, assessing the ability of seabird populations to switch prey types in relation to availability, as well as its demographic implications, will determine how resilient a population may be to additional mortality (e.g. from offshore wind development), in a context of sandeel stock biomass decline in the North Sea.

Predicting the response of seabird populations to changes in prey availability cannot be addressed solely by looking at the relationship between seabird productivity and some averaged indices of prey abundance or biomass, as these indices do not necessarily reflect the availability of prey in specific areas where seabirds forage, and at different periods of the breeding season, including the most energetically demanding periods. Understanding availability of prey at the spatial and temporal scales at which relevant processes occur is therefore key to assess the current and future status of seabird-prey relationships.

At the time of the last breeding seabird census (Seabird 2000, 1998—2002), the UK was home to over 8 million breeding seabirds (Mitchell *et al.* 2004), which traditionally nest in natural sites such as remote islands, moorland and coastal cliffs. One species, the black-legged kittiwake (*Rissa tridactyla*), hereafter referred to as kittiwake, nests on small ledges on coastal cliffs around the UK. There are estimated to be 205,000 breeding pairs within the UK (JNCC 2019), comprising 5% of the world's breeding population of kittiwakes (CAFF 2020). However, evidence shows that UK colonies have declined by around 60% since 1986, and as a consequence, the black-legged kittiwake has recently been red-listed as a species of conservation concern (Eaton *et al*. 2015).

Kittiwakes are known to be particularly sensitive to impacts from OWFs, particularly through collision with turbines and, to some extent, displacement. When considering the potential mortality caused by the Hornsea Project Three windfarm in the southern North Sea, an adverse effect on integrity could not be ruled out, in-combination, on the kittiwake feature of the Flamborough and Filey Coast SPA. Therefore, a kittiwake compensation plan has been developed to compensate for potential collision impacts on breeding adult kittiwakes, with a requirement to implement and monitor the success of artificial nesting platforms (Ørsted 2020).

The Offshore Wind Strategic Monitoring and Research Forum OWSMRF (https://jncc.gov.uk/our-work/owsmrf/) Pilot Year identified several Research Opportunities that would improve understanding of the main pressures affecting kittiwake population persistence and help predict with more confidence population responses to changes in management of these pressures (Ruffino *et al*. 2020). JNCC was requested by Ørsted to develop some thinking around possible future research that would improve understanding of kittiwake-prey interactions and the resilience of kittiwake populations to changes in fish prey availability. This research was requested to align with the commitments of Ørsted Hornsea Project Three of implementing and monitoring the success of artificial nesting platforms for breeding kittiwakes as part of their compensatory measure package. Moreover, as it was stated in the Development Consent Order issued to the project, the kittiwake implementation and monitoring plan ("KIMP") must include for instance "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". This requirement refers to the Appendix 1 of the response from the Ørsted Hornsea Project Three to the Secretary of State's minded to approve letter dated 1 July 2020 (Ørsted 2020).

This report presents the findings of a desk-based review exercise, which aimed to:

a. review the knowledge base on breeding kittiwake diet and foraging distributions in the UK, and associated diet sampling and tracking efforts;
b. identify forage fish datasets and assess resolution of data, focusing on the North Sea region;
c. review the available evidence on the current and future distributions and status of main fish prey species for kittiwake;
d. review UK research projects relevant to kittiwake-prey interactions; and
e. identify key knowledge gaps and a list of research recommendations to fill gaps.

This assessment, alongside the OWSMRF review of kittiwake population dynamics and drivers of population change (Ruffino *et al*. 2020), provides Ørsted with the evidence needed for identifying future research that would address priority ecological questions for Hornsea Project Three whist ensuring the research is complimentary to other existing projects, adds value, and is transferrable to other North Sea regions and seabird species with similar ecology and behaviour.

2 Kittiwake evidence review

2.1 Kittiwake diet at UK colonies

2.1.1 Spatial and temporal variation in diet

Kittiwakes are surface feeding birds, which typically prey on small schooling fish during the breeding season. In the North Sea, the lesser sandeel (*Ammodytes marinus*), a small pelagic lipid-rich fish, has been identified as one main component of breeding kittiwake diet (Furness & Tasker 2000; Coulson 2011). Variation in breeding season diet composition however exists between colonies, regions and years, reflecting availability of different fish prey species. In southeast Scotland, differences in diet were observed at a local scale, with clupeids (sprat and herring) making up most of the diet in estuarine colonies, presumably feeding inshore in more rocky seabed habitats (Bull *et al*. 2004). Inter-colony variation in diet composition was also observed in the Irish Sea; two years of diet study at two colonies highlighted a range of fish prey species (including clupeids, gadids and sandeels) on Lambay, while kittiwake on Rathlin seemed to be relying almost exclusively on clupeids (Chivers *et al*. 2012). Compared to eastern and northern UK colonies, breeding diet studies from western Scotland and the Celtic/Irish Sea region indicated a weaker reliance on sandeels, which are replaced by clupeids and gadoids (Chivers *et al*. 2012; Lauria *et al*. 2013). A recent comparative analysis of breeding kittiwake diet across 18 UK colonies confirmed some of these patterns (Wilson *et al*. 2021). Preliminary analyses of frequencies of occurrence indicated a higher probability of diet samples containing sandeels at eastern and northern colonies and a decline with latitude, while gadoid spp. presented the opposite trend, and clupeid prevalence did not seem to differ between regions. The study also found a positive but weak relationship between breeding success and the proportion of sandeels in kittiwake diet in both the Greater North Sea and Celtic Sea regions. These results may need to be interpreted with caution however due to the small number of regurgitate samples analysed per colony and year (Linda Wilson, pers. comm.).

Although several studies have found a negative association between sandeel fisheries pressure and kittiwake demographic parameters, the relationship is complex. The temporal window at which breeding season diet is assessed is important as kittiwakes shift from preying on one year or older sandeels (1+ group) early in the breeding season to young of the year sandeels (0+ group) when raising their chicks. While 1+ group sandeels are site faithful, 0+ group sandeels are not so closely associated with sandy habitats (Wright *et al*. 2000) and their distribution may vary between years. Availability of both age groups to breeding kittiwakes and chicks is also likely to be affected by climate warming (Lewis *et al*. 2001; Régnier *et al*. 2019); however, the physical and ecological processes that underpin availability of fish prey may operate differently across marine regions and temporal scales (e.g. Lauria *et al*. 2013; Eerkes-Medrano *et al*. 2017).

On the Isle of May, dietary shifts from sandeels to alternative fish prey species (clupeids and juvenile gadoids) were identified concomitant with temporal changes in fish species composition, which can be associated with both sea surface warming and industrial fisheries pressure (Wanless *et al*. 2018). There was also evidence for a decrease in sandeel prey quality brought in for chicks over the 40-year study period. Such changes in diet composition, with an increasing prevalence of alternative prey with different distributions, availability and energetic profitability, can be costly and result in inter-annual differences in foraging distances and trip durations, with consequences on body condition and breeding success (e.g. Christensen-Dalsgaard *et al*. 2018; Trevail *et al.* 2019).

2.1.2 Diet sampling effort across colonies and years

The Marine Ecosystems Research Programme (MERP) has created a seabird diet database for ten species in the British Isles by compiling information from the published literature (Krystalli *et al.* 2019). For kittiwake, the database brings together diet data from 17 different colonies spanning from 1963 to 2015 (101 location-years; see Table 1). Overall, diet studies are unevenly distributed across the UK, with most colonies being sampled in south-east Scotland, the northern Isles and north-east England (Figure 1). While most of the studied colonies have collected diet samples from two or more years, long-term and contemporary diet studies have only been conducted on Canna Island (28 years) and the Isle of May (31 years). At some locations, no contemporary diet information is available (four colonies have data up to 1989, and 11 colonies have data up to 2004). Number of diet samples collected vary widely among locations and years, which reflects the opportunistic nature of the sampling. All data collected during the breeding season came from analyses of regurgitated food samples when handling either or both adults and chicks, and results were mostly reported as presence/absence data, and rarely biomass. Prey age group has been more commonly reported for sandeels than clupeids or gadoids, while fish prey size information (in length) has rarely been reported.

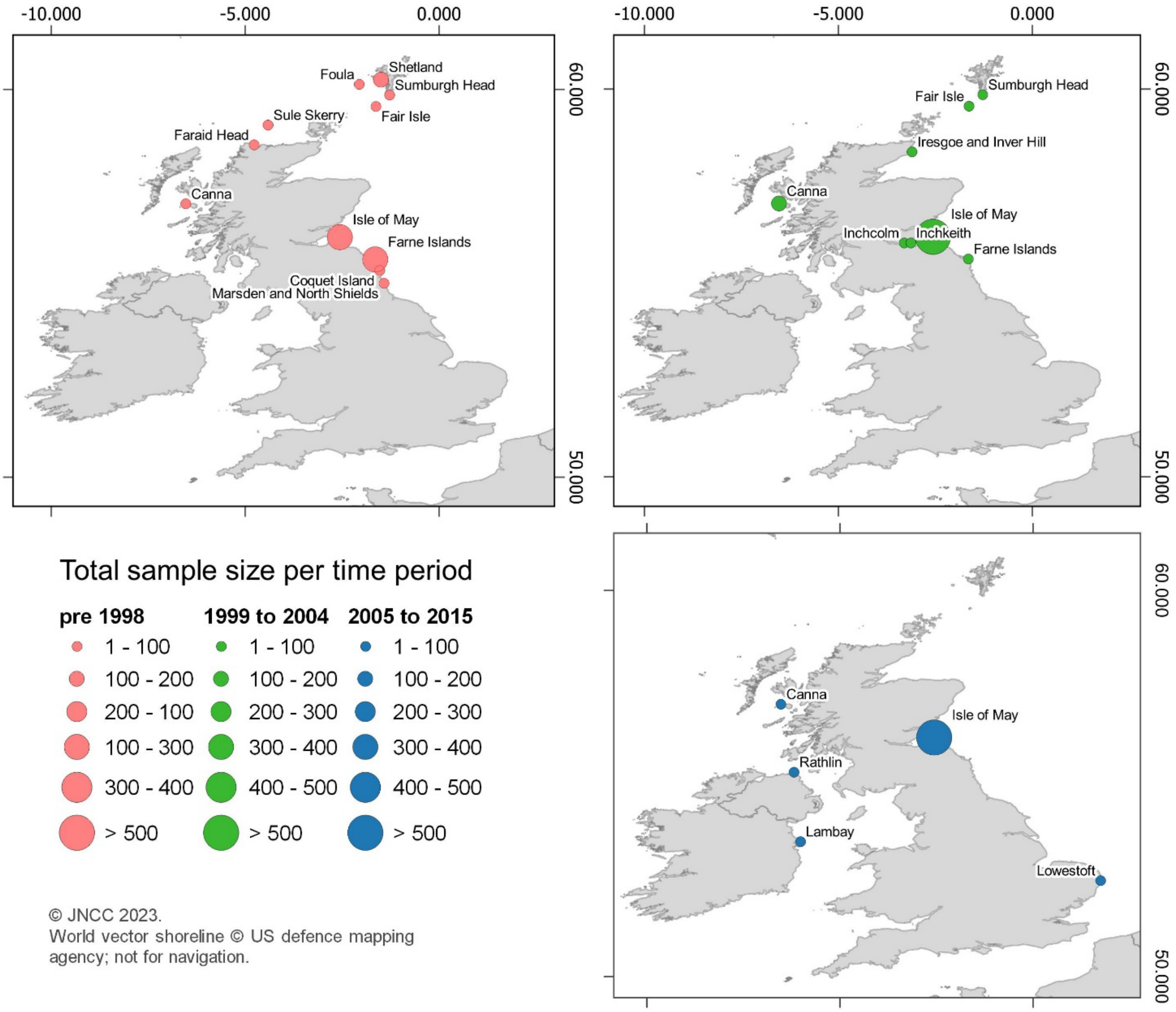

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Figure 1. Total diet sample size across kittiwake colonies and time periods. Data extracted from the MERP database (latest update made on 20 June 2018; Krystalli *et al.* 2019).

Contemporary (i.e. post-2015) collection of kittiwake diet samples has occurred at some UK colonies. Diet information collection is part of the long-term monitoring of seabird colonies on the Isle of May. Diet data has also been obtained more recently from colonies in the Irish Sea (Rockabill, 11 km from Lambay; Stephen Newton, pers. comm.). As part of the RSPB project on geographic variation in kittiwake diet (Wilson *et al*. 2021; see section 3.1.1 for a summary of preliminary results), recent diet data has been collected at the Flamborough and Filey Coast SPA in 2018 (n = 13) and 2021 (n = 6) late June/early July.

It is also worth noting the availability of six years (2008—2013) of dietary information for the Lowestoft colony, in Suffolk, one of the south-eastern-most colony in the UK (Carter *et al.* 2014). The data showed that both sandeels and clupeids (mostly sprat) form a staple food for breeding kittiwakes, while gadoids were supplementing diet in years when sandeels availability was low, with no observed consequences on kittiwake productivity. This dataset could be used to investigate temporal variability in diet composition if further dietary information was to be collected at this colony or region as part of the monitoring of Hornsea

Three artificial nesting platforms, acknowledging however the relatively low number of regurgitates collected per year (ranging from 13 to 32; see Table 1).

Table 1. Summary of kittiwake diet studies at UK colonies for the period 1961—2015, as collated in the MERP database (last version updated on 20 June 2018; Krystalli *et al*. 2019).

Location	**Period**	**Type of diet samples**	**Mean sample size [range]**	**Fish prey**	**Diet variables**	**References**[1]
Canna	1987—2005, 2007—2015	regurgitate	10.9 [2—32]	sandeel, clupeidae, sprat, gadidae, pipefish, rockling	frequency of occurrence, sandeel age group provided for 5 years	32, 71, 72, 73, 77, 78, 79, 75, 76, 81, 82, 83, 84
Coquet Island	2012	regurgitate	17 [17]	sandeel, sprat	frequency of occurrence	66
Fair Isle	1986—1988, 1991, 1998, 2000	regurgitate	20.4 [8—34]	sandeel, gadidae	frequency of occurrence, numerical frequency, biomass, sandeel and gadid age group in one year, sandeel size provided for 2 other years	3, 28, 29, 32, 67, 97
Faraid Head	1986	regurgitate	1 [1]	sandeel	frequency of occurrence, biomass	32
Farne Islands	1961—1963, 1998—2000	regurgitate	79.5 [26—218]	sandeel, clupeidae, gadidae	frequency of occurrence, numerical frequency, biomass, sandeel age group provided for 3 years	10, 62
Foula	1975—1983	regurgitate	n/a	sandeel	frequency of occurrence, prey size provided	22

Location	Period	Type of diet samples	Mean sample size [range]	Fish prey	Diet variables	References[1]
Inchcolm	1997—1998, 2000	regurgitate	10.3 [6—14]	sandeel, clupeidae, gadidae	frequency of occurrence, sandeel age group provided for 3 years	10
Inchkeith	1997—1999	regurgitate	18 [16—21]	sandeel, clupeidae, gadidae	frequency of occurrence, biomass, sandeel prey size provided for one year	10
Iresgoe and Inver Hill	1987—1988	regurgitate	11.5 [8—15]	sandeel, clupeidae, gadidae	frequency of occurrence, biomass, sandeel prey size provided for one year	32
Isle of May	1982, 1986—2015	regurgitate	73.3 [9—217]	sandeel, herring, clupeidae, gadidae, cottidae, pipefish, flatfish, rockling	frequency of occurrence, numerical frequency, biomass, sandeel age group provided for all years except one	8, 9, 10, 17, 23, 32, 35, 36, 39, 44, 51, 52, 53, 54, 56, 57, 58, 59, 60, 64, 91, 95, 96
Lambay	2009—2010	regurgitate	11.5 [8—15]	sandeel, clupeidae, gadidae	frequency of occurence, sandeel and clupeid size provided for both years	13
Lowestoft	2008—2013	regurgitate	[13—32]	sandeel, clupeidae, gadidae, rockling	frequency of occurrence	12
Marsden and North Shields	1968—1973	regurgitate	46	sandeel, clupeidae, gadidae	biomass	16

Location	Period	Type of diet samples	Mean sample size [range]	Fish prey	Diet variables	References[1]
Rathlin	2009—2010	regurgitate	12.5 [4—21]	clupeidae (bulk of diet), sandeel	frequency of occurrence, sandeel and clupeid size provided for both years	13
Shetland	1975—1983, 1988	regurgitate	56 [6—106]	sandeel	number, biomass, sandeel size provided	2, 22
Sule Skerry	1986	regurgitate	4 [4]	sandeel	frequency of occurrence, biomass	32
Sumburgh Head	1987—1988, 1990—1992	regurgitate	4.8 [1—12]	sandeel, gadidae	frequency of occurrence, number, biomass, sandeel and gadoid age group provided for 3 years	32, 97

[1] See Supplementary material 1 (Annex 1) for a full list of references.

2.1.3 Data and knowledge gaps

This review has highlighted gaps in diet study coverage across UK kittiwake colonies. Three obvious geographic areas where data is lacking are the southern North Sea, the western Scottish Isles and the Celtic/Irish Sea region, particularly in Wales. Despite being the largest kittiwake colony in the UK, only a few diet samples have been collected at the Flamborough and Filey Coast SPA, probably due to the difficulty of accessing nests at elevated cliff sections and potential disturbance caused to nesting birds (Saskia Wischnewski, pers. comm.). Gaining a better understanding of breeding season diet in regions where different environmental conditions and prey types prevail compared to the North Sea, would help better appreciate the relative influence of prey resource quality and availability on key demographic components of kittiwake populations.

At present, there is poor understanding of seasonal and annual variation in kittiwake breeding season diet. A great proportion of the diet samples that have been collected so far across UK colonies are 15 years old or older. Given on-going changes in fish prey community composition due to climate change and fisheries pressure, these data may not be representative of current prey availability to breeding kittiwakes. Long-term time series of dietary samples as collected for example on the Isle of May can provide the opportunity to address these questions. There should also be scope for expanding diet sampling coverage through existing tracking and ringing programmes, or other kittiwake field studies, by collecting opportunistic regurgitate or faecal samples at a wider range of key sites.

A key limitation of conventional techniques for collecting dietary data at kittiwake colonies is the opportunistic collection of regurgitated food samples while handling birds. Since fish prey are swallowed by adults and hence cannot be directly observed at colonies as they, sample size is inevitably highly variable across years and sites.

Studies so far have mainly reported diet composition as frequencies of occurrence, which tend to over-estimate the relative importance of small prey items. In addition, many prey items will be incomplete following digestion; therefore, quantifying prey biomass (in weight or volume) and estimating the number of prey of a given size and weight in a dietary sample provide a less biased picture of a predator's meal. Collecting information on prey size (using, for example, otoliths) and energetic quality over years is not common (see, however, Wanless *et al*. 2018) but is key to determining how diet varies in relation to prey abundance and availability and may indicate the minimum biomass requirements of fish prey to maintain healthy kittiwake populations.

Coupling different dietary analysis methods and tools has the potential to overcome some of the biases from traditional analyses of regurgitated food. Genetic approaches for example have allowed the identification of highly degraded prey from marine predators, including seabirds (Nimz *et al*. 2022). They are complementary to morphological diet analyses by capturing a wider diversity of prey items including rare items and addressing longer diet timescales (i.e. allowing to detect degraded prey).

2.2 Breeding kittiwake foraging distributions in the UK

2.2.1 Tracking effort at UK colonies

Kittiwake is one of the most commonly GPS-tracked marine bird species in the UK. This has resulted in a number of studies using GPS tracking data to assess foraging behaviour and at-sea distribution of adult breeding kittiwakes at different spatial scales (Table 2). Although breeding kittiwakes are usually found to travel relatively short distances at sea, Woodward *et al.* (2019)'s review of 37 tracking studies (1,452 individuals) in the UK revealed strong variability in foraging ranges between individuals, sites and years, with a mean maximum foraging distance from colony currently estimated as 156.1 km (+/- 144.5 SD). Further recent analyses of tracking data of four UK-breeding seabird species indicated that uncertainty around maximum foraging distances in kittiwake was mostly explained by between-colony variation (Cleasby *et al*., in prep). Variation in foraging ranges can be explained by a combination of factors, including spatio-temporal changes in prey availability (e.g. Chivers *et al*. 2012; Robertson *et al*. 2014). Foraging ranges have also been recorded to vary between incubation and chick-rearing periods, although studies so far have not revealed any consistent patterns (Robertson *et al.* 2014; Ponchon *et al.* 2014; see, however, Cleasby *et al*. in prep for evidence of larger foraging ranges during incubation). Furthermore, it remains unclear how the demographic impacts of avian-borne diseases, such as Highly Pathogenic Avian Influenza, on UK colonies may affect the foraging behaviour of breeding seabirds in future years, due to potential reductions in intra-specific competition near breeding sites, possibly leading to a shrinkage of foraging ranges.

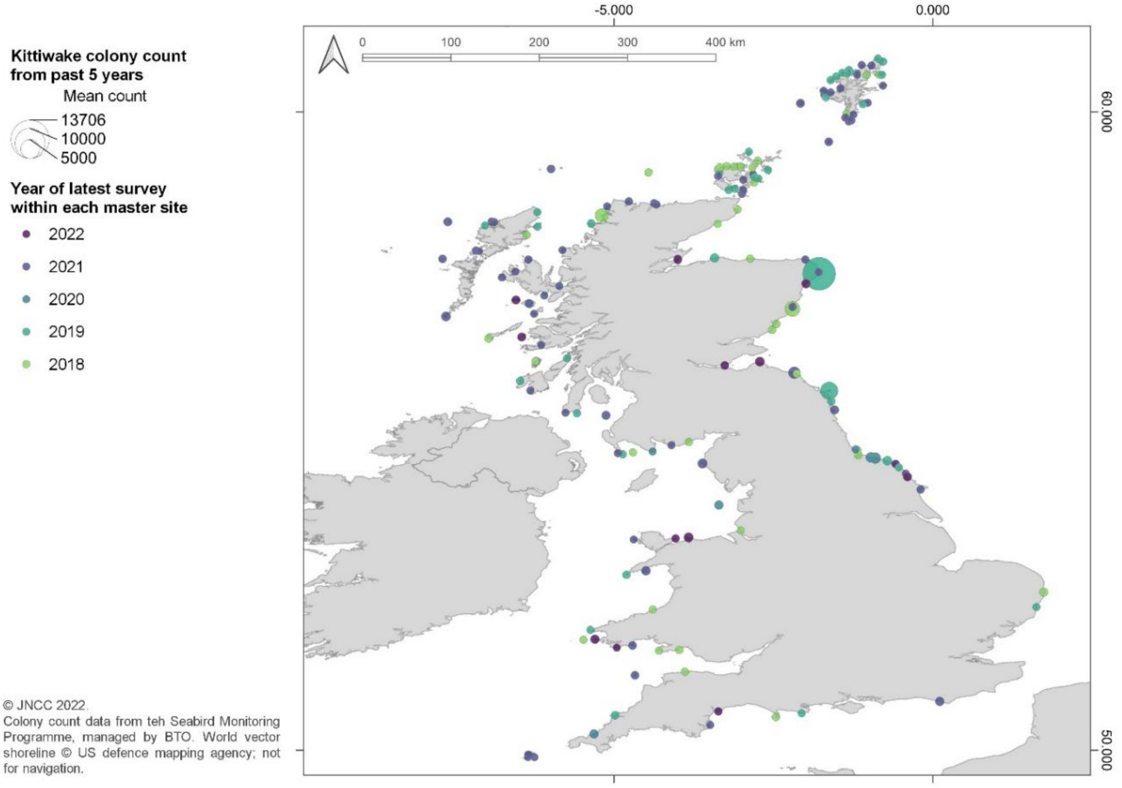
The RPSB-led tracking projects 'FAME' (Future of the Atlantic Marine Environment) and 'STAR' (Seabird Tracking and Research) represent the most comprehensive GPS tracking data collection on breeding kittiwake in the UK. Over the course of these twin projects, substantial effort was put into deploying GPS tags on five species including kittiwake. Data were collected over a four-year period (2010 to 2014) on a total of 583 adult kittiwakes across 20 sites during the late incubation and early chick periods (May to June) (Table 2, Figure 2). From this sample, 464 birds were tracked for more than 24 hours, with a median tracking duration of 42 hours (range 25—51 hours) (Wakefield *et al.* 2017). Most tracking effort was deployed along the northern (6 colonies) and east coast of Scotland (5 colonies), and north-east coast of England (3 colonies), where most densely occupied kittiwake colonies occur (Figure 2). On the western side of Britain, individuals were tracked on the Isles of Scilly (2 colonies), in Wales (2 colonies), and Northern Ireland (1 colony). One colony was tracked in Ireland over this time period.

Some additional tracking data were obtained from the Irish Sea and the Northern Channel in 2015—2017 on Rockabill, Rathlin, Puffin Island and Skomer (Table 2).

Table 2. Summary of breeding kittiwake tracking effort in Britain and Ireland for the period 2010-2022.

Site	**Region**	**Year**	**No. birds tagged**	**Tag type**	**Reference**
Fair Isle	Scottish Northern Isles	2010 2011 2012 2014	2 1 2 2	GPS	Wakefield *et al.* (2017)
Sule Skerry	Scottish Northern Isles	2011	4	GPS	Wakefield *et al.* (2017)
Copinsay	Scottish Northern Isles	2010 2011 2012 2014	11 7 8 3	GPS	Wakefield *et al.* (2017)
Muckle Skerry	Scottish Northern Isles	2010 2011 2012 2013 2014	9 9 12 8 12	GPS	Wakefield *et al.* (2017)
Cape Wrath	Northern Scotland	2014	5	GPS	Wakefield *et al.* (2017)
Bullers of Buchan	East Scotland	2012	5	GPS	Wakefield *et al.* (2017)
Whinnyfold	East Scotland	2012	20	GPS	Wakefield *et al.* (2017)
		2021	20	remote download GPS in 2021	Aonghais Cook, pers. comm.
Fowlsheugh	South-east Scotland	2011 2012	35 15	GPS	Daunt *et al.* (2011a) Wakefield *et al.* (2017)
Isle of May	South-east Scotland	2010 2012 2013 2014 2018 2019 2020 2021	36 17 22 11 16 25 25 50	GPS remote download GPS in 2018/19, coupled with accelerometer and altimeter in 2020/21	Daunt *et al.* (2011b) Wakefield *et al.* (2017) Bogdanova *et al.* (2020a, b, 2021, 2022)
St Abbs	South-east Scotland	2011 2012	25 15	GPS	Daunt *et al.* (2011a) Wakefield *et al.* (2017)
Coquet	North-east England	2011 2012	13 23	GPS	Wakefield et al. (2017)

Site	Region	Year	No. birds tagged	Tag type	Reference
Rathlin	Northern Ireland	2009 2010 2012 2013 2017	13 10 1 8 17	GPS	Chivers *et al*. (2012) Wakefield *et al*. (2017) Trevail *et al*. (2019)
Filey/ Bempton/ Speeton/ Flamborough	North-east England	2010 2011 2012 2013 2014 2015 2017 2018 2022	23 17 9 38 33 26 18 20 35	GPS GPS remote download with accelerometer in 2017/18, reverting to GPS only in 2022	Wakefield *et al*. (2017) Wischnewski *et al*. (2017, 2018, in prep) Trevail *et al*. (2019)
Lambay	Ireland, Irish Sea	2009 2010 2010 2011	12 7 10 4	GPS	Chivers *et al*. (2012) Wakefield *et al*. (2017)
Rockabill	Ireland, Irish Sea	2017	4	GPS	Steve Newton, pers. comm.
Puffin Island	Wales, Irish Sea	2010 2011 2012 2013 2015 2016	15 30 24 4 9 10	GPS	Wakefield *et al*. (2017) Trevail *et al*. (2019)
Skomer	Wales, Irish Sea	2016 2017	11 16	GPS	Trevail *et al*. (2019)
Bardsey	Wales, Irish Sea	2011	8	GPS	Wakefield *et al*. (2017)
St Martins	Isles of Scilly, south-west England	2010 2011 2012	18 14 3	GPS	Wakefield *et al*. (2017)
St Agnes	Isles of Scilly, south-west England	2011 2012	2 2	GPS	Wakefield *et al*. (2017)
Colonsay	South-west Scotland	2010 2011 2012 2013 2014	9 26 24 13 12	GPS	Wakefield *et al*. (2017)



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Colony count data from teh Seabird Monitoring Programme, managed by BTO. World vector shoreline © US defence mapping agency; not for navigation.

Figure 2. Kittiwake colony size in the UK, showing latest count data for the period of 2018—2022 (extracted from the Seabird Monitoring Programme database managed by BTO). Circles show location of each master site, averaged across individual sites.

Using the FAME and STAR tracking data, Wakefield *et al*. (2017) developed habitat use models to predict the at-sea distribution of adult breeding kittiwakes during late incubation and early chick-rearing periods at both colony and regional levels. GPS tracking data were combined with a range of environmental and ecological variables to predict at-sea usage of breeding kittiwakes from both observed and un-observed colonies at a 2 km x 2 km resolution. Outcomes of the model describe the expected time spent by kittiwake populations in a specific area and therefore represent the probability of encountering a kittiwake in that location during a future observation period. Resulting breeding distribution maps revealed the importance of the entire east coast of mainland Scotland and coast of Shetland and the Hebrides, the coast of Yorkshire (southeast of Flamborough Head) and northern Norfolk Banks, the central Irish Sea and Galway Bay (west of Ireland) (Figure 3).

Further analyses of FAME and STAR tracking data were developed to identify kittiwake high density areas using hotspot mapping techniques (Cleasby *et al.* 2020). Hotspot analyses were performed at both the UK-level (all colonies within the UK) and the SPA-level (all colonies within a defined SPA) (Figure 4).

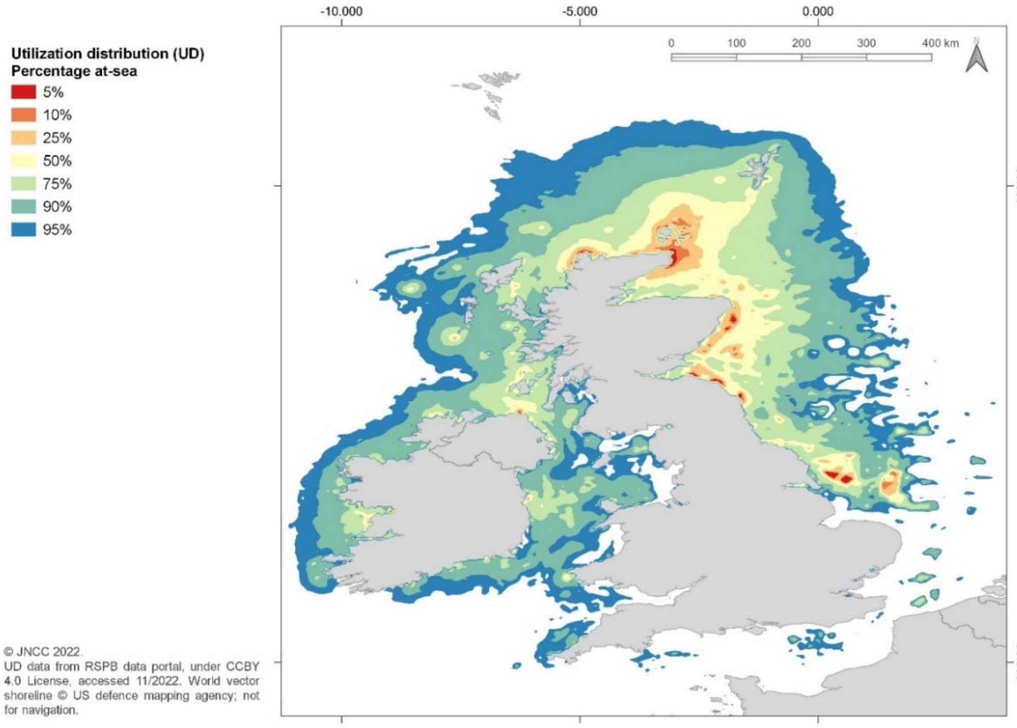


Figure 3. Percentage at-sea utilization distributions of kittiwakes breeding in Britain and Ireland during late incubation/early chick rearing, estimated as functions of colony distance, coast geometry, intraspecific competition, and habitat. Warmer colours indicate higher usage. From Wakefield *et al.* (2017).

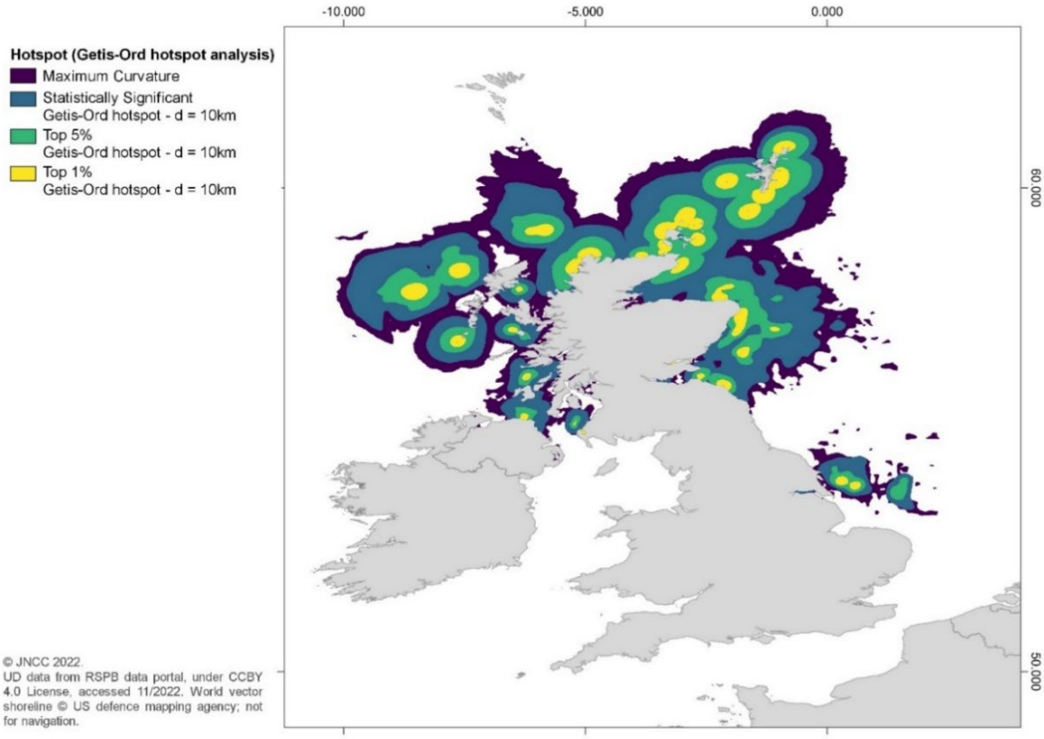


Figure 4. Hotspot analyses for each SPA in which kittiwake are listed as a feature. Hotspot mapping was conducted for each SPA independently and then individual SPA outputs were merged to create a single, combined SPA hotspot map across the UK. From Cleasby *et al.* (2020).

It is important to note that the above predicted at-sea distributions and high-density areas are encompassing all flight behaviours, including commuting, resting and foraging. These areas may therefore be wider than the more discrete locations where kittiwakes actively forage. Behaviour classification is a useful tool to discriminate between different behavioural states. Different classification methods have been applied to kittiwake tracking data in the UK, including the Flamborough and Filey Coast SPA (Wischnewski *et al*. 2017, 2018), which has helped refine foraging locations. Further research led by RSPB is focusing on understanding the mechanisms driving fine-scale behaviours of kittiwake while at sea (Ian Cleasby, pers. comm.). By coupling GPS tracking data (from FAME/STAR) and dynamic environmental features (e.g. tidal fronts), the research aims to assess whether kittiwakes switch from commuting to foraging when encountering a frontal zone, and whether this varies between colonies and years.

In more recent years, RSPB collected additional tracking data from the Flamborough and Filey Coast SPA, which can provide useful information relevant to windfarms in the southern North Sea (Wischnewski *et al.* 2017, 2018; Wischnewski *et al*. in prep) (Table 2). Tags were deployed for a longer period of time (up to 29 days in 2017, and 14 days in 2018) compared to previous studies and at different sections of the SPA. Tracking data from 2017 indicated segregated foraging areas between kittiwakes nesting at the northern and southern parts of the SPA (Wischnewski *et al.* 2017), which confirmed the patterns observed with the analyses of FAME and STAR data (Figure 3 and 4). While at Filey, birds tended to forage to the north of the Hornsea developments, kittiwakes from Flamborough tended to forage further south. Similar patterns have been found in 2018, although data should be interpreted with caution due to potential biases in the sampling regime in offshore areas (Wischnewski *et al*. 2018). Data from 2017 also indicated larger foraging ranges and longer foraging trips than for the FAME and STAR projects. These differences could be explained by the fact that birds were tracked from a longer part of the breeding season, including when adults were provisioning large chicks, which can be left for longer than small chicks.

The Flamborough and Filey Coast SPA is the only SPA where multi-year GPS tracking of kittiwake is on-going in England. Future kittiwake tracking is planned at this site (2023, 2025, 2027, 2029) as part of the strategic monitoring programme aiming at reducing uncertainty around estimates of collision mortality and understanding use of the marine environment (tracking funded by Hornsea Project One).

In Scotland, multi-year GPS tracking of adult breeding kittiwakes has been undertaken on the Isle of May over the past decade. Following on the FAME and STAR programmes (2010—2014), four additional years of tracking were undertaken at the Isle of May in 2018-2021. This work was complimented by similar tracking work at two additional Scottish sites, St Abb’s Head and Fowlsheugh SPAs, and is funded by Forth and Tay developers (NNG, Seagreen, Berwick bank) in agreement with the Forth and Tay Regional Advisory Group and carried out in collaboration with UKCEH and RSPB. In 2021, a total of 50 breeding adult kittiwakes were tracked from the Isle of May, 39 at St Abbs’ Head and 40 at Fowlsheugh (Bogdanova *et al*. 2022). All data were collected during chick rearing, except in three kittiwakes on the Isle of May that were tracked towards the end of incubation. A comparison of breeding kittiwake at—sea distributions from multiple years of tracking on the Isle of May revealed contrasted patterns between years, which could mirror differences in the distribution and availability of fish prey (Bogdanova *et al*. 2022).

In north-east Aberdeenshire, GPS tracking was undertaken at kittiwake colonies by BTO in Whinnyfold in 2021. Tags were attached using glue mounts in mid-June and collected data for a period of 17 to 45 days (BTO, in prep.). Future work at this colony includes the deployment of 25 tail-mounted GPS tags and 30 geolocators on kittiwakes in summer 2023 (Aonghais Cook, pers. comm.). In Northern Ireland, GPS tracking of breeding kittiwakes has been recently conducted at a colony near Newcastle, in county Down, by BirdWatch Ireland as part of the MarPAMM project.

2.2.2 Data and knowledge gaps

Kittiwakes have been the focus of a large number of GPS tracking studies over the past 15 years in the UK. While most of the tracking data has come from the northern and eastern part of Scotland and the north-eastern part of England, less is known about breeding kittiwake foraging distributions in the Irish and Celtic Seas, where environmental conditions differ from the North Sea. More tracking of breeding kittiwakes in Wales, Northern Ireland and Ireland would help reveal for example how birds adapt to different prey types and distributions and assess potential consequences on body condition and breeding success.

Another notable geographic gap in kittiwake tracking data coverage in the east coast of Britain is Farne Islands, with about 4,000 kittiwakes breeding on the SPA (SMP 2019; see also Figure 2). The kittiwake colony holds a strategic position, with potential connectivity to both the south-east Scottish and north-east English waters.

The large body of kittiwake GPS tracking work in the UK reveals marked differences in foraging distances and distributions across years and sites, as well as between periods of the breeding season and sections of a SPA site. Caution should therefore be applied when inferring breeding kittiwake foraging distributions from colonies where a small sample of tracked individuals is unlikely to be representative of the whole colony/SPA, or where data is derived from a small number of years or a short period in the breeding season. Altogether, these differences suggest that repeated tracking studies across spatial and temporal scales is essential to fully capture variability and understand the role of both extrinsic and intrinsic factors in driving at-sea usage.

Prey distribution and availability is one important factor determining where and how far offshore breeding kittiwake travel (Trevail *et al*. 2019). As marine birds track the availability of their main prey in space and time, they are likely to travel shorter distances when prey is more abundant (Chivers *et al*. 2012; Robertson *et al.* 2014). Longer and more costly foraging trip durations have also been associated to poorer breeding success (Christensen-Dalsgaard *et al*. 2018). Therefore, undertaking concomitant monitoring of prey distribution and availability, kittiwake foraging behaviour and distribution, and demographic consequences at colonies, will help better understand the dynamics of kittiwake-fish prey interactions.

3 Forage fish evidence review

3.1 Forage fish surveys and resolution of data

There are a number of forage fish data sources in UK waters, and these can be grouped into two main categories, commercial fisheries datasets and scientific surveys.

3.1.1 Commercial fisheries datasets

Commercial fisheries datasets include landings and effort statistics. There is a requirement for all vessels fishing in UK waters to report their fishing activity to the relevant management authorities (through landings declaration and logbook submission). In the UK, catch landed and effort data are then processed by the MMO (for landings into England, Wales and Northern Ireland and the Isle of Man) and Marine Scotland (for landings into Scotland), and aggregated by ICES rectangle and month. Landings statistics can be accessed for all vessels operating in UK waters by individual species, species group, gear and vessel length. Since fishing activity is not evenly distributed across each ICES rectangle, landing and effort data summaries may not be representative of the activity at localised sections of the rectangle.

Vessel Monitoring Systems (VMS) are monitoring systems that collect the precise location and speed of UK and EU Member States' vessels at a pre-ordained interval (e.g. 2 hrs). It is a legal requirement to transmit VMS data for all UK and EU commercial fishing vessels of 12 metres or over in length. Landings can be combined with VMS data to provide information on fishing activity at a higher spatial resolution than ICES spatial units. VMS data consist of a geographical location taken at regular intervals, but do not provide information on gear used, species targeted, quantities of fish landed or whether vessels are actively fishing or in transit. The data is filtered by speed to only include activity of vessels that are deemed to have been fishing, however, uncertainty remains on where and when exactly fish have been caught along a vessels' fishing track. Combining information from both VMS and logbooks allows to allocate landings (kg) to known effort and thus analyse the spatial dynamics of fishing activities at a more discrete resolution (e.g. kg per 0.05 × 0.05 degree grid) (ICES 2019). However, fish distribution inferred from fisheries datasets only does not reflect the occurrence and density of fish in areas where fishing does not occur.

3.1.2 Fishery-independent scientific surveys

The scientific surveys that collect information on sandeel, sprat and herring populations in the North Sea are coordinated by the International Council for the Exploration of the Sea (ICES), and used to inform fish stock assessments in the ICES area (Table 3):

- The International Bottom Trawl Survey Working Group (IBTS WG) coordinates multispecies bottom-trawl surveys across ICES regions in the Northeast Atlantic area (see Figure 4). While IBTS is designed to catch demersal gadoid species, pelagic species such as herring and sprat can be opportunistically caught. Non-target pelagic species are recorded, but not used as the basis of stock assessments. In the North Sea, the surveys are undertaken in quarters (Q) twice a year (15 days at sea, 45 trawl stations per quarter). Length-at-age data is collected for the target species. The IBTS undertaken in Q1 adds a pelagic component to the survey (IBTS-MIK) to sample eggs and larvae from winter spawning herring in the southern North Sea and Channel. A recent pilot study revealed that using a MIK net as part of the Q3 IBTS surveys had the potential to provide sprat larvae abundance estimates, although the use of this new sampling method to assess recruitment would need further investigation (ICES 2022a). Moreover, although sandeels can be caught opportunistically by the trawl surveys, the mesh size of the trawl is too coarse to provide reliable estimates of sandeel abundance (Wright *et al*. 2019). It has been found however that an additional small ring net attached to the MIK ring on the Q1 herring larvae surveys to sample cod and plaice eggs could also be used to catch small sandeel larvae (ICES 2022a).

- The Herring Acoustic Survey (HERAS) is an ICES-coordinated survey with five countries that collects data to assess herring stocks with coverage from the southern North Sea to north of Shetland and down the shelf edge as far as the Republic of Ireland. Fish shoals are identified using echosounder and fishing operations are then carried out to sample fish. Samples of all species caught are measured for length and weight to establish a length-weight relationship.

- The North Sea Sandeel Surveys (NSSS) sample sandeels buried in the seabed in November and December and compare catches (number and age composition) with previous year's collections to assess current year-class strength in ICES areas 1r, 2r and 3r (Figure 5).

- The International Herring Larvae Survey programme aims to provide quantitative estimates of herring larval abundance, which are used as a relative index of changes of the herring spawning-stock biomass in the assessment. The surveys are carried out in specific periods and areas, following autumn and winter spawning activity of herring.

Table 3. Summary of ICES-coordinated stock assessment surveys in the North Sea. See also Figure 6 for Subareas and Divisions locations.

Survey	Period of survey	Geographic area sampled	Frequency of survey	Survey method	Fish species
IBTS North Sea (NS-IBTS + IBTS-MIK) https://datras.ices.dk/	Quarter 1 (Q1)	North Sea; ICES Subarea IV and Division IIIa and VIId	Every year	Bottom trawl; pelagic net for herring larvae	Cod, haddock, whiting, saithe, Norway pout and herring larvae (targeted species) + opportunistic catch (e.g. herring, mackerel, sprat, sandeels)
IBTS North Sea (NS-IBTS) https://datras.ices.dk/	Quarter 3 (Q3)	North Sea; ICES Subarea IV and Division IIIa	Every year	Bottom trawl	Cod, haddock, whiting, saithe, Norway pout (targeted species) + opportunistic catch (e.g. herring, mackerel, sprat, sandeels)
North Sea Herring Acoustic Survey (HERAS) https://acoustic.ices.dk/	Quarter 2 (Q2)	North-western North Sea and North of Scotland	Every year	Echosounder + midwater trawl	Herring, sprat (targeted species) + opportunistic catch (e.g. mackerel, gadoids)
North Sea Sandeel Survey (NSSS) https://datras.ices.dk/	Quarter 4 (Q4)	North Sea known sandeel habitats	Every year	Modified dredge	Sandeel species
International Herring Larvae surveys (IHLS) https://eggsandlarvae.ices.dk/	Quarters 3 and 4 (Q3, Q4)	North Sea; ICES Subarea IV and Division IIIa	Every year	Modified plankton net	Herring (targeted species) + opportunistic catch (e.g. sandeel, cod, plaice)

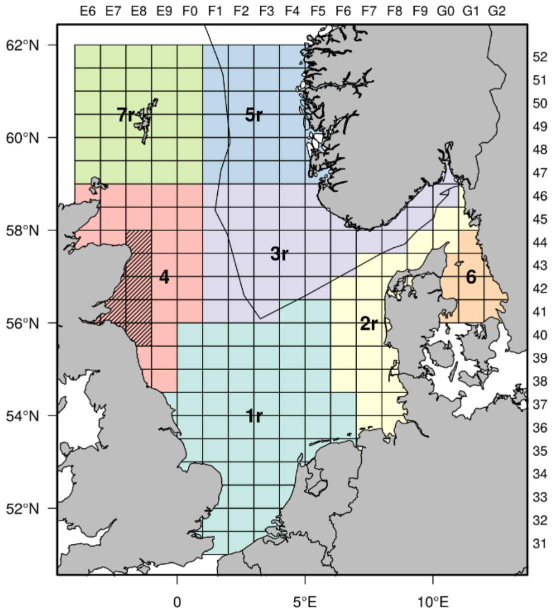


Figure 5. Sandeel assessment regions as defined by ICES (ICES 2022b). The black line indicates Norwegian EEZ limit. The hashed area indicates the fisheries area closure part of Sandeel Area 4.

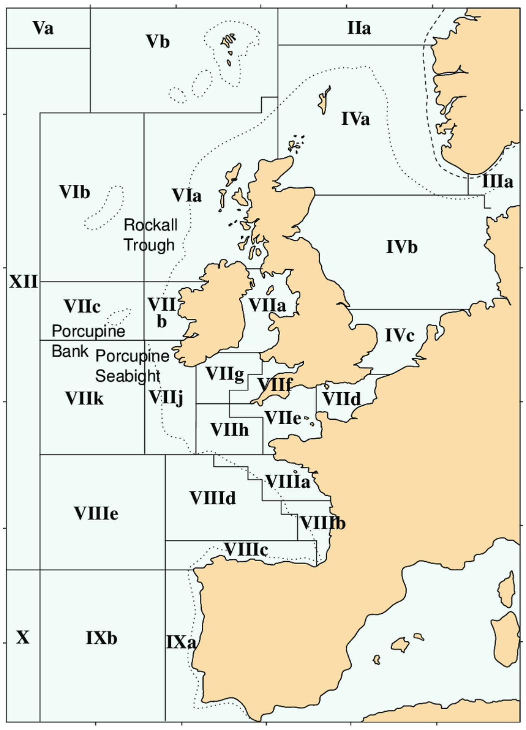


Figure 6. ICES Sub-areas and Divisions.

Scientific surveys are also conducted for herring and sprat in the Western British Isles. Some examples are provided below:

- The industry-science survey programme of herring is a collaborative partnership between the fishing industry and institutions from Scotland, Netherlands and Ireland established in 2016 with the aim to estimate herring spawning stock size in ICES divisions IVa/VIIc. Surveys are conducted every year in September using acoustic sampling. The data is submitted to ICES to assist in assessing herring stocks.

- In the Irish and Celtic Seas, a range of scientific (demersal) surveys have been undertaken by CEFAS in the period of 2008—2021, mainly covering the months of February to April and September to December (Campanella & van der Kooij 2021) and targeting species including sandeel, sprat and herring.

- The PELTIC pelagic survey (acoustic and trawl methods) was initiated in 2013, sampling several clupeid species, and covering the western English Channel, eastern Celtic Sea and more recently Cardigan Bay.

- Several acoustic surveys are conducted in the Irish and Celtic Sea region, including the Celtic Sea Acoustic Survey (sprat, in October), the Celtic Sea herring acoustic survey (October), and surveys carried out by the Agri-Food and Biosciences Institute of Northern Ireland (herring and sprat, September).

- In the western Scottish waters, the Scottish West Coast IBTS is a groundfish bottom trawl survey (Q1 and Q4) that catches sprat throughout the survey area.

3.1.3 Data and knowledge gaps

The main limitation with the currently available fish datasets is the spatial and temporal resolution of the data. Scientific fish surveys are currently the best dataset source for inferring regional fish distributions. However, since the data collected at sampling stations are amalgamated at the scale of ICES rectangles, this data format cannot be used to assess predator-prey relationships at the scale of breeding kittiwake foraging patches. Finer resolution data (e.g. at the scale of sandbanks for sandeels) may be requested from relevant scientific organisations; however, the relatively low intensity of survey data in some areas would still limit the spatial resolution of predictions.

Similarly, the temporal resolution of available fish distribution datasets does not necessarily match the periods when kittiwake reproduce, particularly when energy requirement is maximal (i.e. during the chick-rearing period). For sandeels, trawl sampling is usually done in December when they are buried in the sand. However, sandeel sampling in winter cannot be used to inform the availability of sandeels 1+ and 0- groups during the kittiwake breeding season. As kittiwakes feed at the sea surface, timing of sandeel availability in the water column is key, and this varies with sandeel growth rate (Thomas Régnier, pers. comm.) There is yearly variation in sandeel growth rates, and hence in the timing of when 1+ group sandeels emerge from the sand early spring and when they bury again end spring/early summer (Thomas Régnier, pers. comm.). In eastern Scotland, the Stonehaven coastal biological station samples plankton (including ichtyoplankton) at the sandbank once every 7—10 days using echosounders and pelagic nets; this sampling allows to detect the timing of sandeel larvae hatching. As there is some degree of regional spatial synchrony in sandeel hatching timing, the data from this coastal station may help inform the availability of 0+ group sandeels in kittiwake foraging areas in the region (Thomas Régnier, pers. comm.), however this is unlikely to extend to the North Sea.

For herring, surveys in the North Sea are covering relatively well the entire breeding season (with acoustic surveys conducted in April to June), whereas for sprat surveys in the North Sea there is a gap in coverage during the critical period of April to June.

Recent advances in statistical modelling techniques have overcome some of the data issues highlighted above. For example, combining survey and commercial fishing data sources has proven successful for enhancing spatio-temporal coverage and resolution, and hence improving understanding of fish population dynamics (e.g. Gonzalez *et al*. 2021). Species distribution models, combining habitat variables with survey data, have also been developed to predict the occurrence and density of sandeels in parts of the North Sea and Celtic Sea regions (Langton *et al*. 2021).

3.2 Distribution, status and trends of forage fish populations

A comprehensive literature review was carried out to evaluate the current and possible future distribution of three key prey species for breeding kittiwake in the North Sea; sandeel, herring and sprat. Below are described the findings of this review for each of the species in turn, detailing the current distribution and stock status in the North Sea, projected changes in distribution and a brief summary of other potential impacts of rising sea temperatures.

3.2.1 Sandeel species

Sandeels are small eel-like fish that play an important role in marine food webs. They are a major prey for predator species (marine mammals, seabirds, predatory fish; Rindorf *et al*. 2000; Daunt *et al*. 2008; Herr *et al*. 2009) and support the largest single fishery in the North Sea.

The sandeel family (*Ammodytidae*) includes several genera with a total of 18 species, five of which are found in UK waters, with *Ammodytes marinus* (Raitt's sandeel) and *Ammodytes tobianus* (lesser sandeel) as the two most common species in the North Sea. All *Ammodytes* species*,* hereafter commonly referred to as sandeels, are a schooling fish, often forming large aggregations when free in the water column and returning to the sediment at night or when approached by predators (Winslade 1974a, 1974b, 1974c).

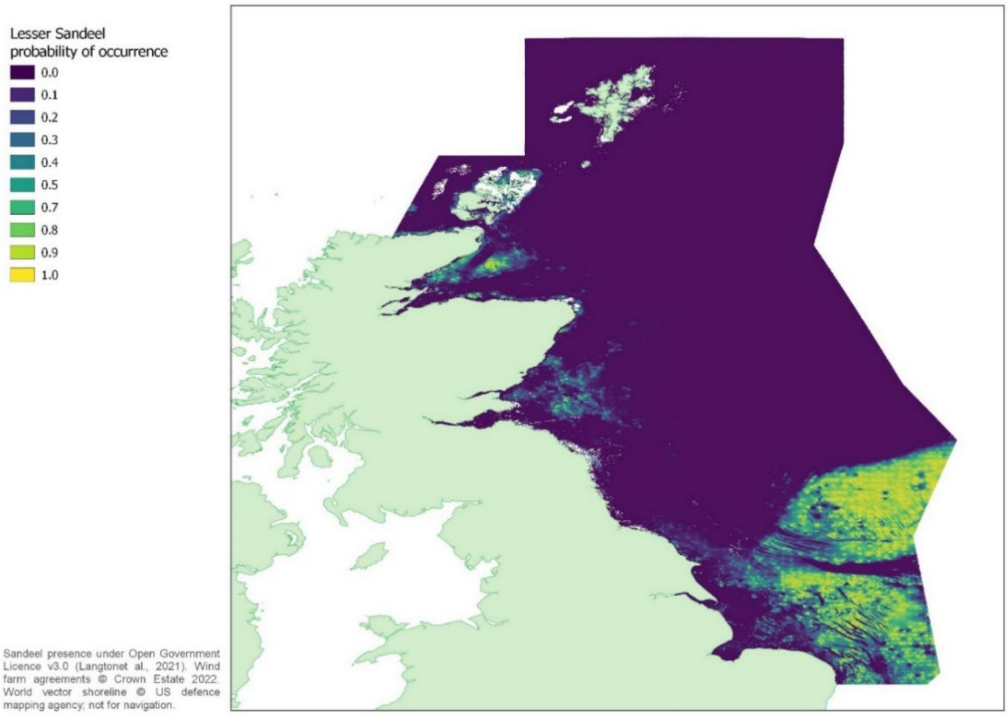
Sandeels typically inhabit offshore waters at a 20—80 m depth (Wright *et al*. 2000). The distribution of sandeels is highly fragmented in the North Sea with mixing among subpopulations dependent on dispersal of planktonic larvae over long distances and the movement of pre-settled juveniles between colonised habitat patches (Wright & Bailey 1996; Proctor *et al*. 1998; Jensen *et al*. 2008).

3.2.1.1 Stock status

Sandeel distribution within their North Sea geographic range is patchy (Wright *et al*. 2000). They have a specific habitat niche and are strongly associated with coarse sandy habitats once settled after their pelagic larval stage (Wright *et al*. 2000; Jensen *et al*. 2011; Rindorf *et al*. 2019; Langton *et al*. 2021). Sandeels then burrow into the sediment from September to March, which is interrupted in January when they emerge for their spawning period and begin feed on zooplankton in the water column (Henriksen 2021). Sandeel populations disperse during the pelagic larval life stage but have low dispersal and high site fidelity after settlement and into adult life stages (Jensen *et al*. 2011; Rindorf *et al*. 2019; Sadykova *et al*. 2020).

Much of the current understanding of sandeel distribution is based on commercial fisheries data, therefore is focused on the fishing grounds where sandeels aggregate to feed (Jensen *et al*. 2011) or trawl data, which is not designed for sandeel monitoring and hence can only provide relative abundance estimates (Wright *et al*. 2019). Recent research has attempted to predict the distribution and density of lesser sandeels (*Ammodytes marinus*) in the North Sea, using prediction models based on grab sample data, to gain a better understanding across their whole range (Langton *et al*. 2021). The authors suggested that the composition of the seabed habitats can reliably predict lesser sandeel distribution and density, with percentage silt and sand being the most important predictor of distribution, and slope as a significant predictor of density. This study found that the highest concentration of sandeel distribution was over the Dogger Bank and Norfolk sandbanks in the southern North Sea (Figure 7), which is consistent with previous studies (Wright *et al*. 2000; Jensen *et al*. 2011;

Rindorf *et al*. 2016; Wright *et al*. 2019). The model presented by Langton *et al*. (2021) improves inference on sandeel prey availability to large marine predators, such as kittiwake, and can be repeated and refined as new habitat data becomes available.



Sandeel presence under Open Government Licence v3.0 (Langtonet al., 2021). Wind farm agreements © Crown Estate 2022. World vector shoreline © US defence mapping agency; not for navigation.

Figure 7. Predicted occurrence of lesser sandeel in the North Sea (Langton *et al*. 2021)

Of the five species found in UK waters, lesser sandeel *Ammodytes marinus* (also known as Raitt's sandeel) supports the largest single fishery in the North Sea (Wright *et al*. 2000). Since the 2000s, sandeel stock has rapidly declined in the North Sea, with about 50% drop in catch in the early 2000's (ICES 2022b; Figure 8). The population abundance has remained low despite of fishery quota restrictions during this time period, suggesting a complexity of factors affecting sandeel biomass and recruitment (Henriksen 2021).

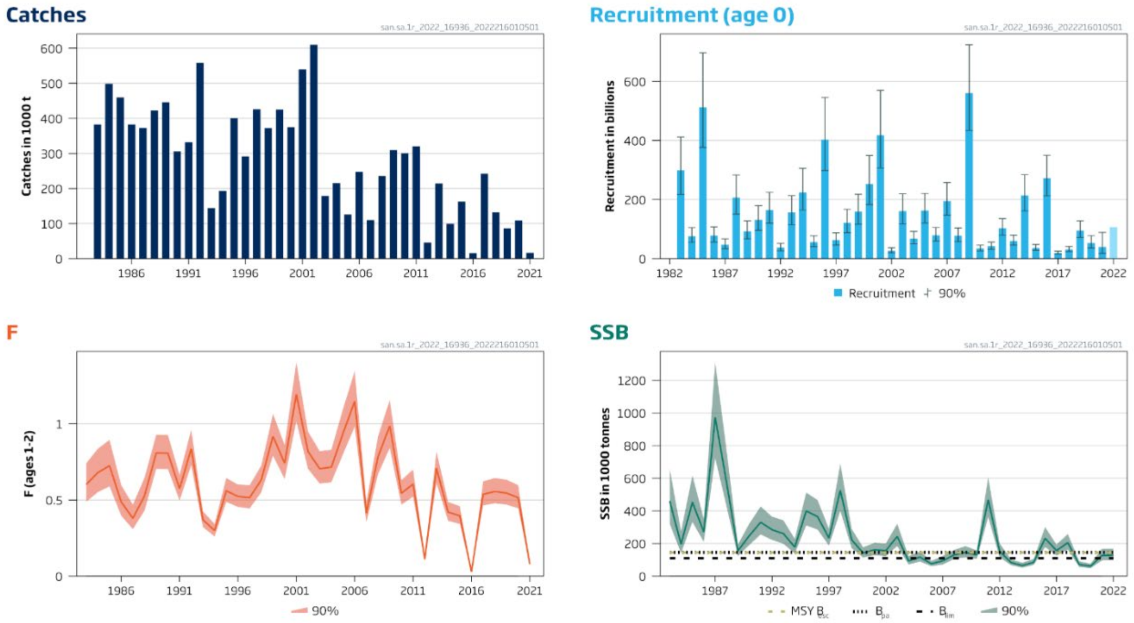


Figure 8. Sandeel stock summary of assessment of Area 1r (Southern North Sea) with associated uncertainties for fisheries catch, recruitment, fish mortality (F) and spawn stock biomass (ICES, 2022b).

3.2.1.2 Projected changes in distribution

A large body of literature suggest that sandeels are unlikely to shift their distribution in response to changing conditions, for example, changes in temperature regime, physical removal of preferred habitat, or changes in environmental conditions due to climate change (Heath *et al*. 2012). Sandeels tend to remain faithful to the area of initial settlement habitat (Gauld & Hutcheon 1990) and are rarely found further than 15 km away (Wright & Bailey 1996; van der Kooij *et al*. 2008). Review of the drivers of changes in fish distribution to inform predictions of past, current and future distributions of fish species revealed that sandeels show no apparent latitudinal shift, which may be explained by the specific habitat niche of settled sandeel communities (Heath *et al*. 2012). This study highlights the potential inability for sandeel populations to respond spatially to changes in sea temperature, due to their specialised habitat requirements.

Sadykova *et al.* (2020) used environment variables and data on the past distribution of kittiwake and sandeel to estimate changes in distribution of areas of spatial overlap for both kittiwake and sandeels; comparing present spatial distribution (1986—2014) and future projected spatial distribution (2037—2062) based on the “business-as-usual, worst-case” climate change scenario. They suggest sandeels could experience a 42.5% decrease in areas of occurrence of both predator and prey, with a general northwest shift of on average 98.1 km, towards coastal waters of the UK. The results of this study differ from results of other work (see references above), which indicate that sandeels are unlikely to shift spatial distribution in response to temperature change. These differences could be explained by the predictor variables used for sandeel distribution modelling by Sadykova *et al.* (2020); for example, net primary production (NNP) and a proxy for water column mixing (potential energy anomaly; PEA) were used, but benthic habitat preference of sandeels as a limiting factor was not represented. The authors acknowledge the complexity of predator-prey relationships and habitat preferences and therefore the limitations of their results. The method of this study could be replicated to include known habitat preference of sandeel to improve accuracy and detail for sandeel predator-prey spatial overlaps.

Inter-annual variation in sandeel populations (Régnier *et al*. 2017) and differences in abundance, size, reproductive timing across space (Rindorf *et al*. 2016) make investigations into the drivers of variation and change difficult. Recent studies are beginning to shed light on these relationships, so future research may be able to factor such temporal and spatial variations (Rutterford *et al*. 2015; Wright *et al*. 2020; Katara *et al*. 2021). In their PhD thesis, Henriksen (2021) explored the relationship and importance of intrinsic factors (such as growth and density dependence) and extrinsic factors (such as food availability, habitat, temperature and predation) influencing variations of sandeel abundance and distribution. Key life history events for sandeel populations, such as hatching and settlements, are influenced by a complexity of factors. For instance, temperature changes can influence the timing of hatching, leading to a match or mismatch with food availability for newly hatched sandeels. This will have a knock-on impact on survival. Temperature can also affect the metabolic rate of adult fish influencing energy demand and potentially spawning and recruitment processes. Distance to suitable habitat is related to the success of settlement, but this is further complicated by density dependence. MacDonald *et al.* (2019) further showed that low growth rate corresponded with a decline in abundance and attributed recent changes in length to prey availability. Table 4 outlines the driving factors and their interaction, summarised from Henriksen (2021).

Table 4. Summary of the driving factors influencing sandeel abundance and distribution in the North Sea, as described by Henriksen (2021): a) Driving factors for egg and larval stages; b) Driving factors for adult.

a) Driving factors for egg and larval stages	**Possible influence on driving factor**			
	Oceanography	Food availability	Temperature	Habitat
Food availability	Yes	No	Yes	No
Predation	No	No	Yes	No
Density dependence	No	No	No	Yes
Growth	Yes	Yes	Yes	No

b) Driving factors for adult stage	**Possible influence on driving factor**			
	Oceanography	Food availability	Temperature	Habitat
Density dependence	No	No	No	Yes
Temperature	Yes	No	No	No
Habitat	Yes	No	No	No
Predation	No	No	Yes	No
Fisheries	No	No	No	No

Although sandeels are very important commercial fish species, uncertainty remains around their population dynamics due to their life history strategy (short-lived species with variable recruitment). There is not a simple linear relationship between fishing effort and sandeel abundance. Disentangling the effects of fisheries pressure and climate can be challenging, especially across large regions (Wright *et al*. 2020).

3.2.1.3 Impacts of increased sea temperature

Increasing sea temperature could have impacts at population levels, as sandeel populations are unlikely to be able to shift their range, which is limited by the availability of preferred habitat. The effects of increasing temperature that can cause changes in populations have been investigated through the present literature review. Key elements are listed below but should not be considered as an exhaustive review of impacts. Variations observed in sandeel populations such as poor growth, decreased reproductive investment and increased predation have been linked to changes in sea temperature (van Deurs *et al*. 2009; Régnier *et al*. 2017; Lindegren *et al*. 2018; Régnier *et al*. 2019; Henriksen 2021).

Decrease in body size: there is evidence for a negative relationship between sea temperature and the abundance, size and quality of sandeel populations (van Deurs *et al*. 2009; MacDonald *et al*. 2019). Between 1989 and 2014, a 12% decrease in the mean body length of sandeels has been observed in the North Sea (Howells *et al*. 2017). Rindorf *et al*. (2016) showed evidence of spatial variability, with fastest growth (smaller individuals) occurring in southern UK waters and off the Norwegian coast and slowest growth off Shetland.

Decrease in reproductive investment: higher overwintering temperatures can have a negative impact on the available energy for reproductive organ development and therefore on overall reproductive success (Wright *et al*. 2017).

Trophic mismatch: differences between the timing of key live stages of sandeels and timing of prey availability due to changes in environmental conditions can have catastrophic consequences (i.e. starvation). A mismatch in timing between higher abundance of prey zooplankton species and sandeels impacts on the growth and fitness of individuals and therefore population abundance (Henriksen 2021).

3.2.2 Herring

Atlantic herring (*Clupea harengus*) is a widespread and abundant clupeid fish of both commercial and ecological importance (ICES 2006; Hislop *et al*. 1991; Thompson *et al*. 1997; Santos & Pierce 2003). In the North Sea, the population is mixed throughout the year, with adults forming large shoals that undertake vertical migrations through the water column. During the day, they are found below the thermocline but migrate upwards towards to the surface overnight (Maravelias 1997). Herring have large larval movements and adult annual migrations, therefore are found in different habitat niches at different life stages and seasons (Rose 2005; Sadykova *et al.* 2020). For spawning, subpopulations split away to undertake seasonal migrations. North Sea herring have four distinct spawning components; Shetland/Orkney, Buch, Banks and Downs (Dickey-Collas *et al*. 2010), and spawning grounds are typically characterised by offshore gravel banks in depths between 5—150 m in areas of high-water movements (Blaxter 1985; Maravelias *et al*. 2000). Spawning can occur year-round but is typically observed during a short period in autumn in the North Sea (Daan *et al*. 1990), and spawning timing is known to vary between the four regional components. Outside of the spawning season, key characteristics of herring habitat remain unclear, although studies have suggested that they might prefer hard rocky substrates and topographic features such as ridges and escarpments (Reid & Maravelias 2001) and temperatures at 60 m depth between 9ºC and 11ºC (Maravelias 1997).

3.2.2.1 Stock status

Herring populations are distributed widely around the North Sea and form one the largest components of forage fish biomass, providing key ecosystem services to the North Sea (Figure 9 and 10; ICES 2021). The North Sea has several sub-stocks of herring, each with differing population dynamics, morphology and physiology, which likely reflects different environmental conditions (ICES 2021). The three northern components of autumn spawners show similar recruitment trends, but these differ from the Downs winter spawning sub-stock, likely due to different environmental drivers. The relative contribution of each to the North Sea herring stock is still unclear, particularly for the Downs winter spawning population.

North Sea herring stocks have declined significantly since 2016 as a result of low recruitment in the populations (Figure 11). However, there is some evidence that the decline may be slowing down with the 2020 spawning stock estimated at 1.5 million tonnes (2019 estimates were 1.55 million tonnes), and recruitment estimated at 30 billion recruits, 28% higher than the mean over the last decade (ICES 2021). The most recent abundance figures from the ICES Herring Assessment Working Group (HAWG) estimates the 2020 abundance of North Sea autumn spawning herring at 8,915 million fish, compared to 10,295 million in 2019 (ICES 2021).

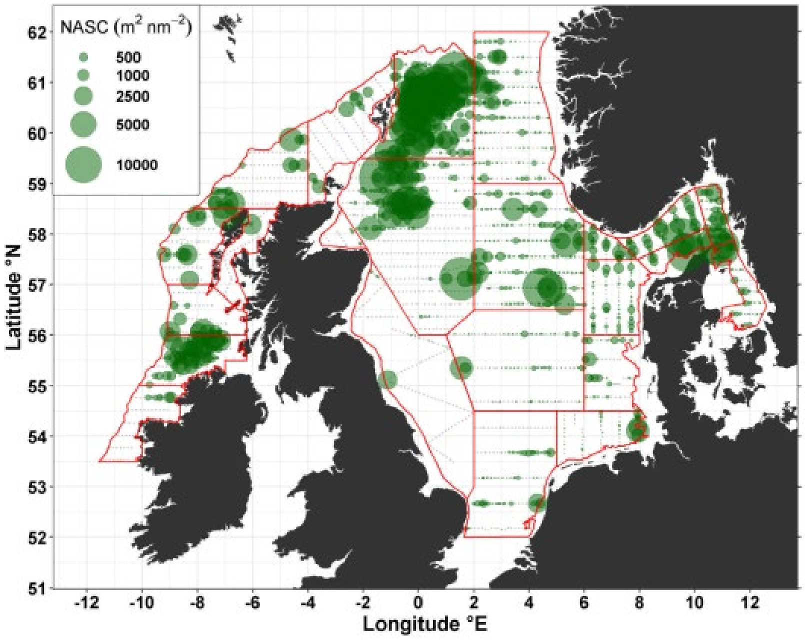


Figure 9. NASC (Nautical Area Scattering Coefficient) distribution plot of herring in HERAS 2020. Small light grey dots represent the acoustic intervals, and the green circles represent the size and location of herring aggregations (ICES 2021).

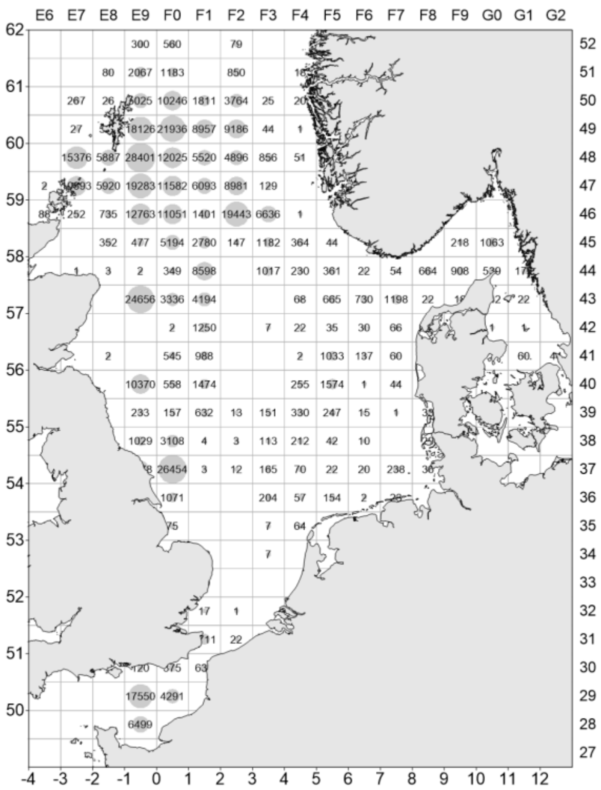
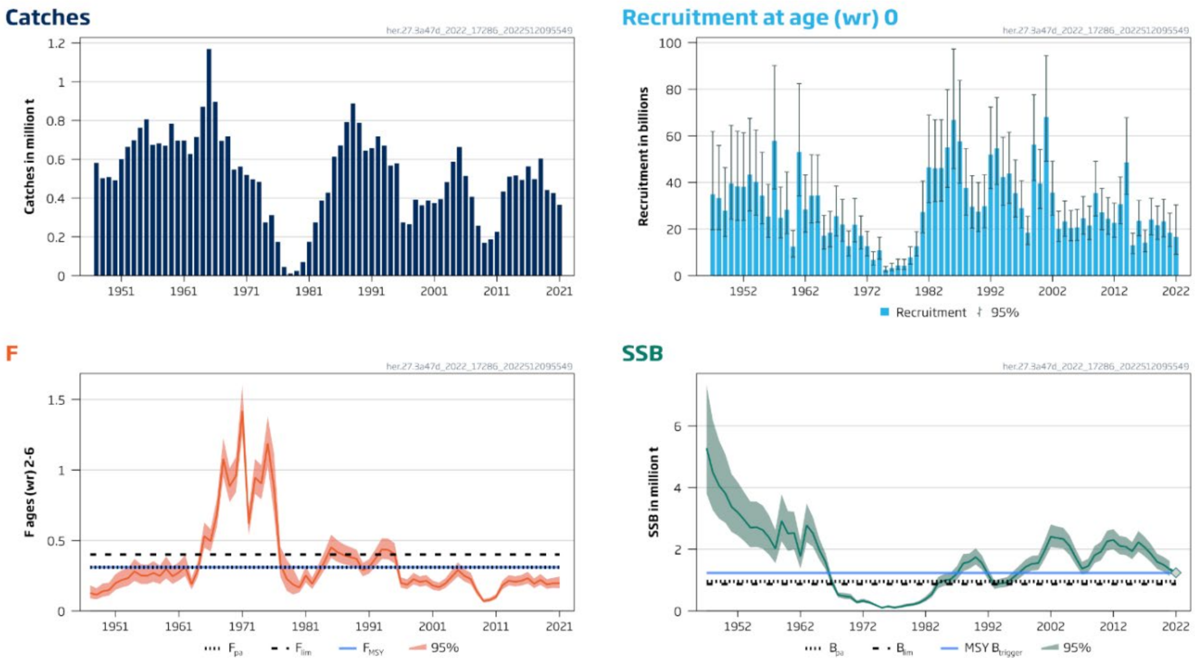


Figure 10 Herring catches (in tonnes) in the North Sea in all quarters for 2020 by statistical rectangle (ICES 2021).


Catches

Recruitment at age (wr) 0

F

SSB

Figure 11. Herring stock assessment summary of autumn spawners in Subarea 4 (North Sea) and divisions 3a and 7d with associated uncertainties for fisheries catch, recruitment, fish mortality (F) and spawn stock biomass (SSB) (ICES 2022c).

3.2.2.2 Projected changes in distribution

Climate models indicate that continued increases in temperature and changes in wind, cloud cover and precipitation may impact on the overall productivity of herring stocks in the North Sea rather than distribution, with decreases in the mean weight-at-age since the early 1980s (ICES 2022c) and low recruitment in autumn spawning herring stock since 2002 (Payne *et al*. 2009). However, impacts of climate change may be different between age classes. Sadykova *et al*. (2020) predicted distribution change under the "business-as-usual, worst case" climate change scenario and showed that herring age 1 could be less impacted by climate change (20—48.2% change) than herring age 2+3 (74.8%—82.4% change). This difference was attributed to the potential energy anomaly having less of an influence on herring age 1 (Sadykova *et al*. 2020).

Furthermore, using multi-species models to predict changes in distribution of predator-prey in the "business-as-usual, worst-case" climate change scenario Sadykova *et al*. (2020) suggested a 30.5% decrease in the size of area common to both kittiwake and herring (available space for both predator and prey) and an eastward shift of on average 11.6 km by 2050. This is consistent with some other studies over the last decade (e.g. Röckmann *et al*. 2011). However, a northward shift has also been identified in more recent studies, with herring shifting in response to warming climates (Fernandes *et al*. 2020; Jourdain *et al*. 2021).

3.2.2.3 Impact of increase temperature on herring

Evidence suggests that the distribution of herring in the North Sea is linked to the bottom substrate, water depth and upwelling zones (Reid & Maravelias 2001; Sveegaard *et al*. 2012). Therefore, the distribution of adult herring may be less directly impacted by changes in temperature in comparison with other fish stocks in the North Sea (Roberts 2020). Any changes that may be observed are thought to be indirectly related to temperature and the resulting changes to primary production such as zooplankton composition and food quality (Akimova *et al*. 2016; Fernandes *et al*. 2020). A range of potential impacts of increasing sea temperature, other than changes in distribution, have been recorded on herring, for example:

Smaller body size: Historically, warmer sea temperatures have been associated with a smaller mean body size and slower swimming speeds in herring (Avaria-Llautureo *et al*. 2021).

Changes in habitat use for larvae: During the development of early life stages, herring larvae may show preference for the upper littoral or pelagic habitats, both of which are at risk of disappearing or changing significantly with continued environmental change (Polte *et al*. 2017).

Changes in stock recruitment: Recruitment success in several North Sea herring stocks showed a strong negative correlation with increased sea surface temperatures from the 1960's onwards (Ottersen *et al*. 2013) and is thought to be at least one of the causes of the decline observed in the North Sea since 2016 (ICES 2021).

Changes in spawning stock biomass: There is evidence of a positive correlation between spawning stock biomass and temperature across the North Sea; thus, increasing temperatures may allow for greater stock biomass through changes in zooplankton composition (Akimova *et al*. 2016). However, more work is needed to better understand mechanisms of impact as stock biomass has been declining in the North Sea since 2016 with increasing temperatures (ICES 2021).

3.2.3 Sprat

Spat are short lived shoaling forage fish found in the central and southern North Sea with concentrations along the North Sea coastal regions and estuaries (Kvamme 2022). The spawning season ranges from January to July with the seasonal peak in spawning activity varying between regions; in the North Sea spawning peaks in late spring/early summer (Campanella & van der Kooij 2021).

Sprat populations in the North Sea are dominated by young fish with year one individuals making up an average of 62% of landings (ICES 2021). The population is concentrated in the southern region and along the southern North Sea and coastal estuarine regions with little seasonal variation (Figure 12).

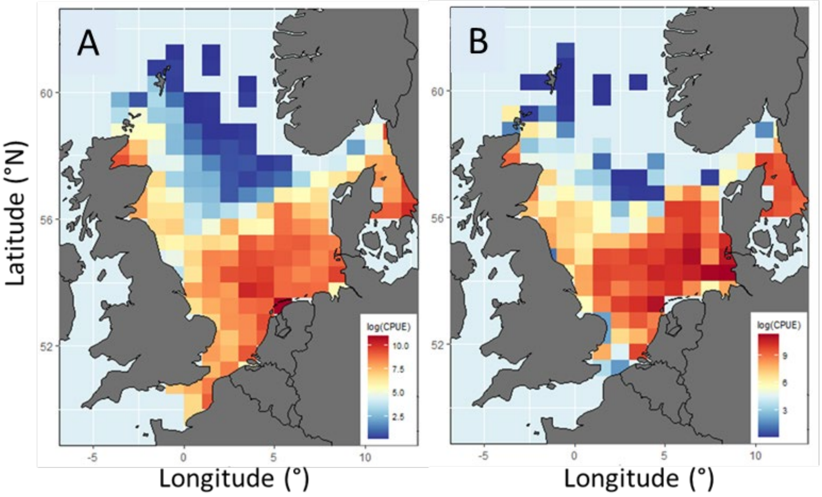


Figure 12. Spatial distribution of mean abundance of sprat in the North Sea based on IBTS trawl survey data from the A) 1st quarter (January to March) during the time period from 1982—2019 and B) 3rd quarter (July to September) during the time period from 1991—2019.

3.2.3.1 Stock status

The North Sea region is assessed for sprat as single ICES unit since 2018 (ICES 2018) based on genetic studies of the species population dynamics (Lindegren *et al*. 2018; Quintela *et al*. 2021; Saltalamacchia *et al*. 2022) (Figure 13). Recent genetic and population dynamics studies are suggesting that there is demographic connection between the Celtic Sea, English Channel, North Sea and Bay of Biscay management areas (Lindegren *et al*. 2022), which would need further investigation into whether this should be incorporated into stock assessments.

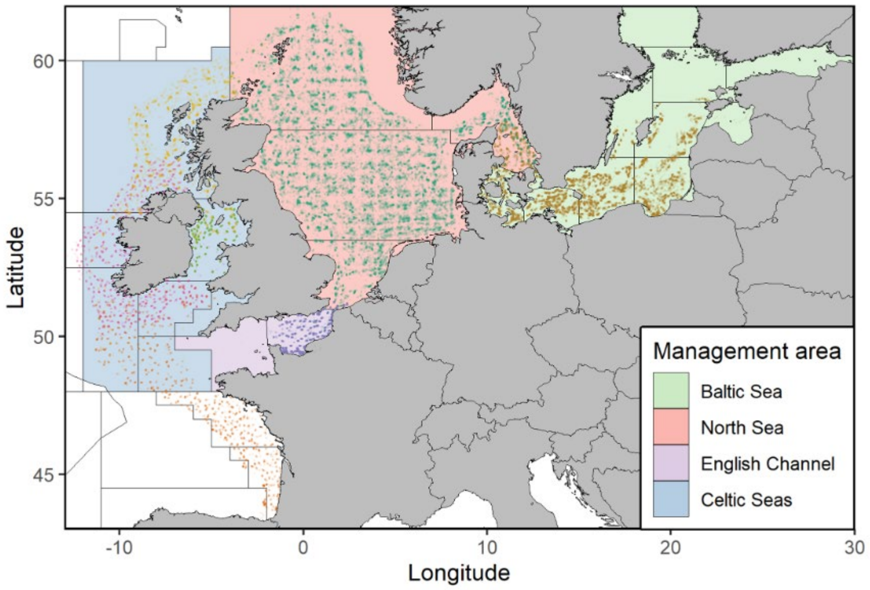


Figure 13. Map of the current Sprat ICES management units for the North Sea, Baltic Sea, English Channel and Celtic Sea. Coloured points show the sampling sites for bottom-trawl monitoring. The coloured dots illustrate data collected through different monitoring programmes, which contribute data to ICES DATRAS (Lindegren *et al*. 2022).

North Sea annual commercial catch for sprat, recruitment and spawning stock biomass have dramatically declined since the 1980s and have since remained low but stable (Figure 14). However, there are unknowns, such as the abundance and proportion of mature fish during the spawning season, which means that stock assessment data cannot be used to accurately account for interannual changes observed in the populations (ICES 2022d).

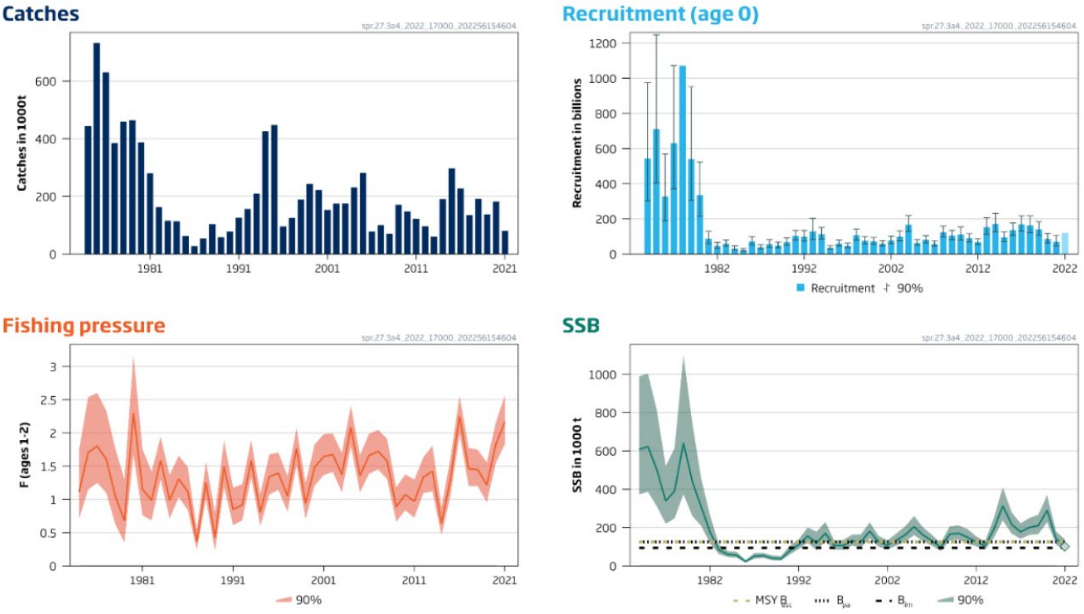


Figure 14 North Sea sprat ICES assessment summary (ICES 2022d) with associated uncertainty for fisheries catch, recruitment, fish mortality (F) and spawn stock biomass (SSB).

3.2.3.2 Projected changes in distribution

Drivers of observed variation in sprat populations are complex, and may not be singly linked to fishing pressure, environmental or oceanographic changes (Lawrence & Fernandes 2021; van der Molen & Pätsch 2022). Studies in the Bristol Channel found links between the observed decline of sprat populations since the 1980s with changes in temperature and global climate pattern (Henderson & Henderson 2017). However, more recent evidence suggests that the impacts of climate change are not clear and do not corroborate the changes in sprat populations in the North Sea (Fernandes *et al*. 2020; ICES 2021), and the evidence is unclear in identifying an appropriate model for sprat recruitment (ICES 2009b). The evidence, therefore, highlights the complexity and lack of understanding of the dynamics North Sea sprat population and influence of environmental variables.

The high degree of interannual variation in weight and abundance of sprat further complicates projections of future population abundance and distribution. Inaccuracies in stock assessment models have shown high mean errors and deviation from observed levels in abundance (Lindegren *et al*. 2020; ICES 2022d).

3.2.3.3 Impacts of increased temperature on sprat

Sprat have differing environmental requirements for each life stage, as with herring and sandeels. Current knowledge on the effects of climate change on sprat populations is limited, with recent research focusing on the effects of changes in temperature, prey availably and salinity (Lindegren *et al*. 2020; Felice *et al*. 2021). Generally, current evidence suggests weak correlation between temperature and sprat recruitment (ICES 2021), but there may be secondary effects through temperature-related changes in the resource availability and interspecies interactions; i.e. competition and predator-prey relationships, as outlined below.

Smaller growth and weight: During the larval stage, there is evidence for small direct impact of temperature on the feeding success or growth rate of larval sprat; while the optimal environmental envelope for sprat egg survival and growth is between 5°C and 17°C, the highest growth rates occur between 18°C and 22°C (Engelhard *et al*. 2014).

However, evidence suggests a secondary link between sprat growth and weight and prey availability due to temperature change. Changes in sea temperature are affecting the distribution and abundance of zooplankton in the North Sea. As these form a critical part of the bottom of the food web, the observed changes are having bottom-up effects on both the weight and abundance of sprat (Montero-Serra *et al*. 2015; Lindegren *et al*. 2020).

The observed variability in sprat weight over time may also be density dependent, with increasing population density negatively affecting individual growth and weight, likely due to increase competition for food resources (Lindegren *et al*. 2020).

Changes in interaction between forage fish species: Sprat and herring have similar diets (which vary at the different life stages). Changes in each population may change the interaction between species either through competition for food or through predator-prey relationships (Engelhard *et al*. 2014). Increasing sprat populations are known to have a negative impact on herring weight and condition in the Baltic Sea; however, the reverse has not been documented. Whether this competition between herring and sprat is present in the North Sea is unclear and requires further investigation. Equally, consideration of the interactions with other forage fish species would also be important, particularly those species that are increasing in the North Sea, such as European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) (Lindegren *et al*. 2020).

3.2.4 Summary of findings

The most significant impact from climate change on marine species populations is related to changes in prey availability (Howells *et al*. 2017). Increasing temperatures may lead to range expansion of warmer temperature species, affecting fish communities, food-web structure, competition and predator-prey interactions. With respect to kittiwake and their prey, this general understanding may hold true; a recent study has predicted that under the “business-as-usual, worst case” climate change scenario, the common area (available space for both predator and prey) for sandeel and herring with kittiwake may decrease by 42.5% and 30.5%, respectively (Sadykova *et al*. 2020). However, the present literature review has also highlighted that secondary impacts such as reduced body size, changes in recruitment success or reproductive investment, changes in trophic interactions and trophic mismatches are more likely to occur than adult populations shifting their distribution in response to changing environmental conditions for all three species (e.g. Ottersen *et al*. 2013; Akimova *et al*. 2016; Régnier *et al*. 2017; Wright *et al*. 2017; Régnier *et al*. 2019; Lindegren *et al*. 2020; Avaria-Llautureo *et al*. 2021). This is most likely due to current distributions being driven by a wide range of factors and correlated with key topographic features or sediment types (Wright *et al*. 2000; Reid & Maravelias 2001; Sveegaard *et al*. 2012; Rindorf *et al*. 2019; Lawrence & Fernandes 2021; van der Molen & Pätsch 2022). Several key evidence gaps remain, which make difficult to fully appreciate the mechanisms and strength of the impact of environmental change, especially for sprat populations.

3.2.5 Data and knowledge gaps

Disentangling the effects from fisheries and climate change can be challenging, especially across large regions, such as the MSFD assessment units (Wright *et al*. 2020). Investigation into long-term changes in North Sea forage fish populations should consider the effects of environmental change, effects of fisheries pressure and the influences of food-web dynamics as well as inter- and intra-specific interactions (Engelhard *et al*. 2014).

The 2021 MCCIP report highlighted the need for validation and testing of model assumptions and outputs in relation to projected changes in species distribution, suggesting that combining modelling approaches as well as further empirical studies are needed to improve input parameters (Wright *et al*. 2020). The North Sea region provides an opportunity for such testing, due to existing long-term monitoring data.

Research has mainly focused on annual or seasonal average temperatures, therefore there is little understanding of the impacts from short extreme variations in temperature such as heat waves, which are predicted to increase in frequency caused by climate change (Wright *et al*. 2020).

The ICES 2022 sprat stock assessment recommended further research into assumptions on European sprat natural mortality recruitment and changes in fishing patterns to increase the accuracy of stock assessments and forecasting (ICES 2022d). Better understanding the influence of underlaying factors on sprat weight and growth could be accounted for in stock assessment models, to improve accuracy of short-term stock forecasting (Lindegren *et al*. 2020).

Further research is also needed to better understand the potential oceanographic and atmospheric factors influencing the hydrodynamic regime in the North Sea and how climate change may affect these (van der Molen & Pätsch 2022). Continued monitoring of the influx of warmer water species into the North Sea and their interactions within the existing ecosystem should continue. Studies have suggested that increasing species richness in the North Sea could increase competition and predator impacts on important forage fish, but this area requires further study.

4 Review of UK research projects relevant to kittiwake and fish prey interactions

In addition to the kittiwake diet and tracking projects described in the above sections, a review of recent and on-going research of relevance to the topic of kittiwake and fish prey interactions in the UK was undertaken by contacting a range of organisations, including academic institutions, Statutory Nature Conservation Bodies, RSPB and Marine Scotland Science. A full list of projects is provided in Table S2 (Annex 2), with a summary below presenting the most relevant projects and how they may overlap or complement each other. While the list compiled below is thought to be reflecting the most directly relevant projects to the topic of kittiwake and fish prey relationships, further information on other recently completed or on-going projects on, for example, seabird/fish ecology and behaviour may be found in the Offshore Wind Evidence Register (OWEER) version 04.

The Crown Estate, with support from the Department for Environment, Food and Rural Affairs, the Department for Energy Security and Net Zero, and the Natural Environment Research Council, recently funded two ambitious research programmes, OWEC (Offshore Wind Evidence and Change) and ECOWind (Ecological Consequences of Offshore Wind), to facilitate the sustainable expansion of offshore wind in UK waters. A number of successfully funded projects are tackling questions around environmental impacts of offshore windfarms, particularly focusing on predator-prey interactions and ecosystem-level effects.

4.1 Predators and Prey Around Renewables Energy Developments (PrePARED)

In Scottish waters, OWEC-funded project PrePARED aims to assess how predator behaviour and distribution may change in response to the presence of offshore windfarms as well as potential windfarm-induced changes in fish prey behaviour, distribution and communities. In the Forth region, concurrent data will be collected on both fish prey and seabirds, including kittiwake.

4.2 Ecosystem Change, Offshore Wind, Net gain and Seabirds (ECOWINGS)

In parallel and in the same geographic area as PrePARED, ECOWIND-funded project ECOWINGS is looking at the ecological processes that underpin offshore windfarm impacts and strategic compensation. One component of ECOWINGS aims at better understanding the mechanisms driving seabird-fish prey dynamics (including kittiwake), particularly the linkages between seabird behavioural changes and demography. The project will focus on prey patch (i.e. finer) scales, and will collect simultaneous high-resolution data on both seabirds (including kittiwake) and fish prey over offshore windfarm gradients. ECOWINGS will seek to quantify the demographic consequences of changes in fish prey abundance, quality and phenology, as well as fisheries management, on seabird populations (including kittiwake) to inform strategic compensatory measures and their robustness to future climate change scenarios.

As part of ECOWINGS, a PhD project has been recently advertised (in collaboration with UKCEH, ZSL and MacArthur Green; Francis Daunt, pers. comm.) to

i) investigate spatial variation in the diet of kittiwake in the UK combining morphological analyses and DNA metabarcoding;
ii) ii) relate seabird demography to annual estimates of local sandeel and sprat biomass; and

iii) iii) quantify how much sandeel and sprat biomass needs to increase to allow elevated seabird recruitment and survival to compensate for increased OWF mortality.

4.3 Ecological implications of accelerated seabed mobility around windfarms_(ACCELERATE)

ECOWIND-funded project ACCELERATE is addressing impacts of both large-scale offshore windfarms and climate change on benthic ecosystems, with bottom-up consequences on fish and seabird predators. Predator-prey interaction research is focused on seabird fine scale foraging behaviour and energetics, with concurrent data being collected on both seabirds and fish in the Eastern Irish Sea. A key objective of the project is to better understand why seabirds forage where they are observed to do so, by quantifying the relationships between seabed characteristics, prey availability and seabird foraging behaviour.

4.4 Predicting seasonal movement of marine top predators using fish migration routes and autonomous platforms (PREDICT)

With the increasing recognition that marine species distributions are influenced by a range of dynamic environmental drivers, researchers from project PREDICT are combining survey and commercial fisheries datasets with environmental data to assess fish population growth rates in the North Sea and identify mechanisms driving variability in annual fish migrations movement patterns, which is the most likely cause of high variation in top predator distributions. One key outputs of the project will be a series of dynamic seasonal fish distribution maps that would inform the locations and timings of where multiple fish species are available as common prey in the North Sea.

4.5 Physics-to-Ecosystem Level Assessment of Impacts of Offshore Wind Farms (PELAgIO)

PELAgIO, the third ECOWIND-funded project, takes a step further by addressing the linkages between the physics, fish and top predators. The project is investigating bottom-up drivers of predictability of fish availability and foraging opportunities to top predators. There is potential for synergies between PELAgIO, PrePARED and ECOWINGS through the use of the same concurrent seabird GPS tracking data, and also the deployment of complementary fish monitoring technology that capture fish density and distribution at different depths of the water column and spatial resolutions.

4.6 Kittiwake behavioural responses to tidal fronts

Some further research on the linkages between seabird foraging behaviour and dynamic environmental features is currently undertaken by RSPB, using kittiwake GPS tracking data from the FAME and STAR programmes (2010—2014) from colonies in the North Sea ranging from Flamborough and Filey in the South to colonies in Orkney and Fair Isle in the north (Ian Cleasby, pers. comm.). The aims of the project are to assess

i) fine-scale behavioural responses of foraging breeding kittiwakes to tidal fronts, and
ii) habitat usage patterns as a response to changes in environmental conditions.

4.7 Remote Tracking of Seabirds at Sea

Novel tracking technology is being developed and tested on kittiwake through the OWEC-funded “Remote Tracking of Seabirds at Sea” project, which involves deployment of MOTUS-type automated radio telemetry network on both OWF platforms and on land to assess year-round bird behaviour and movements. When the technology is ready to be deployed, it may be possible to couple these novel data with fish distribution and availability data collected as part of other OWEC or ECOWIND-funded projects, extending therefore our understanding of multi-level interactions beyond the limited temporal window of the GPS tracking.

4.8 Seabird feasibility tagging study for the Sectoral Marine Plan

Further kittiwake tracking work is being planned at northern and north-eastern Scottish colonies. A desk-based review project is being conducted by BTO to evaluate relevant data and ongoing tracking studies, available technology, key evidence gaps and feasibility of undertaking tracking work to fill these gaps. This work will provide recommended approaches for undertaking further tagging at key sites.

4.9 Interaction between seabird populations, prey abundance and fisheries management

Other projects have looked at the effects of North Sea fisheries management on seabirds. For example, statistical modelling of kittiwake populations at the Flamborough and Filey Coast SPA, based on Carroll *et al*. (2017), quantified the impact of a reduction in fishing pressure in the stock management area SA1 on chick survival and then kittiwake population size (DMP Statistical Solutions 2020). Modelling outcomes indicated that a 4% reduction in fishing mortality resulted in a median of 190 additional adults after five years. However, these results rely on a number of major assumptions and should therefore be treated with caution.

McGregor *et al*. (2022) delivered a quantitative assessment of the likely effectiveness of a range of compensatory measures that may be proposed to offset predicted OWF collision impacts on the kittiwake population of the Flamborough and Filey Coast SPA. The assessment highlighted that across different OWF impact scenarios, sandeel fisheries closure was likely to result in substantial increases in the FFC SPA kittiwake population compared to a scenario in which productivity remained at its current low level. The model structure used in this exercise did not allow however for seabird movements between populations, and results should be interpreted with this caveat in mind.

The Sandeel North Sea Natural Capital Account project looked at responses of both surface-feeding and diving seabirds to different sandeel fishing regimes (Eftec & ABPmer 2022). Compared to the baseline (all stocks fished at maximal sustainable yields), the biomass of surface-feeding birds (including kittiwake) was predicted to increase by 15% in the absence of sandeel fisheries, and by 7% when fishing effort was reduced by 50%, mainly within the first 15 years. Further work in ongoing to refine seabird functional relationships and estimate responses separately by species (Jacob Bentley, pers. comm.).

The complex interactions between seabirds, their prey and commercial fisheries is further investigated in a Sheffield University PhD project, which is looking at prey consumption models related to predator needs in order to inform sustainable management efforts whilst maintaining healthy seabird populations (Sylvan Benaksas, pers. comm.). For a range of seabird species, including kittiwake, the project is combining fish prey distribution data in the North Sea with breeding seabird diet data to estimate seabird functional responses.

4.10 Kittiwake and forage fish in the Irish/Celtic Sea region

A couple of recent review pieces of work have recently been completed in the Irish and Celtic Sea. An assessment of kittiwake populations in Wales highlighted a decline in kittiwake abundance and productivity, with variation in trends between colonies possibly related to local prey abundance and availability (Johnston *et al*. 2021). A review of forage fish communities and pressures in Welsh and surrounding waters combined data from different fisheries-independent surveys to update the distribution and status of a range of species, including herring, sprat and sandeels (Campanella & van der Kooij 2021).

5 Conclusion and recommendations for future work

The black-legged kittiwake is one of the most studied seabird species in the UK, and this is reflected by the large body of evidence on their ecology and behaviour. Although there is evidence for geographic and annual variation in breeding season diet and productivity, uncertainty remains as to whether varying biomass contributions of sandeels, herring and sprat in the diet relates to different levels of demographic rates, and ultimately population size. Furthermore, better understanding the numerical and functional relationships between kittiwake predators and their fish prey is needed to target fisheries management measures that are sustainable at the scale of the entire ecosystem. Another key question relates to temporal changes in fish prey distribution, abundance, quality and availability, and potential consequences on kittiwake foraging behaviour and energetic costs. Assessing where and when highly profitable prey become available to surface-feeding seabirds at key periods of the breeding season, and the mechanisms underpinning annual variation in availability, is needed to understand why some colonies perform better or worse in some years or compared to other colonies.

We understand that some of these knowledge gaps will be filled by ongoing or recently funded research projects. With this novel research, the emphasis is on the mechanisms driving variability in predator and prey: we are now moving from mapping static to dynamic distributions of prey and predicting where seabirds are likely to forage by linking the physics to the species and validating model predictions with empirical data. The processes driving predator-prey dynamics are being tackled at the temporal and spatial scales that matter, through the concurrent collection of data on both seabirds and fish. Predicting sandeel availability in the water column is being investigated through analyses of sandeel growth rates and environmental variables. Novel genetic tools are proposed to be developed for a more robust analysis of kittiwake diet and investigate relationships between fish prey biomass and seabird breeding success. The complex interactions between seabirds, prey and fisheries pressure are being addressed through the use of predator-prey consumption models. Improvements are also being made to refine modelling predictions of climate-change driven changes in fish distributions. Within the next two to four years, a substantial body of evidence will become available through this novel research, which all together will help further refine our understanding of kittiwake and prey relationships, and the sustainability of these in the future.

Below we present a list of possible research ideas that could be developed to address questions that are relevant to Hornsea Project Three and more generally to the southern North Sea region:

- Linking diet composition, foraging behaviour and demographic rates through concurrent collection of diet, tracking and colony monitoring data. While the primary focus of this research would be colonies in north-east England where little is known about breeding kittiwake diet but tracking at colonies is on-going, there would be potential for expanding the geographic coverage of the study to other regions in the UK, particularly to areas where long-term datasets exist (e.g. Isle of May). Effort should also be made to compare regions where environmental conditions differ from the southern North Sea, or at a more local scale compare colonies where different habitats prevail. The project would involve the collection of data across years, and possibly also across periods of the breeding season, to capture both annual and seasonal availability of prey; this would help better understand for example why some natural or artificial breeding sites perform better or worse than others. Improvements of existing kittiwake diet sampling and analysis methods should be investigated to allow for increased geographic coverage, increased sample sizes, quantification of biomass, detection of rare prey and increased diet timescales.

- Improving predictions of fine-scale kittiwake foraging behaviour by linking tracking data to environmental variables. This project would build on the preliminary findings of RSPB's on-going project on the influence of tidal fronts on kittiwake foraging behaviour by expanding the analyses to more recent and extensive datasets, including at FFC SPA but also in marine regions where environmental conditions differ from the North Sea (e.g. Irish and Celtic Seas). This project could also consider the use of a range of tracking technology (e.g. accelerometery, although potential multi-sensor tag effects would need to be carefully considered) and machine learning tools to investigate the fine-scale movements and behaviour of birds while at sea.

- Determining the fish prey biomass requirements to maintain healthy kittiwake populations to inform an ecosystem-based approach to fisheries management. This project would build on the previous findings and model developments from Cury *et al.* (2011), the Sandeel North Sea Natural Capital Account project, and ongoing PhD research at Sheffield University. It would further develop model functionality to more realistically quantify kittiwake functional responses to fish density and biomass, and the identification of tipping points and prey thresholds above which kittiwake productivity can be maintained at high levels and below which it cannot. Assessing how differences in diet and foraging behaviour translate to breeding success and ultimately population size is key to determining population persistence, and critical to that is understanding how density-dependence operates both at sea and at the colony. The project should therefore consider novel ecological evidence that could be collected to inform density-dependent processes.

It is worth noting that there may be overlap between some of the research ideas described above and the questions that will be tackled by some of the more recent research projects described in Section 5. Therefore, it is recommended to maintain close engagement with project leaders to update on progress, avoid duplication of effort and seek synergies.

Although evidence points to prey availability being a major driver of seabird population dynamics, the mechanisms and processes governing predator-prey interactions across spatial and temporal scales are not well understood. Key to predicting resilience of kittiwake populations to changes in environmental conditions is improving our knowledge of the complex demographic and behavioural factors and processes that are at play, such as movements between colonies, positive and negative density-dependence feedbacks both at sea and at colonies, and further research should be directed to collect the empirical evidence that is needed to improve predictions of population dynamics models.

Documentation supporting this report can be found on the report entry:

Annex 1: Supplementary Material Table S1: MERP Diet Studies References

Annex 2: Supplementary Material Table S2: Summary of recently completed/on-going UK research projects relevant to kittiwake-fish prey interactions

6 References

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