A literature review of the lesser (Raitt's) sandeel *Ammodytes marinus* in European waters

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Introduction

Effective species' management requires knowledge of a species' status and ecology, the drivers of variation in populations, actual and potential threats faced by a species and the role of the species in an ecosystem context (Shaffer 1981; Pikitch et al., 2004; Thomas et al., 2009). The status of species that act as trophic links within communities should be considered of particular significance for conservation as this has implications for many species within an ecosystem (Cury et al. 2000; Lindegren et al., 2011; Smith et al., 2011). Such species include those at intermediate-trophic levels that feed on primary producers and lower trophic levels and are themselves predated on by higher trophic species (Cury et al. 2000; Delibes-Mateo et al., 2007; Prugh et al., 2009). However, understanding the factors impacting intermediate-trophic species can be particularly complex because they experience both "bottom-up" pressures (such as the availability of food and environmental suitability) and "top-down" pressures (such as predation) (Frederiksen et al., 2006; Lindegren et al., 2011).

One such intermediate-trophic species in the North Sea is the lesser sandeel, *Ammodytes marinus* (Raitt 1934). Lesser sandeels feed on phytoplankton and zooplankton and are themselves targeted by piscivorous predators; therefore they provide a crucial link between primary production and higher trophic levels (Reay, 1970; Malzahn and Boersma, 2009; Eliasen et al., 2011). The high lipid content and shoaling behaviour close to the surface of the water make sandeels an important source of food for many seabirds (Furness and Tasker, 1999, 2000; Cabot and Nisbet, 2013). In addition to avian predators and piscivorous fish, lesser sandeels are prey for marine mammals, such as harbour porpoise, harbour seal and minke whale (Santos & Pierce, 2003; Pierce *et al.,* 2004; Sharples et al., 2009). Sandeels are also targeted by a large, offshore, Danish-led industrial fishery in the North Sea for the production of fish oil and fish-meal (Naylor et al., 2000; Furness, 2003; European Parliament, 2004).

Catches of the lesser sandeel have declined substantially since the 1990s (ICES, 2012), coinciding with large declines in the breeding populations of many seabirds (Bailey et al., 1991). Although the decline in sandeels is likely to have been driven primarily by reductions in the availability of planktonic prey due to large-scale climatic change (Beaugrand et al., 2002; Reid, et al., 2003; van Deurs et al., 2009), additional pressures may have exacerbated the decline (Furness, 2004; Poloczanska et al., 2004). Given the importance of *A. marinus* for the North Sea ecosystem, long-term sustainable management of the species is essential. This requires a comprehensive understanding of the species' ecological role in the North Sea and the potential vulnerability of the species to pressures in addition to climate change. Here we review current knowledge of *A. marinus*. We begin with a summary of the ecology and distribution of the species to provide background knowledge. We then discuss long-term trends and spatio-temporal fluctuations with consideration of the likely drivers of variation. This is followed by a summary of the importance of the species for seabirds, piscivorous fish and marine mammals. Finally, we discuss some of the threats faced by *A. marinus*.

Ecology

Life history

The lesser sandeel, *A. marinus*, is a small pelagic fish of the sand lance family (Ammodytidae) and the most common of the five species of sandeel found in the North Sea (ICES, 1997; Cabot and Nisbet, 2013). Whereas its close relative *A. tobianus* (Linnaeus 1785) typically occurs in inshore areas, *A. marinus* is predominantly found in offshore waters (Reay, 1970). Lesser sandeels can live for 10 years (Muus and Nielson, 1999) and tend to reach reproductive maturity around 2 years of age, although this varies regionally (Gauld and Hutcheon, 1990; Boulcott et al., 2007). They typically spawn in December and January (Macer, 1966; Bergstad et al., 2001) and produce between 2,700 and >15,000 eggs depending on size and location (Gauld and Hutcheon, 1990). The eggs are covered in a glutinous secretion enabling them to stick to the seabed (Proctor et al., 1998), where they remain until hatching in February or March (Macer, 1966; Wright and Bailey, 1996). The planktonic larvae then enter most depths of the water column (Conway et al, 1997). During this time, larval drift between areas of the North Sea is driven by the prevailing sea circulation, leading to considerable inter-annual variation in larval dispersal from spawning grounds and local sandeel abundance (Wright, 1996; Proctor et al., 1998; Christensen et al., 2008). Metamorphosis of larvae to juvenile fish typically occurs in late May to early June or 33-90 days after hatching (Wright and Bailey, 1996). After this, these 0-group fish actively search for areas with suitable substrate into which they can burrow and remain hidden when not foraging (Macer, 1965; Proctor et al., 1998). The larval and juvenile period is one of relatively low survival, with the natural mortality rates of 0-group fish being on average 4 times higher than 2-year old fish (Cook, 2004).

Once settled, juvenile and adult lesser sandeels are largely resident and rarely disperse over distances greater than 30 km (Frederiksen et al*.,* 2005). During spring and summer sandeels emerge from the seabed at dawn and ascend the water column in large schools, often along the edges of sandbanks, to feed on a range of available zooplankton (van der Kooij et al., 2008). Although this behaviour applies to most individuals, schools occasionally remain close to the seabed during daylight hours (Freeman et al., 2004). This localised, schooling behaviour during the daytime coupled with a highly specific habitat association (see *Habitat Requirements*) renders local aggregations vulnerable to overfishing (Engelhard et al., 2008; Heath et al., 2012). Approaching dusk, the schools descend towards the seabed and bury into the sediment for the hours of darkness, although small numbers may remain in the water column close to the seabed (Freeman et al., 2004). Thus when not foraging, and during low light intensities, adult sandeels tend to remain buried in the sand (Winslade 1974; Freeman et al., 2004).

Sandeel activity also varies throughout the year and is influenced by water temperature, availability of prey and body condition (Winslade, 1971; van Deurs et al., 2011). Early studies identified a seasonal switch in sandeel behaviour. Macer (1966) found that, although sandeels could be caught in all months of the year, few fish were caught swimming in the water column during the winter months and those that were tended to be juveniles. This was supported by the observation that although sandeels could be caught by a modified scallop dredge in winter, they could not be caught by trawls (Cameron, 1958). Further, in southern England, *A. tobianus* collected from the sand were found to have empty stomachs during the winter months but full stomachs from late March to November, suggesting foraging was avoided in winter (Reay, 1970). Indeed, in winter most sandeels remain buried in the sediment and only emerge to spawn (van der Kooij et al., 2008), although bioenergetic models suggest individuals <9.5 cm length do not have adequate reserves to survive the winter without food (van Deurs et al., 2011) and some seabirds continue to catch sandeels in winter (Harris et al, 2015). Suggested functions of sandeel burrowing behaviour include avoiding displacement from suitable areas by underwater currents, minimising energy expenditure when not foraging (due to the absence of a swim-bladder in sandeels, active swimming is required to remain clear of the seabed) and avoiding predation (Reay, 1970; Wright et al., 2000). However, there is evidence to suggest that some piscivorous fish, such as haddock and whiting, and diving birds, such as the European shag (Figure 1), are able to target buried sandeels in the seabed (Temming et al., 2004; Watanuki et al., 2008).

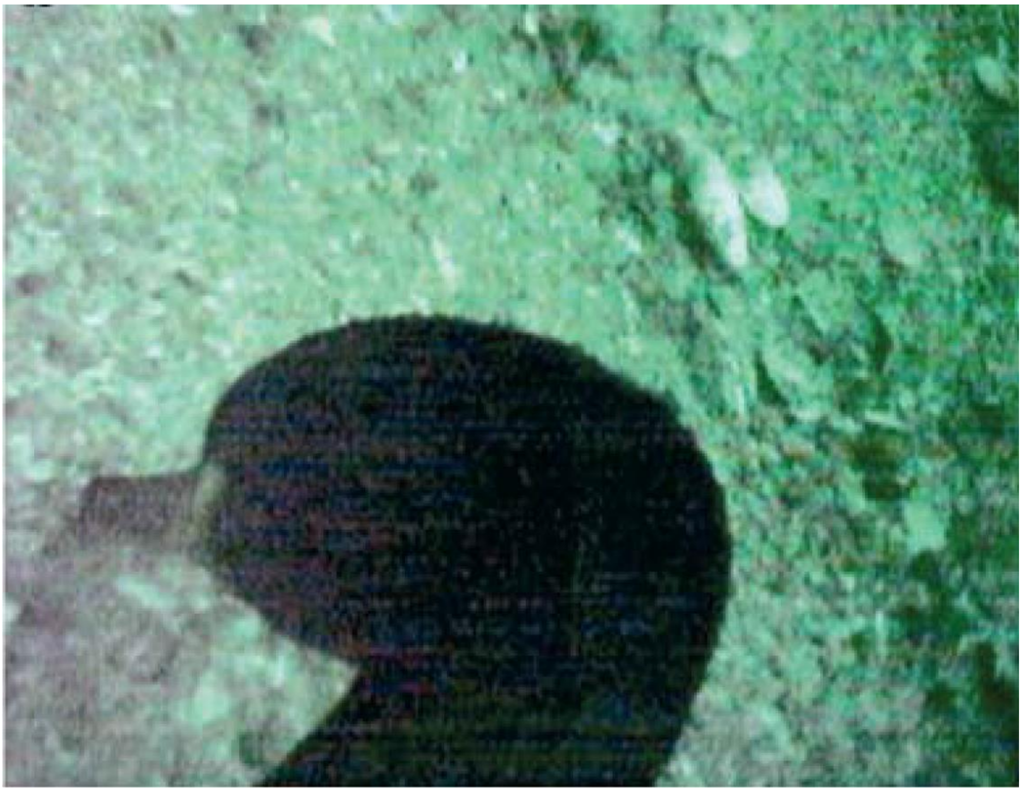

Figure 1. A European shag probing its bill into the sand, probably searching for lesser sandeels. Reprinted with permission from Watanuki et al. (2008), © Inter-Research.

Habitat requirements

Burrowing lesser sandeels have been found to demonstrate high habitat specificity. Studies show *A. marinus* has a preference for medium/coarse grained sands (0.25 – 2 mm) (Wright et al., 2000; Holland et al. 2005), is absent from sediments with >10% silt content (Wright et al., 2000) and decreases in density with >2% silt or >20% fine sand (Holland et al., 2005). This is possibly due to greater permeability, and thus higher oxygen concentrations, of large-grained sediments compared to those containing silt (Lohse et al., 1996; Wright et al., 2000). The closely related *A. tobianus* has been shown to experience physiological stress in hypoxic conditions, with a critical partial pressure of oxygen of 4.1 kPa at 10°C below which basal metabolic requirements cannot be maintained (Behrens and Steffensen, 2007). However, sandeels appear more tolerant of hypoxia than many demersal and pelagic species; they survive in low oxygen conditions when burrowing by reducing their metabolic rate and thus oxygen dependence (Behrens and Steffensen, 2007). As the oxygen concentration is highest in the top layer of sediment, burrowing sandeels tend to occupy the top 4 cm of the substrate and actively transport fresh, oxygenated water into the sediment using gill ventilation to enhance advection and by wriggling (Behrens et al., 2007).

In addition to requiring well-oxygenated and coarse-grained sandy substrate, *A. marinus* occupies turbulent, fairly shallow waters (<100 m) with an optimal depth of 30-70 m, such as along sandbanks (Proctor et al., 1998; Wright et al., 2000; Lynam et al., 2013). Further, within areas occupied by sandeels, the areas of greatest abundance were found to have a bottom temperature of 8.5-9.0°C and a surface salinity of 34.9-35.0 ppt (van der Kooij et al., 2008). These narrow habitat and environmental preferences mean lesser sandeels are unlikely to be able to relocate in response to changing conditions, and are therefore considered particularly vulnerable to the effects of climate change and localised fisheries depletion (Engelhard et al., 2008; Heath et al., 2012).

Prey

The availability of prey after the larval sandeel hatching period in early spring is an important determinant of larval growth rates, which affects early survival rates and recruitment (Wright and Bailey 1996; Gurkan et al., 2012). Young larval sandeels feed on phytoplankton, such as diatoms and photosynthetic dinoflagellates, and copepod eggs and nauplii, whereas older larvae feed predominantly on Appendicularia and copepod nauplii (Ryland, 1964; Arnott and Ruxton, 2002). Post-larval stages tend to target larger food items such as older stages of copepods, particularly *Temora* and *Calanus* species (Macer 1966). During a study in the North Sea, Macer (1966) found copepods to be in the stomachs of all sampled *A. marinus* individuals. The most important copepod prey was *Temora*, while *Calanus* copepods were found to be in about 30% of *A. marinus* and 5% of *A. tobianus* stomachs (Macer, 1966). However, more recent studies have found that sandeels will preferentially feed on larger copepods, such as *Calanus* species, over smaller copepods, such as *Temora* (van Deurs et al., 2013).

Of the *Calanus* copepods in the North Sea, *C. finmarchicus* seems to be a particularly important prey species for *A. marinus* (van Deurs et al., 2009; van Deurs et al., 2013). Sandeels feeding on large *C. finmarchicus* consume more food (i.e. have a higher stomach content weight) than conspecifics feeding on smaller copepods, possibly due to reduced handling time (van Deurs et al., 2013). Further, *C. finmarchicus* is critical for the survival of sandeel larvae due to temporal overlap in larval emergence and egg production by this copepod (van Deurs et al., 2009). However, the abundance of *C. finmarchicus* in the North Sea has declined since the mid-1980s and has coincided with an increase in the congeneric *C. helgolandicus* (Planque and Fromentin, 1996; Beaugrand et al., 2003). While *C. finmarchicus* egg production peaks in March and abundance peaks in April-June, *C. helgolandicus* has high egg production but low abundance in May, with peak abundance in July-September (Planque and Fromentin, 1996; Jónasdóttir et al., 2005). Therefore, while egg production in *C. finmarchicus* coincides with the hatching period and early life of larval sandeels, that of *C. helgolandicus* does not (van Deurs et al., 2009). This difference in phenology has important implications for larval sandeel survival (see *Trends*, below).

Distribution

A. marinus exists in offshore waters in the North Sea (Reay, 1970) and shows high habitat specificity (see above). The patchy distribution of suitable habitat and limited movement of mature sandeels between areas results in distinct aggregations exhibiting population-specific dynamics (Pederson et al., 1999; Frederiksen et al*.,* 2005; Boulcott et al., 2007; Boulcott and Wright, 2011; Jensen et al., 2011). Ellis et al. (2012) presented several sources of information regarding the distribution of sandeels around the UK using previous information (from Coull et al., 1998) and more recent groundfish and ichthyoplankton survey data. Figure 2 shows a map of sandeel nursery grounds, taken from Ellis et al. (2012), based on the presence and abundance of juvenile sandeels: large, dark circles indicate high abundance and high occurrence (present in >70% of tows); small, dark circles indicate low abundance but high occurrence. Including more recent survey data indicates a more extensive distribution of juveniles (yellow areas) than previously reported by Coull et al. (1998; striped polygons). Figure 3 shows a map of spawning grounds, taken from Ellis et al. (2012), based on the presence and abundance of sandeel larvae and eggs: large circles indicate high abundances of larvae (orange) or eggs (brown). Although the spawning grounds reported by Coull et al. (1998; striped polygons) largely correspond with those identified using the more recent data (yellow and blue areas), additional spawning grounds in the Irish Sea and Bristol Channel become apparent with addition of the more recent survey data. Jensen et al. (2011) presented a map of sandeel habitat areas thought to hold high densities of non-buried sandeel in the North Sea and Skagerrak based on the distribution of fishing effort and catch rates. The total area of suitable habitat was 33,566 km^2, equal to 5% of the total area of the North Sea and Skagerrak (Jensen et al., 2011).

Prior to 2010, sandeels in the North Sea were assessed as a single stock (ICES, 2010). However, based on the high habitat-specificity of lesser sandeels (Wright et al., 2000; Holland et al., 2005), the patchy distribution of suitable habitat (Jensen et al., 2011), limited movement between areas once settled (Frederiksen et al*.,* 2005; Christensen et al., 2008) and large regional variation in demography and population dynamics (Boulcott et al., 2007; Frederiksen et al., 2007a; Boulcott and Wright, 2011), sandeels in the North Sea have been treated as seven discrete populations since 2010 (ICES, 2010). The seven sandeel areas (SAs) are shown in Figure 4. The area divisions were based on the locations of sandeel fishing grounds and simulations of larval drift between different areas, such that larval retention within an area was high but movement between areas was low (ICES, 2010). The identification of seven distinct units was broadly supported by otolith chemistry, which showed limited movement of individuals between areas (Gibb et al., 2017).

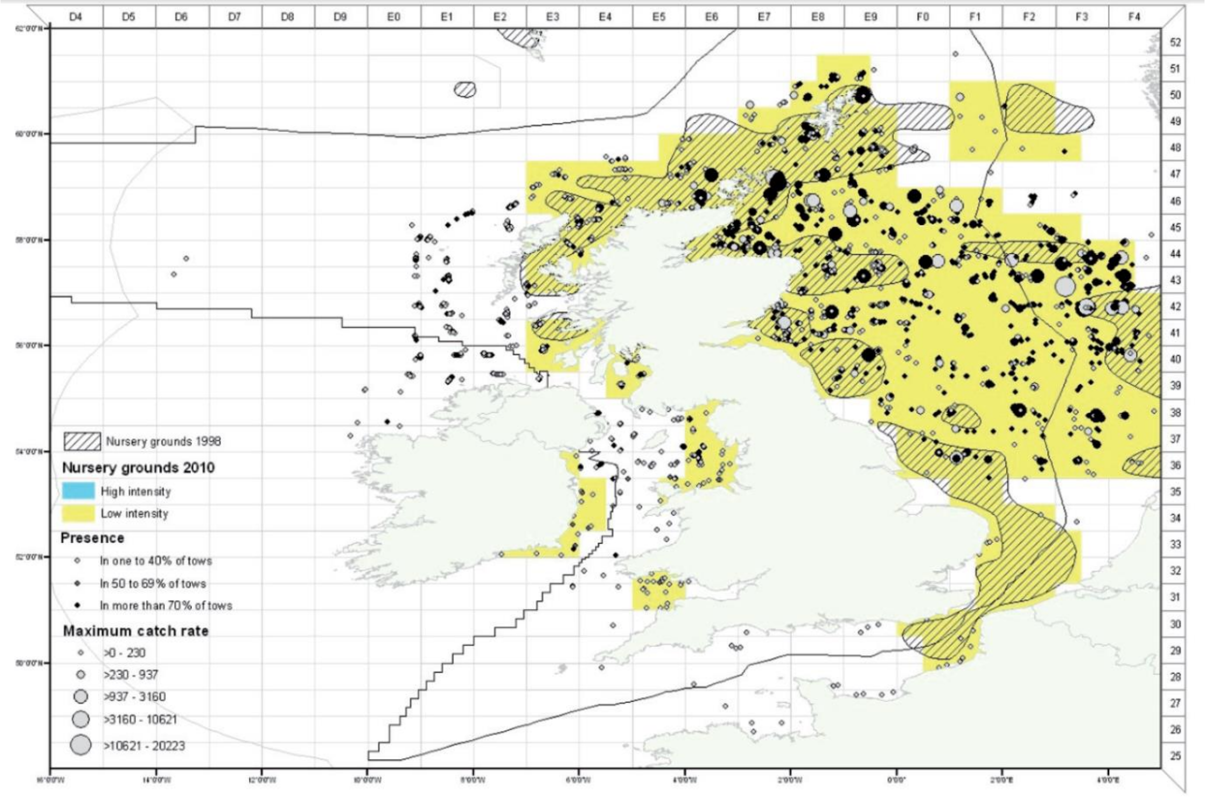

Figure 2. Distribution of sandeel nursery grounds around the UK indicated by the presence of juveniles in groundfish surveys. North Sea sites originally included by Coull et al. (1998; striped polygons) are also shown. Reprinted with permission from Ellis et al. (2012), © Crown copyright, 2012.

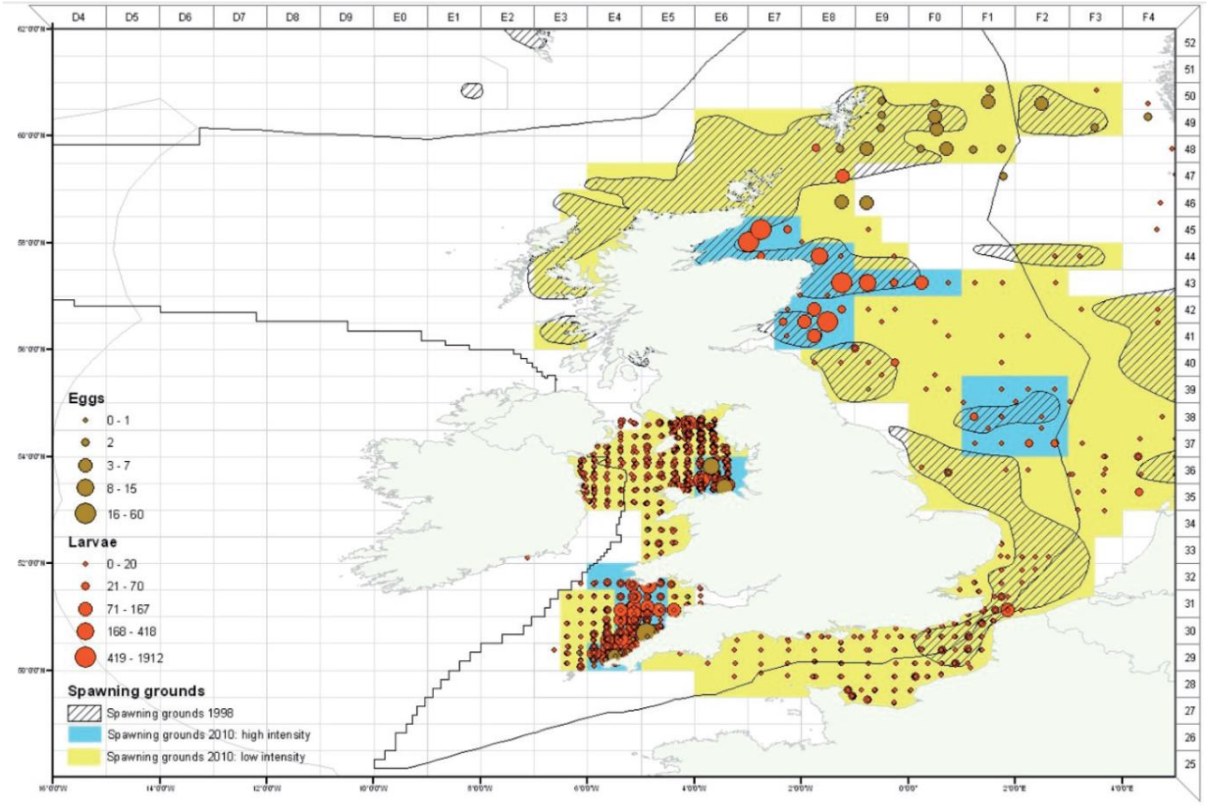

Figure 3. Distribution of sandeel spawning grounds around the UK based on the areas identified by Coull et al. (1998; striped polygons) and recent larval data from ichthyoplankton surveys. Reprinted with permission from Ellis et al. (2012), © Crown copyright, 2012.

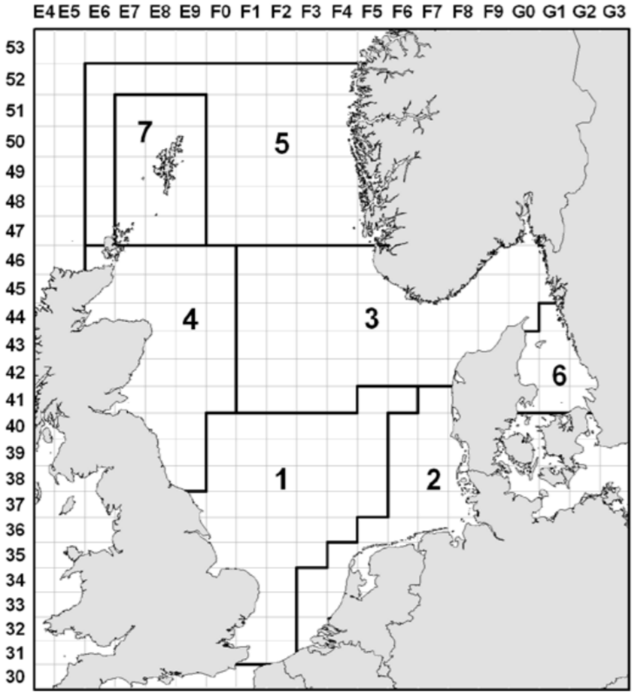

Figure 4. Map of sandeel areas (SAs) in the North Sea and Skagerrak. Reprinted with permission from ICES (2014).

Monitoring populations

Sandeels are important prey for many seabirds, piscivorous fish and marine mammals (see *The importance of sandeels as prey*, below), but are also the target of the largest (by weight) single-species commercial fishery in the North Sea (ICES, 2004). Due to the potential impacts on sandeel-dependent species of local and regional depletion of stocks by industrial fisheries, and to ensure long-term sustainability of the fishery, it is important to monitor sandeel abundance (ICES, 2010; Greenstreet et al., 2010b).

Sandeels are usually surveyed using dredges, grab surveys or non-invasive acoustic surveys at known fishing grounds (Hoines and Bergstad, 2001; ICES, 2010). Dredging for sandeels uses a modified scallop dredge to measure sandeel abundance in the seabed (ICES, 2010), whereas grab surveys involve a bucket of sediment being dredged from the seabed (Hoines and Bergstad, 2001). Acoustic surveys operate by sending regular sound pulses into the water beneath a vessel and using the returning echo to estimate the abundance of the target species, to which the transducer and echosounder are calibrated, in the water column (Fernandes et al., 2000; Greenstreet et al., 2006). Due to the absence of a swimbladder, schools of sandeels produce a distinctive acoustic signature (van der Kooij et al., 2008). As the sampling methods employed rarely have a catchability efficiency (i.e. the proportion of sandeels caught during surveys in a given area) of 1, most surveys can only provide relative indices in abundance rather than absolute total abundance (Greenstreet et al., 2010).

It has been suggested that density estimates of sandeels from grab surveys may give the closest representation of absolute density (Greenstreet et al., 2010), whereas dredge surveys may be less reliable. Johnsen and Harbitz (2013) showed the catchability of survey dredges increased with the density of sandeels, leading to biased results. Further, when compared with grab surveys, dredge catchability was very low, with an efficiency of only 5% that of grab surveys (Johnsen and Harbitz, 2013). Catchability is also known to vary with vessel size and location (ICES, 2010). For example, although they employ similar survey methods, there are differences in age-specific catchabilities between SAs 1 and 3 and SA 4 (ICES, 2010). This is suggested to be a result of the lower selection of the gear for fish <8.5 cm, and the reduction in length-at-age in SA 4 compared to SAs 1 and 3 (ICES, 2010). Additional evidence suggests that estimates based on different survey methods may not be directly comparable. When monitoring sandeels on the Wee Bankie before and after closure of the East Scotland sandeel fishery in 2000, Greenstreet et al. (2010b) found that, although both the acoustic survey and dredge survey showed sandeel biomass initially increased following the closure and then declined, the annual variation in biomass estimated from the two survey methods was uncorrelated ($R^2 = 0.087$). This is perhaps due to dredge surveys estimating sandeel biomass within the sediment while acoustic surveys estimate sandeel biomass in the water column (Greenstreet et al., 2006). This indicates that different survey methods can give considerably different estimates of sandeel biomass even when employed at a similar time.

The daily variation in the amount of time sandeels spend in the water column or buried in the seabed during the spring and early summer (Greenstreet et al., 2006), and the near-continuous burrowing behaviour of adults from late summer, may have contributed to a lack of sandeel monitoring surveys (Johnsen and Harbitz, 2013). However, following a large decrease in North Sea landings in 2003, annual assessments of commercial catch per unit effort (CPUE) have been used to monitor the abundance of 1-group sandeels (ICES, 2010, 2012; Johnsen and Harbitz, 2013). In addition, dredge surveys have been carried out by Denmark and Scotland since 2004 and 2008, respectively, in late November to early December when most 0-group and older sandeels are burrowed in the seabed (ICES, 2010). Further, an acoustic survey in Norway, carried out in the spring, began in 2005 (Johnsen et al., 2009). The data collected from these surveys are used by the International Council for the Exploration of the Sea (ICES) to provide advice on the management and Total Allowable Catch (TAC) of sandeels in the North Sea, with the size of the TAC in a given year predicated on the strength of recruitment. When a dredge survey indicates sandeel recruitment for a given year is outside the range of previous observations and believed to be spurious, Real-Time Monitoring (RTM) is recommended (ICES, 2012). This involves additional surveys that take place in April-May to determine CPUE and thus estimate stock abundance of 1-group sandeels at the start of the fishery season (Vinther and Rindorf, 2016). For example, due to very low results from the dredge survey in November-December 2015 in SA 1 (Figure 4), and following a request from Denmark, TAC for 2016 in that area was informed by CPUE of 1-group sandeel during RTM in early 2016 (ICES 2016). It was argued that RTM allows a more responsive management procedure to stock abundance (ICES, 2016).

Relationships between seabird breeding success and other variables thought to correlate with sandeel abundance have been studied in the absence of regionally-explicit sandeel abundance data (Frederiksen et al., 2007b). Larval sandeel data from the Continuous Plankton Recorder (CPR) have been shown to correlate temporally with larval sandeel data from plankton surveys, 0-group trawl data and recruitment data for some periods and locations (Lynam et al., 2013). Arnott and Ruxton (2002) found that sandeel recruitment in the southwestern part of the North Sea was negatively associated with sea temperature, particularly at the surface, during the egg/larval stages and positively associated with *Calanus* abundance. A study investigating the effects of sandeel abundance on black-legged kittiwake productivity used winter sea surface temperature (SST) and the abundance of copepods as proxies for *A. marinus* abundance (Frederiksen et al., 2007b). However, proxies of sandeel abundance do not always show good predictive power. For example, Eerkes-Medrano et al. (2017) showed that, although kittiwake breeding success was significantly correlated with 0-group sandeel abundance, neither winter SST nor *Calanus* abundance were reliable predictors of sandeel abundance during their study.

Long-term trends

An increase in the sandeel total stock biomass from 1974 to 1984 was followed by a rapid decline between 1984 and 1987 (Anonymous, 1989). Around Shetland there was a marked decline in the total abundance of 0-group sandeels from 1982 to 1988 and a decrease in total production from 1983 to 1987 (Bailey et al., 1991). This was accompanied by a shift in many species of seabird from a predominantly sandeel-based diet to greater consumption of alternative prey, with concurrent declines in several populations (Bailey et al., 1991). The most severe decline was observed in the Arctic tern population which, following a decrease in the percentage of sandeels in the diets of breeding adults from 100% to 20%, underwent a 70% decline in the number of breeding pairs by 1988 relative to 1981-1983 numbers (Bailey et al., 1991). Sandeel landings in the North Sea in recent years are around 50% of those in 1980-2000, and are due largely to a decline in landings from the Dogger Bank area (SA1) (ICES, 2014).

Between 1973 and 2002 mean length-at-date of 0-group *A. marinus* on the Wee Bankie aggregation declined by 11.1 mm, while the mean length-at-date of older sandeels declined by 19.4 mm, corresponding to a 40% decline in energy content (Wanless et al., 2004). A later study extended the period to show the mean length-at-date declined from 1973 to 2006 by 22%, corresponding to a 60% decrease in energy content (Frederiksen et al., 2011). The larger reduction in energy content in the latter study is due to a sharper decline since 2002 (Frederiksen et al., 2011). Further, a study in the Dogger Bank area showed a general reduction in mean length-at-date of 0-group and 1-group lesser sandeels from 1987 to 2011, but no trend in total stock biomass (van Deurs et al., 2013). Although initially driven by later hatching dates, more recent reductions in length-at-date are suggested to have been driven by lower growth rates and changes in size-dependent mortality (Frederiksen et al., 2011). These changes may be a consequence of climate-related shifts in the distributions of copepod prey and other planktivorous fish that compete with *A. marinus* (Frederiksen et al., 2011; van Deurs et al., 2013). For example, van Deurs et al. (2014) observed that the increase in sandeel length-at-date before 1987 and the subsequent decline corresponded with an increase and then decline in the abundance of *C. finmarchicus* before and after the mid-1980s (Planque and Fromentin, 1996). Higher temperatures are associated with a lower abundance of *C. finmarchicus* but a higher abundance of the congeneric species, *C. helgolandicus* (Planque and Taylor, 1998). As discussed above, the annual peak in abundance and egg production of *C. finmarchicus* coincides with the early larval stages of *A. marinus*, whereas that of *C. helgolandicus* occurs later in the year (Planque and Fromentin, 1996; Jónasdóttir et al., 2005; van Deurs et al., 2009). Thus, a climate-induced shift towards a more *C. helgolandicus* dominant community is likely to lead to a mismatch between the timing of copepod prey availability and larval sandeels (van Deurs et al., 2009). The impacts of climate change on sandeels are discussed in greater detail below.

Spatial and temporal variation

Sandeel abundance is controlled by both bottom-up (e.g. availability of food) and top-down (e.g. predation) processes (Frederiksen et al., 2007a), and as a result sandeel population dynamics show high spatial and temporal variability. In the southern North Sea, Malzahn and Boersma (2007) showed that of at least 42 taxa surveyed, only the lesser sandeel showed significant inter-annual variation in abundance. Investigations of length-at-date and age-at-maturity of *A. marinus* found large regional variation across the North Sea, with sandeels in the Firth of Forth maturing later and at a smaller size than elsewhere (Boulcott et al., 2007). Populations also experience regional and seasonal variation in body condition, with better body condition in the northeast sandeel stocks than the northwest and the best body condition attained in summer (Rindorf et al., 2016). Variation in length-at-date between the East Central Grounds of the North Sea and the Norway coast has been inferred as evidence for regional differences in average growth rate (Bergstad et al., 2002). Further, regional variation in the fecundity of lesser sandeel populations has been observed, with low fecundity in the Firth of Forth compared to fishing grounds in central areas of the North Sea (Boulcott and Wright, 2011). Evidence from studies investigating this variation suggests multiple factors contribute to these observed differences.

Inter-annual variation in year-class strength in *A. marinus* populations around the Shetland Isles has been linked to variation in juvenile growth rates, influenced by hatching date of sandeel larvae (Wright and Bailey 1996). Investigation into variation in hatching date found that embryonic development times are influenced by the prevailing temperature and oxygen concentration (Winslade 1971). The degree of synchrony between *A. marinus* hatching date and the spring burst of plankton prey, when copepod densities increase from <200 m^{-3} to >1000 m^{-3}, affects larval growth rate, larval survival and reproductive output throughout life (Wright and Bailey 1996; van Deurs et al., 2010; Gurkan et al., 2012; Gurkan et al., 2013). Other studies have shown recruitment of lesser sandeels is affected by zooplankton availability and abundance (Arnott & Ruxton, 2002; Frederiksen *et al*., 2006), and van Deurs et al. (2009) found that recruitment of *A. marinus* was related specifically to the abundance of the copepod *C. finmarchicus* during the early larval stages.

A range of studies suggest density-dependent effects may contribute to observed spatio-temporal variation in sandeel populations. Arnott and Ruxton (2002) found a negative relationship between abundance of 1-year old sandeels and recruitment. Lynam et al. (2013) showed a pattern of annual cycles between high and low recruitment in the Dogger Bank and Wadden Sea areas. van Deurs et al. (2009) showed that in years with a large population of 1-group sandeels, the positive relationship between spawning stock biomass and recruitment was decoupled. Further, following the initial recovery in sandeel abundance after closure of the fishery off Northeast Scotland and Northumberland in 2000, abundance then declined to very low levels (Greenstreet et al., 2010b). However, this decline coincided with increased survival of larvae ≤20 days old, implying that mortality rates of hatchlings increased as densities of older fish declined (Heath et al., 2012). Possible mechanisms for this density dependence include competition for food and intra-specific predatory behaviour of mature sandeels on younger age classes (van Deurs et al., 2009). Cannibalism of older sandeels on juveniles and larvae has been observed at unexpectedly high rates, with one third of captured individuals from a single haul being confirmed as cannibals and larger fish shown to be more likely to perform cannibalism (Eigaard et al., 2014).

Environmental conditions also contribute to variation in sandeel populations, such as the impact of the prevailing sea circulation on larval advection and recruitment. High displacement of larvae away from spawning grounds has been shown to coincide with years of low recruitment at those sites, whereas years with high larval transport towards spawning grounds coincide with years of high recruitment (Proctor et al., 1998). The poor recruitment around the Shetland Isles in the late 1980s is likely to have been caused by changes in oceanic currents disrupting the immigration of larval sandeels from Orkney spawning grounds into the area (Wright, 1996). Further, the time of day and degree of stratification in the water column have been shown to drive diurnal variation in the vertical distribution of larval sandeels, with night-time distributions being more homogenous than day-time, and a greater abundance of larvae in surface waters in less stratified areas during the day (Jensen et al., 2003).

The importance of sandeels as prey

Sandeels are important prey for a wide range of species (Engelhard et al., 2014). They have been identified as an important intermediate-trophic species, providing a link between primary productivity and top predators (Eliasen et al., 2011; van Deurs et al., 2013). However, the nutritional quality of the lesser sandeel as a prey species shows large variation between seasons and regions in the North Sea (Rindorf et al., 2016). For example, populations in the warmer seas of the north-eastern and northern sandeel banks have higher growth rates and better body condition than populations in the southern and north-western areas (Rindorf et al., 2016). Sandeel condition also changes seasonally, from a relatively low value following spring emergence to a peak in June (Rindorf et al., 2016). Due to the importance of sandeels for many predators, substantial research has been carried out into relationships between sandeels and the species that target them, particularly seabirds (Monaghan, 1992; Engelhard et al., 2014; Macdonald et al., 2015).

Seabirds

Seabirds consume an estimated 200,000 tonnes of sandeels every year in the North Sea alone (Furness and Tasker, 1997). For many species of seabirds in this region, sandeels make up a major component of chick diet (Harris and Wanless, 1991; Wilson et al, 2004; Harris et al., 2005). The internationally important seabird colonies at Shetland are particularly dependent on sandeels during the breeding season due to a lack of other small, lipid-rich prey (Tasker et al., 1987; Bailey et al., 1991; Furness and Tasker, 1997), notably sprats which have been absent from Shetland since the late 1970s (Corten, 1986). The distributions of some seabirds, such as the shag and common guillemot, have been shown to correlate with areas of high sandeel availability (Wright and Begg, 1997; Wanless et al., 1998).

Many studies have been carried out on the black-legged kittiwake *Rissa tridactyla* in the North Sea due to large population declines since the 1990s (Wanless et al., 2007), and the use of this species as an indicator of the state of the marine environment in relation to sandeels (Furness and Tasker, 2000). Kittiwakes feed predominantly on sandeels, exhibiting a seasonal switch from 1-group sandeels in April-May to 0-group sandeels in June-July (Lewis et al., 2001). Thus, breeding success of kittiwakes is positively correlated to the size and abundance of both 0-group sandeels and older age classes (Harris and Wanless, 1997; Lewis et al., 2001; Daunt et al., 2008). Fishery pressure has been shown to have a detrimental impact on kittiwakes in the North Sea, demonstrated by a negative relationship between an annual indicator of breeding success and the annual proportion of the sandeel stock harvested by the fishery (Cook et al., 2013). During operation of the sandeel fishery off the east coast of Scotland, kittiwake breeding success on the Isle of May was found to be severely depressed, and was negatively correlated with fishery effort (Frederiksen et al., 2008). Although closure of the fishery in 2000 caused an initial recovery in kittiwake breeding success, in 2004 this species and many other seabirds suffered breeding failure (Proffitt, 2004). The observed breeding success of kittiwakes in 2004 was much lower than was predicted based on proxies of sandeel abundance, namely SST in the preceding winter, larval biomass in 2003 and the absence of fishery pressure (Wanless et al., 2007). However, dietary monitoring data of kittiwakes and other species in 2004 revealed low availability and nutritional content of 1-group sandeels in addition to a late appearance and small average body size of 0-group sandeels (Wanless et al., 2005; Wanless et al., 2007), details that were not discernible from the variables employed as proxies of sandeel abundance.

Studies by Daunt et al. (2008) and Frederiksen et al. (2008) found that, excluding kittiwakes, there was little evidence of a relationship between sandeel abundance or fishery activity and the breeding success of other seabird species. This may be due to different foraging strategies and a higher sensitivity of surface-feeding species, such as the black-legged kittiwake, to local and regional depletion of sandeel prey (Daunt et al., 2008; Frederiksen et al., 2005; Frederiksen et al., 2008). Furness and Tasker (2000) provided an index to estimate breeding success sensitivity of different seabird species to reduced sandeel abundance, based on five variables. Within the category quantifying the ability to dive, the greatest vulnerability rating was given to surface feeders. Additional vulnerabilities arose from a strong reliance on a small number of prey species and a limited foraging range. Based on this index, they identified that the majority of sensitive sandeel-dependent seabirds breed in Shetland and Orkney and that the species most vulnerable to local depletion of sandeels are terns, followed by kittiwakes. Indeed, during operation of a sandeel fishery near the Shetlands, a decline in landings since the mid-1980s coincided with large declines in the breeding success of surface-feeding seabirds, particularly Arctic terns and black-legged kittiwakes (Bailey et al., 1991; Monaghan, 1992; Furness and Tasker, 1997). Further support comes from Eliasen (2013), who found that ~55% of the annual variation in the breeding success of Arctic terns and black-legged kittiwakes at the Faroes could be explained by local variation in 0-group sandeel abundance, with less strong relationships shown for common guillemots and northern fulmars.

Other studies have shown that both surface-feeding and diving seabirds are negatively affected by low sandeel abundance (Rindorf et al., 2000). A long-term study of seabirds at Foula, Shetland, between 1976 and 2004 showed that the annual estimated total stock biomass of sandeels in the Shetland area could explain annual variation in the breeding success of both surface-feeding and diving seabirds moderately well (black-legged kittiwakes $R^2 = 64\%$, Arctic terns $R^2 = 52\%$, Arctic skuas $R^2 = 71\%$, great skuas $R^2 = 42\%$) (Furness, 2007). However the shape of the relationship varied between species. The effect of increasing sandeel biomass on breeding success of kittiwakes and skuas was logarithmic, with the greatest impact observed at very low sandeel biomass and levelling off at higher values. In contrast, the effect of sandeel biomass on breeding success of Arctic terns was linear, with breeding success continuing to increase up to the maximum estimate of ~150,000 tonnes of sandeels (Furness, 2007). Between 1997 and 1998, a switch in the diet of fulmar chicks from a high proportion of sandeels to a complete absence of sandeels correlated with a reduction in breeding success from 87% to 55% (Gray et al., 2003). However, the chicks that survived to fledge in 1998 were heavier than those in 1997, indicating a higher mortality of lighter chicks, possibly due to a lower tolerance to unfavourable weather conditions (Gray et al., 2003). At Shetland, a decline in the availability of sandeels correlated with a 75% reduction in breeding success of great skuas from 1988-1990 (Klomp and Furness, 1992), with another study between 1994 and 2003 finding a similar pattern (Oswald et al., 2008). Additionally, declines in Arctic skua breeding success and chick growth rates at Shetland were shown to coincide with declines in local sandeel availability (Caldow and Furness, 1991; Phillips et al., 1996).

A study on the Wee Bankie found that the breeding success of common guillemot, black-legged kittiwake and European shag were negatively affected by low 1-group sandeel abundance in June

(Rindorf et al., 2000). In addition, the findings suggested that in years where adult sandeel availability peaked earlier than June, breeding success was lower. Wright (1996) showed that the size and timing of 0-group sandeels in relation to chick hatching were important determinants of seabird breeding success at Shetland. Temporal overlap between sandeel emergence and the timing of breeding is also suggested to be important for shags on the Isle of May, where sandeels are the main prey item fed to chicks (Harris and Wanless, 1991). Thus, seabirds are affected by both sandeel abundance and timing of availability.

As well as being driven by inter-annual fluctuations in sandeel dynamics, phenological mismatch can arise when long-term trends in the timing of critical seabird activities lag behind trends of sandeels. Between 1983 and 2006 the mean date at which 0-group sandeels reached a threshold size became significantly later, with an average delay of almost two weeks per decade (Burthe et al., 2012). Over the same period, the timing of seabird chick rearing in some species on the Isle of May became later (Burthe et al., 2012). However, the phenological shift in chick rearing lagged behind shifts in 0-group size, resulting in a net decline in the length of 0-group sandeels being fed to chicks (Burthe et al., 2012). Despite the assumed reduction in energy value with the observed decline in 0-group mean length, there has been no apparent impact on breeding success on the Isle of May, although this may be due to importance of alternative prey (such as 1-group sandeels) for which data were not available (Burthe et al., 2012).

Disparities between the findings of different studies may arise from variation in the sensitivity of seabirds to different sandeel parameters. A study investigating the effects of sandeels on breeding productivity of multiple-prey loading seabirds found the biomass of larval sandeels was positively related with breeding success in the subsequent year, indicating a dependence of these species on the abundance of 1-group sandeels (Frederiksen et al., 2006). In contrast, breeding productivity of the single-prey loading common guillemot was related to the size and energy content of individual sandeels (Frederiksen et al., 2006). Another factor that may contribute to variation in findings between studies is spatial and temporal intra-specific variation in prey consumption. For example, guillemot chicks are generally fed high energy adult sandeels, whereas adult guillemots feed on smaller, typically 0-group sandeels (Wilson et al, 2004). However, a study of the diet of guillemots around the UK from 2006 – 2011 found that, although sandeels were the most common prey fed to chicks, they contributed a higher proportion of the diet on the west coast relative to the east (Anderson et al., 2014). Further, comparing recent diet data to data collected a few of decades earlier suggests there has been a general decline in the proportion of sandeels in the diet of Guillemot chicks at colonies bordering the North Sea (Anderson et al., 2014).

A low availability of sandeels can also change inter-specific seabird interactions, resulting in additional threats for some species. For example, to compensate for declines in sandeel availability as well as lower fishery discard rates, great skuas have been shown to increase predation rates on other seabirds, such as kittiwakes, and conspecifics (Hamer et al., 1991; Oro and Furness, 2002; Votier et al., 2004; Votier et al., 2008). When sandeels are less abundant foraging adults may have to spend more time away from the nest, leaving their chicks unattended and more vulnerable to predation (Hamer et al., 1991). Rates of kleptoparasitism may also increase as a result of reduced food availability, such as by yellow-legged gulls on Audouin’s gulls and Audouin’s gulls on terns in the Mediterranean in response to reduced availability of discards (Oro and Martinez-Vilalta, 1994; Oro, 1996), and possibly by great skuas on gannets at Shetland during a period of low sandeel availability (Ratcliffe et al., 1998).

Although here we have mostly focussed on seabirds in the UK during the breeding season, sandeels are also important prey elsewhere and during other periods. For example, sandeels are important overwinter prey for puffins on the Faroe Islands, and razorbills and common guillemots in Iceland (Lilliendahl and Solmundsson, 1997; Lilliendahl, 2009; Harris et al., 2015).

An important note when considering the importance of the lesser sandeel for seabirds is that accurate differentiation between *A. marinus* and the inshore congeneric species, *A. tobianus*, is difficult without detailed morphological or molecular examination. This is often not possible during studies of seabird diet and chick provisioning. Distinguishing between the two species can be achieved using molecular analyses, such as protein electrophoresis or mitochondrial DNA analysis (Donaghy et al., 1995; Mitchell et al., 1998). However, for many studies molecular analysis is not feasible. Morphologically the two species differ in the arrangement of scales, such as on the belly and around the caudal and dorsal fins, and the number of elements, such as dorsal-fin rays and vertebrae (Thiel and Knebelsberger, 2016). However, such distinguishing characteristics are difficult to identify without handling the fish, and differentiation between the two species based on morphological features is even more problematic when the sandeels are a small size (Donaghy et al., 1995; Thiel and Knebelsberger, 2016), as they tend to be when fed to young seabird chicks (Lemmetyinen 1973; Frick and Becker, 1995; Stienen et al., 2000). Despite this, many studies that report the importance of *A. marinus* for seabirds are based on observations of prey fed to chicks or consumed during courtship feeding (e.g. Uttley et al., 1989; Monaghan et al., 1992; Robertson et al., 2016). Due to the difficulty of identifying the morphological features described above during observational studies of seabirds, in some cases sandeel observations assumed to be *A. marinus* may have been *A. tobianus*.

Fish

Sandeels are important prey for many piscivorous fish, being the main prey of plaice and dab in Norway (Hoines and Bergstad, 2002), cod on the Faroe Shelf (Magnussen, 2011) and significant prey for anglerfish (Laurensen and Priede, 2005). A study in the North Sea showed that five predatory fish species, including three of high commercial value, had better body conditions in areas or years with high densities of sandeels (Engelhard et al., 2013). In the Tana River in Norway, which holds the largest wild Atlantic salmon stock in the world, it has been suggested that the high abundance of sandeels provides sufficient prey to prevent predation of salmon smolt by piscivorous fish (Svenning et al., 2005).

Predation from piscivorous fish is likely to contribute significantly to top-down pressure on sandeels (Frederiksen et al., 2007a). In fact, the quantity of sandeels taken historically by predatory fish exceeds the quantity taken by the industrial sandeel fishery (Furness, 2003). Following the collapse of the North Sea stock of mackerel in the 1970s, this predator’s annual consumption of sandeels fell from around 2 million tonnes to less than 100,000 tonnes by the mid-1980s (Furness, 2003). The reduction in piscivorous predatory pressure may have allowed seabird populations to increase and coexist with fisheries (Furness, 2003). Therefore, recovery of piscivorous fish stocks in the North Sea may have adverse effects on the availability of sandeels for seabirds, particularly in combination with current fishing pressure (Furness, 2002, 2003). Indeed, a negative correlation between the abundance of herring and sandeels suggests recovery of herring stocks may have resulted in increased top-down pressure on sandeels (Furness, 2004).

Marine mammals

In addition to seabirds and fish, sandeels are also targeted by marine mammals, including porpoises (Santos and Pierce, 2003; Jansen et al., 2013), minke whales in spring (Macleod et al., 2004; Anderwald et al., 2012) and seals (Sharples et al., 2009). Harbour seals that haul out in south-east Scotland are particularly dependent on sandeels, and since closure of the nearby fishery the average size of sandeels consumed by these seals has increased (Sharples et al., 2009).

Impacts of climate change

Over the last 30 years the mean sea surface temperature (SST) of the North Atlantic has increased, with 2000 – 2009 being the warmest decade on record (IPCC, 2007). In particular, the SST around the UK and Ireland is warming at a rate of up to six times faster than the global average (Dye et al., 2013). Within this region SST has increased by 0.1 to 0.5°C per decade, and to a greater extent in coastal waters, since the 1980s due to global climate change and natural variability attributed to the Atlantic Multi-decadal Oscillation (AMO) (Dye et al., 2013). Temperature rises at both the surface and sea bottom of the North Sea are projected to continue late into the 21st Century (Figure 5, Rutterford et al., 2015), with the average annual sea temperature around the UK projected to be 1.5-4°C warmer by the end of the 21st century relative to the 1961-1990 baseline (Lowe et al., 2009).

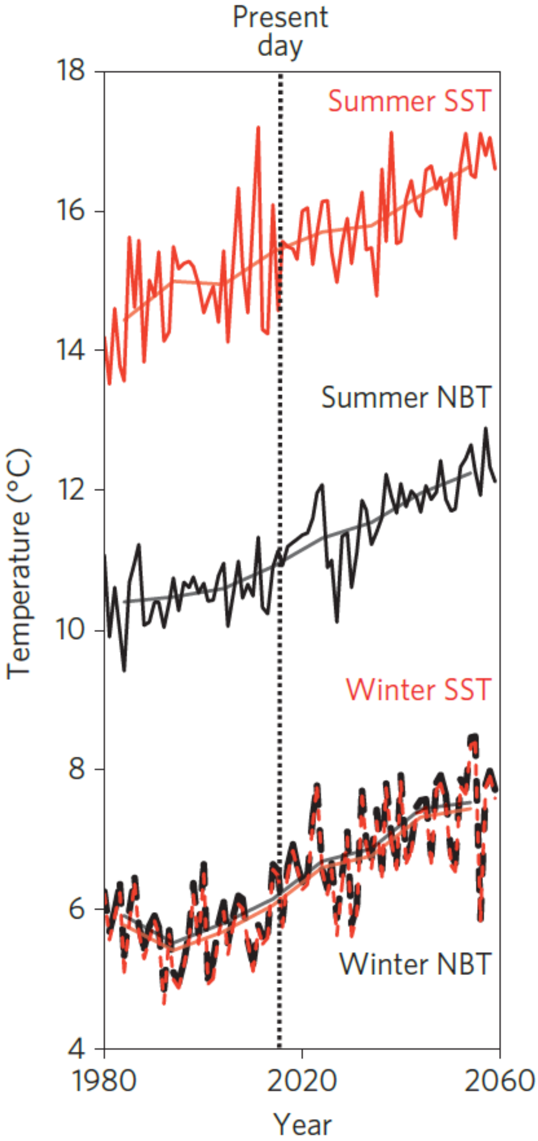

Figure 5. Mean SST (red) and Near Bottom Temperature (NBT; black) in 84 1° x 1° latitude-longitude cells in the North Sea in the summer (July-September, top two plots) and winter (January-March, bottom plot) from 1980-2060, projected by the QUMP_ens_00 northwest European shelf seas climate model. Reprinted with permission from Macmillan Publishers Ltd: Nature Climate Change (Rutterford et al., 2015), copyright (2015).

The distributions of many species of fish in the North Sea have shifted rapidly in response to recent increases in sea temperature, with most species moving northwards or into deeper water (Perry et al., 2005). Of 15 demersal fish species that have exhibited mean latitudinal shifts in response to warming temperatures between 1977 and 2001, 13 shifted northwards (Perry et al., 2005). An increase in the winter bottom temperature in the North Sea of 1.6°C from 1980 to 2004 coincided with a fish assemblage of 28 demersal species shifting into deeper waters at a rate of 3.6 m per decade, with some species shifting up to 10 m per decade (Dulvy et al., 2008). Although some species have exhibited shifts southwards, this may be explained by the greater inflow of warmer waters from the North Atlantic Current into the northwestern North Sea in winter, coincident with a northward shift in the Gulf Stream and a long-term shift towards a positive North Atlantic Oscillation (NAO) phase (Strahler and Strahler, 1997, cited by Perry et al., 2005; Perry et al., 2005; Dulvy et al., 2008). This causes the winter sea bottom temperature to be higher in the northwestern North Sea than in more southerly areas of the North Sea (ICES, 1993; Dulvy et al., 2008). For example, the average winter sea bottom temperature for the period 1980-89 was 7-8°C in the northern North Sea, but 5-6°C in the central and southern North Sea (Figure 6; ICES, 1993). Although many marine species have responded to climatic conditions by moving into deeper or more northerly waters, sandeels are unable to shift in response to warming sea temperatures due to their strong association with sandy, coarse grained sediments and water <100 m deep (Proctor et al., 1998; Holland et al., 2005; Heath et al., 2012).

Multiple studies have found that sandeel recruitment in the North Sea is lower in warmer waters (Arnott and Ruxton, 2002; Frederiksen et al., 2004; Wright et al., 2017), and a decline in recruitment around northern Britain since 2002 has been shown to be negatively associated with increasing temperature (Heath et al., 2012). It is likely there are multiple mechanisms through which an increase in sea temperature affects sandeels, including higher metabolic costs in warmer winters. Van Deurs et al. (2011) estimated the critical length below which *A. marinus* must forage for food during the winter, based on the total energy required for overwintering when excluding reproductive investment, and found that this increases with temperature. The critical length in waters at 10°C was estimated to be 9.5 cm, with an increase of 1°C resulting in an increase in critical length of roughly 1 cm. This was supported somewhat by Wright et al. (2017), who observed that the loss in wet mass of *A. marinus* was greater at higher temperatures, consistent with a higher metabolic cost. However, Wright et al. (2017) found that their oxygen consumption estimates for *A. marinus* at a given temperature were lower than those of van Deurs et al. (2011), who based their estimates on *A. tobianus* due to difficulties in transporting live *A. marinus*. Further, it was argued that the estimates of Wright et al. (2017) better explained gonad size because, based on the predictions of van Deurs et al. (2011), *A. marinus* <12 cm in length and overwintering at 12.5°C would have no surplus energy for reproductive investment. However, although reproductive investment (gonad mass) of *A. marinus* kept at 12.5°C (including individuals <12 cm) reduced proportionally with gutted mass compared with individuals at 7.4°C, it was not halted (Wright et al., 2017). Wright et al. (2017) also observed that somatic energy loss did not differ between sandeels kept at higher and lower temperatures; therefore the difference in mass between the warm and cool treatments was attributed to the change in gonad mass only. This suggests that an increase in overwintering sea temperatures may result in reduced (rather than halted) reproductive investment but may not affect overwinter survival, as there was no impact on somatic mass.

A further potential impact of rising sea temperatures on sandeels is through a reduction in the oxygen content of sediment. Hypoxia has increased in sandy sediments as a result of warming seas, causing a reduction in the amount of suitable habitat for *A. tobianus* by as much as 23% in severe years (Behrens et al., 2009). The proportion of sediments with levels of hypoxia that are lethal for *A. tobianus* is predicted to increase with future temperature increases, resulting in a loss of as much as 40% of suitable habitat in the inner Danish waters during extreme climatic events (Behrens et al., 2009). Although this applies to *A. tobianus*, it is plausible that a similar increase in hypoxia may occur in sandy habitats occupied by *A. marinus*.

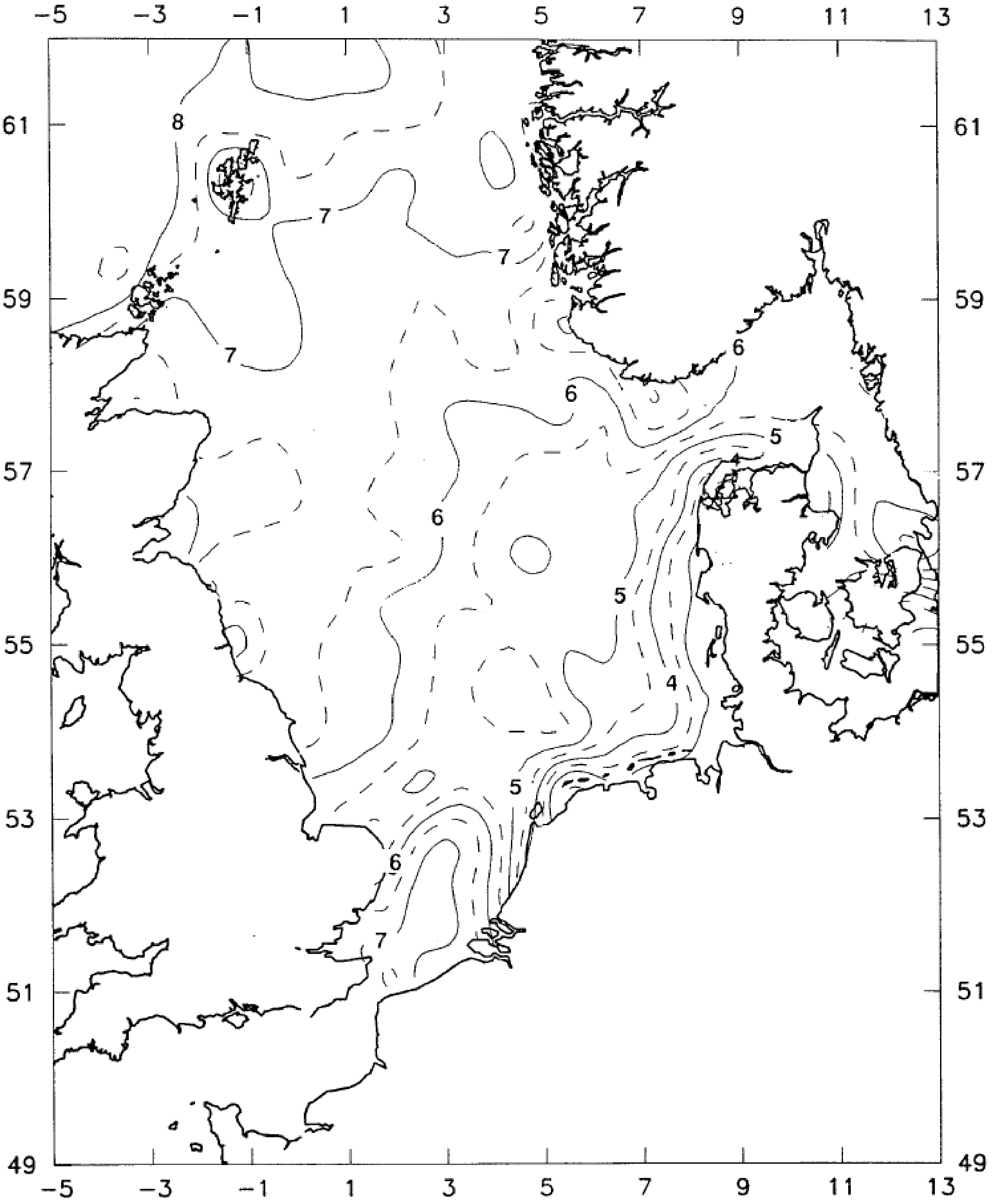

Figure 6. Average winter sea bottom temperature (°C) in the North Sea, 1989-90. Data from the ICES Oceanographic Data Bank. Reprinted with permission from ICES (1993).

However, the greatest impact of climate change on sandeels in the North Sea is likely to act indirectly through a reduction in the availability of their main prey, *C. finmarchicus*. In addition to shifts in fish assemblages in response to increasing temperatures (see above), changes have also been observed in plankton communities (Beaugrand, 2004). A major biogeographical boundary that separates boreal and temperate zooplankton systems, represented by a critical SST threshold of 9-10°C, has shifted northwards by 22 km per year since the 1960s (Beaugrand et al., 2008). Beaugrand et al. (2002) showed that between the 1960s and 1990s zooplankton assemblages associated with warmer temperatures (including *C. helgolandicus*) have shifted northwards at a rate of 250 km per decade in the North Sea, whereas the number of cold-water species (such as *C. finmarchicus*) in this region has decreased. *C. finmarchicus* is a boreal species with the southern limits of its range in the North Sea and a SST thermal optimum of 4.5 – 8.5°C, above or below which occurrence becomes rapidly reduced (Reygondeau and Beaugrand, 2010). Since the 1960s the biomass of *C. finmarchicus* in the North Sea has declined by 70% (Macdonald, et al., 2015), coincident with a decline in climatic suitability (Frederiksen et al., 2013). In contrast, there has been a gradual increase in abundance of the pseudo-oceanic temperate species *C. helgolandicus* since the mid-1980s (Jaschnov, 1970; Beaugrand et al., 2002; Beaugrand et al., 2003). Whereas *C. finmarchicus* was previously the most abundant *Calanus* copepod in the North Sea, data from the CPR shows that since the early 1980s *C. helgolandicus* has been consistently more abundant (Reid et al., 2003; Figure 7). This regime shift coincided with the start of a warm event in the region, caused by higher oceanic inflow of waters originating from more southerly or Mediterranean areas passing around the northwest of Ireland and northwest Scotland and into the North Sea (Reid, et al., 2003). The greater inflows are driven by changes in the strength and patterns of the wind, associated with a positive NAO phase (Reid, et al., 2003).

Mechanisms through which the distribution and abundance of *C. finmarchicus* may be influenced by temperature include impacts on development, mortality, growth rates and ingestion rates (Wilson et al., 2015; Wilson et al., 2016). Further, the maximum potential duration of diapause (a period of reduced metabolic activity in response to low food availability during the winter) is likely to decline with increasing overwinter temperature, as metabolic costs increase with temperature and therefore the lipid reserves upon which the copepods rely are used up at a greater rate (Wilson et al., 2016b). In addition to observed declines in climatic suitability around east Scotland and southern Iceland, further declines are expected to occur in Norway and the Faroes by the mid-late 21st century (Frederiksen et al., 2013). Thus declines in the abundance of this copepod in the North Sea are projected to continue and expand (Frederiksen et al., 2013).

In addition to a reduction in the biomass of the preferred *Calanus* prey of lesser sandeels, there has been a concurrent decline in mean calanoid size by a factor of 2 between the 1980s and 1999 (Beaugrand et al., 2003). Changes in the availability and quality of *Calanus* prey are likely to have serious consequences for lesser sandeels. Recruitment of *A. marinus* is dependent on the abundance of large *C. finmarchicus*, rather than *C. helgolandicus* or overall copepod abundance; thus an ongoing decline of *C. finmarchicus* in the North Sea is likely to be increasingly detrimental to sandeels (van Deurs et al., 2009; van Deurs et al., 2013). The increase in *C. helgolandicus* is unlikely to offset the impact of declining availability of *C. finmarchicus* on sandeels as this copepod has a lower lipid content than *C. finmarchicus* (Macdonald et al., 2015), and, crucially, has a later spring burst which does not coincide with the hatching of sandeel eggs (Jónasdóttir et al., 2005; van Deurs et al., 2009).

Additional potential impacts of climate change on sandeels include the possibility of increased larval predation and competition for food as a result of growing numbers of invasive planktivorous species, such as the comb jelly *Mnemiopsis leidyi* which has been implicated in the collapse of fish stocks in the Black and Caspian Seas (Shiganova et al., 2003; Collingridge et al., 2014). Warmer temperatures are likely to increase overwinter survival of *M. leidyi* in the North Sea, leading to increased abundance and reproduction in the summer (Collingridge et al., 2014).

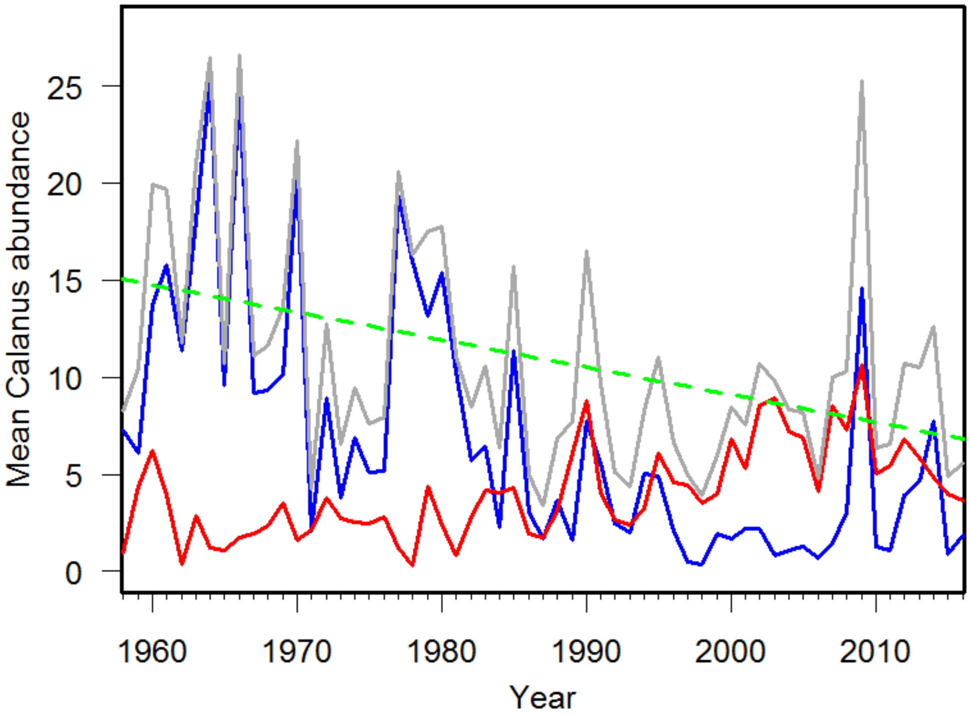

Figure 7. Mean annual *Calanus* abundance in the central North Sea (54N to 58N, 3W to 11E), using data from the Continuous Plankton Recorder provided by SAHFOS. Blue line = *C. finmarchicus*, red line = *C. helgolandicus*, grey line = total *Calanus* abundance, dashed green line = total *Calanus* trend.

Impacts of fisheries

Targeted fisheries

The sandeel fishery began in the late 1950s, following collapse of the heavily fished herring and mackerel stocks, and is now the largest single-species industrial fishery in the North Sea (Furness, 2003). Initially fished at a low level, by 1989 sandeel catch exceeded 1 million tonnes (Furness, 2003), and between 1983 and 2002 the average annual landing was >800,000 tonnes (ICES 2012). However, following a large peak in the late 1990s the annual landings declined, and between 2003 and 2010 the average annual catch was 313,000 tonnes (ICES 2012). The annual landings by sandeel area between 1982 and 2014 are shown in Figure 8, showing the large decline in the early 2000s (ICES, 2014). The decline in stocks of predatory fish, particularly mackerel, and consequent decline in piscivorous consumption of sandeels occurred concurrently with an increase in fishery catches of sandeels, such that between the mid-1970s and mid-1990s the overall consumption of sandeels in the North Sea remained relatively constant (Furness, 2002, 2003). If stocks of mackerel recover and the industrial fishery continues at the current level of effort, the increased competition for sandeels is likely to have a detrimental impact on large populations of seabirds (Furness, 2002).

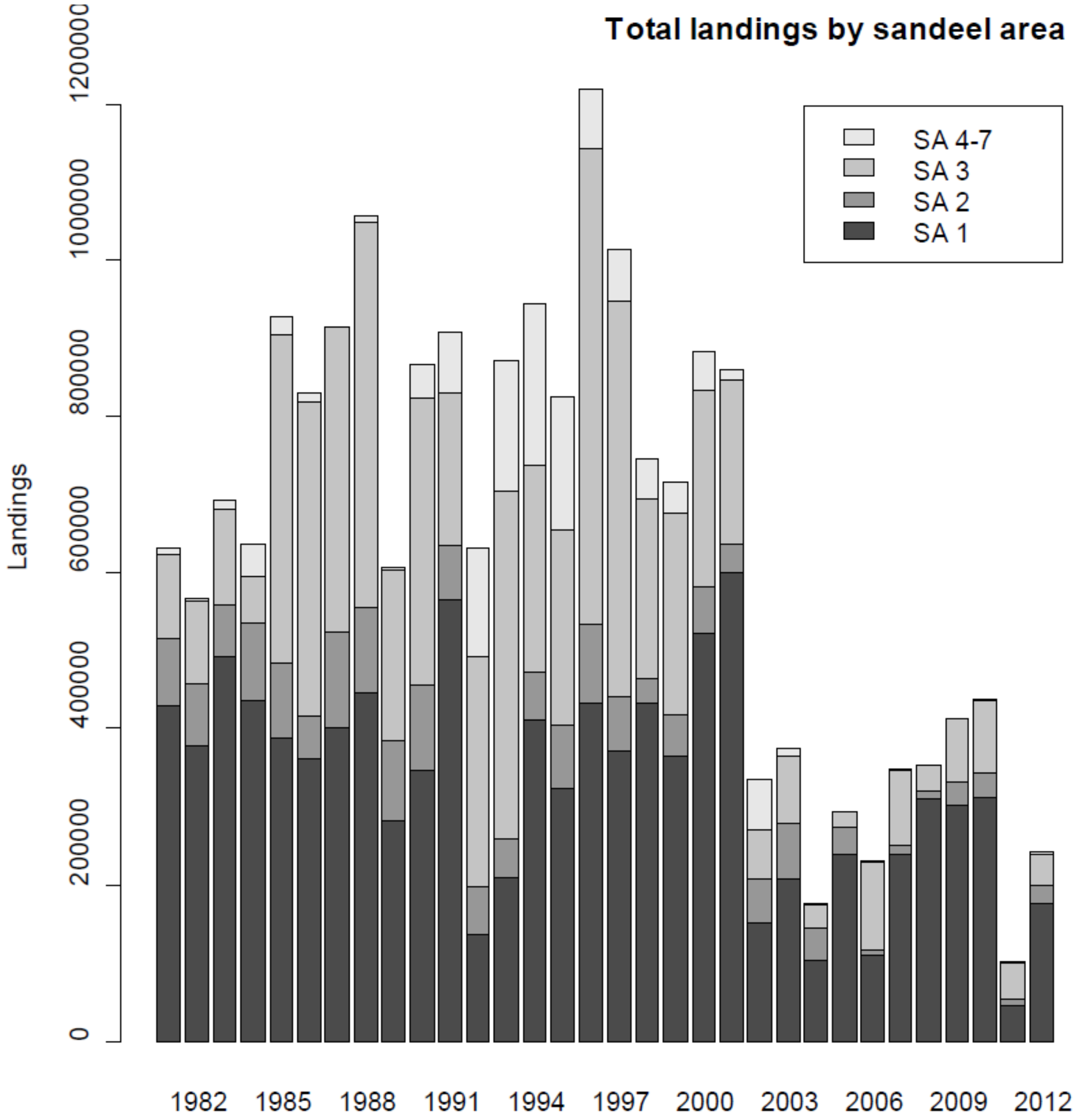

Figure 8. Total landings (tonnes) of sandeels by area from 1982 - 2013. Reprinted with permission from ICES (2014).

During early operation of the North Sea sandeel fishery it was suggested the fishery had no impact on breeding seabirds (Furness, 2003). However, concern about the potential impact of fishing sandeels on seabird breeding success has occasionally led to temporary or long-term closure of a fishery (Greenstreet et al., 2010b). A small, inshore sandeel fishery at the Shetland Isles opened in 1974, with annual landings peaking at just 52,000 tonnes (Dunn, 1998). Despite its small size, the fishery overlapped substantially with foraging areas of internationally important seabird colonies breeding at Shetland (Dunn, 1998). Collapse of the Shetland fishery and the subsequent decline in seabird breeding success around the Shetland Isles in the 1980s led to the precautionary closure of the fishery in 1990 (Hamer et al., 1993; Dunn, 1998; Rindorf et al., 2000; ICES 2005; Greenstreet et al., 2010b). However, although the sandeel population declined during fishery operation and recovered following its closure, this is more likely due to variation in 0-group immigration and survival than changes in fishery pressure (Wright, 1996). The Shetland fishery re-opened in 1995 under restrictions of a TAC of 7,000 tonnes and closure during the months of June and July to prevent competition with seabird colonies (ICES 2005).

Although the small Shetland fishery is unlikely to have been the cause of seabird breeding failure within that area, there is evidence that local depletion of sandeel stocks by a larger sandeel fishery in the North Sea had adverse effects on seabirds (Frederiksen et al., 2004; Frederiksen et al., 2008). A section of the larger, Danish-led industrial sandeel fishery in the North Sea was closed permanently in 2000 due to concerns regarding the negative impact the fishery was having on sandeel-dependent seabirds, particularly kittiwakes (Camphuysen 2005; Daunt et al, 2002; Frederiksen et al., 2008). The closure area, which remains in place today, includes the Wee Bankie, Marr Bank and Berwick Bank and extends from northeast Scotland to Northumberland (Figure 9), covering an area of 20,000 km^2 (De Santo and Jones, 2007; Daunt et al., 2008). The closure appears to have caused an immediate recovery of sandeels within the area, with an observed increase in the biomass of 0-group and 1+ sandeels on the Wee Bankie within the first year; thus, the expected lag in the recovery of stocks was not observed (Greenstreet et al., 2006). This suggests high recruitment and low mortality of sandeels in 1999, possibly due to low levels of fishing effort in the area (Greenstreet et al., 2006). However, by 2007 the spawning stock biomass (SSB) had declined to levels similar to those when the fishery was operating, indicating the operation of other limiting factors (Greenstreet et al., 2006; Greenstreet et al., 2010b). This decline indicated that, even without fishing mortality, sandeel abundance will decline if recruitment cannot compensate for natural mortality (Greenstreet et al., 2006; Greenstreet et al., 2010b). Thus, in addition to monitoring the abundance of sandeels while a fishery is active, it is also important to monitor sandeel abundance after a fishery closes in order to assess the effectiveness of the closure (Greenstreet et al., 2010b). This is often difficult because much of the data used to assess sandeel stocks comes from operating fisheries; therefore, without presence of a fishery-independent monitoring programme, closure of a fishery removes the source of sandeel data (Greenstreet et al., 2010b).

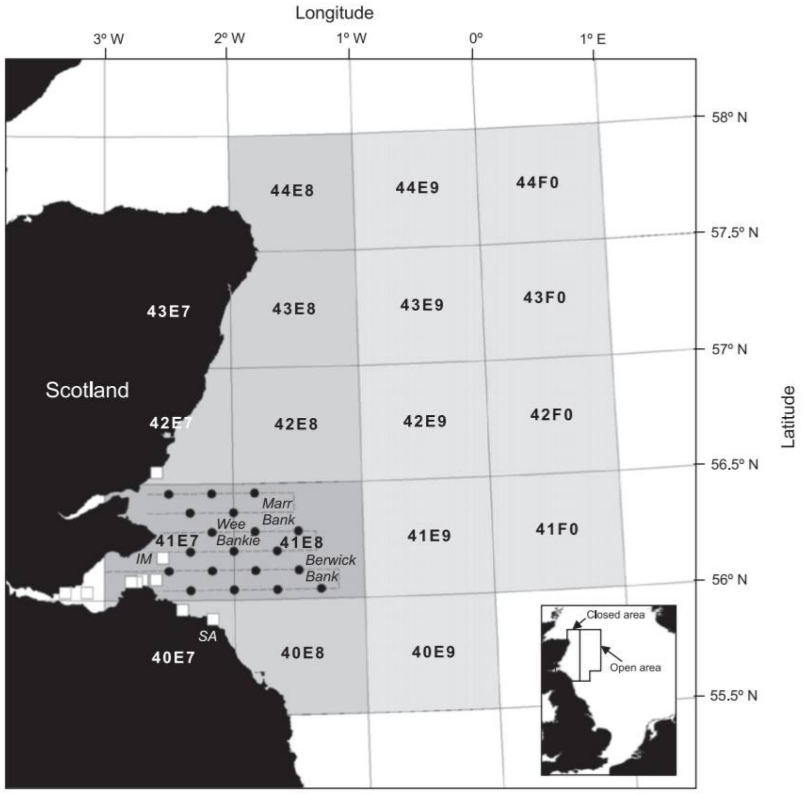

Figure 9. Map of 18 ICES rectangles. The darkest and second darkest rectangles (44E8, 43E8, 42E8, 41E8, 40E8, 43E7, 42E7, 41E7 and 40E7) indicate the area of sandeel fishery closure. Reprinted with permission from Daunt et al. (2008). © Canadian Science Publishing or its licensors.

Although removal of fishery pressure does not guarantee recovery of sandeel stocks (Greenstreet et al., 2010b), it does increase the likelihood that the stock will recover in years of good recruitment, as demonstrated by the immediate increase in biomass on the Wee Bankie following closure of the fishery off the east coast of Scotland. At Shetland, the decline in seabird breeding success and sandeel landings in the 1980s is more likely to have been driven by low recruitment, caused by low rates of larval advection to Shetland from spawning grounds, than by fishing pressure (Wright, 1996). The Shetland population is known to experience high variation in sandeel recruitment (ICES, 2002), and simulations have demonstrated that, even with very limited fishery activity, seabird populations in this area would suffer breeding failure on average every 6 years (Poloczanska et al., 2004). Therefore recruitment may be a more important driver of population dynamics than fishing mortality. However, the risk of sandeel stock collapse increases with fishing pressure (Poloczanska et al., 2004).

Current operation of the sandeel fishery on Dogger Bank may be having an impact on piscivorous fish and seabirds, due to overlap between areas of high fishery effort and foraging areas of multiple predatory species (Engelhard et al., 2008; Carroll et al., *in press*). Carroll et al. (*in press*) found kittiwake breeding success at a colony on the east coast of England was positively associated with high sandeel SSB in the preceding winter, but negatively correlated with sandeel fishing mortality at Dogger Bank two years earlier. The effect of fishing mortality on kittiwake breeding success remained significant after accounting for temporal trends, indicating that this is a robust relationship (Carroll et al., *in press*). In addition, intensive fishery activity in this area may disrupt larval advection and thus reduce the abundance of larval biomass in areas dependent on this spawning ground, thus indirectly influencing recruitment (Cook et al., 2013). Finally, exploitation from industrial fisheries has been shown to affect the age and length composition of sandeel populations in the North Sea, with narrower age and length distributions found in fished areas (Bergstad and Hoines, 2001).

Other fisheries

The North Sea herring and mackerel stocks collapsed in the 1970s due to overfishing and unfavourable environmental conditions (Hay et al., 2001; Jansen, 2014). The coincident increase in sandeel biomass may have been the result of the replacement of the mid-sized predators by the smaller, opportunistic sandeels (Sherman, 1981) and a release of sandeel larvae from predation pressure (Furness 2004; Frederiksen et al., 2007a). Recovery of piscivorous fish stocks in the North Sea may result in increased top-down pressure on sandeels; it is possible that an increase in herring SSB with a concurrent decline in sandeels at Shetland since the early 1980s is the result of such a relationship (Frederiksen et al., 2007a).

Potential impacts of Marine Protected Areas

MPAs are established to protect and conserve marine species, habitats, ecosystems and ecological processes (OSPAR Commission, 2013). For a species such as the lesser sandeel, MPAs may have dual benefits for populations within a region. First, recovery of sandeel stocks within the protected area is likely to occur as a result of the removal of fishing-related mortality (Christensen et al., 2009). Secondly, the abundance of sandeels in adjacent areas and those connected to the MPA by oceanic currents may increase as a result of increased larval spillover from within the protected area (Christensen et al., 2009).

The North-West Orkney MPA was designated in 2014 based on the importance of the area for sandeels and geomorphological features, such as sand banks and sediment wave fields (JNCC, 2014). Larvae from this spawning ground are transported by sea currents and recruit to other grounds, including Shetland, thus playing an important role in supporting Scottish sandeel populations (JNCC, 2014). Although no sandeel fishing is allowed within the MPA due to it overlapping an area of zero TAC, fishing activities targeting several other species do occur, including demersal seine netting, pelagic trawling, creeling and otter trawling (JNCC, 2014). JNCC state that these activities are not capable of affecting the sandeels or sand banks within the North-West Orkney MPA, and therefore have proposed that they require no management interventions (JNCC, 2014). In the Mousa to Boddam MPA off the southeast coast of Shetland, also designated to protect sandeels and sandy habitat, demersal fishing activities such as trawling, dredging and creeling were considered by SNH to be capable of affecting the protected features (SNH, 2013). In particular, sub-surface abrasion and penetration caused by fishing gear was considered to be a potential pressure on sandeels, with the greatest impacts expected from hydraulic gear followed by other dredges (SNH, 2013). It has been reported that hydraulic dredging can leave furrows up to 20 cm deep in the seabed (Gilkinson et al., 2003), while scallop dredging can penetrate up to 6 cm into the sediment (Currie and Parry, 1996). Given that sandeels tend to burrow within the top 4 cm of the seabed (Behrens et al., 2007), it seems likely that surface abrasion to depths of 6 cm could impact a large proportion of the sediment suitable for sandeels. In the case of the Mousa to Boddam MPA, it was recommended that pressures associated with demersal hydraulic gear should be removed or avoided in the MPA. Despite identifying the potential impact of other demersal fisheries, such as scallop dredging, no additional management was recommended (SNH, 2013).

As management of both MPAs is yet to be finalised there are currently no restrictions on fishing in these areas as a result of the MPA designation. A consultation on the Mousa to Boddam MPA is expected to open in October 2017; consultations of the North-West Orkney MPA are ongoing.

Potential impacts of offshore wind farm development

Offshore wind farms may be beneficial in some marine systems by acting as artificial reefs (Wilhelmsson et al., 2006). However, marine communities on sandy areas, such as the North Sea, are very different to those on reefs (van Deurs et al., 2012). Van Deurs et al. (2012) conducted a study into the short-term and long-term effects of an offshore wind farm off western Denmark on three sandeel species: *A. marinus*, *A. tobianus* and *Hyperoplus lanceolatus*. A short-term positive effect of the wind farm on sandeel density was observed, but this effect was driven only by changes in the most abundant species, *H. lanceolatus*. It is possible this increase was due to a reduction in the silt-clay content of the seabed as a consequence of the wind farm, although this may have been coincidental (van Deurs et al., 2012). There was no significant effect of the wind farm on the less abundant *A. marinus* or *A. tobianus*, but both species experienced declines in the impact area and within a closely-situated control area. The decline was greatest for *A. marinus* and may have been driven by low rates of larval advection into the area (van Deurs et al., 2012). In another study, an observed switch in dominance from herring to sandeels occurred immediately after construction of an offshore wind farm in the Dutch North Sea (Lindeboom et al., 2011). However, this was observed within both the impact and control areas (Lindeboom et al., 2011), and therefore could not be attributed to a wind farm effect.

In addition to potentially acting as an artifical reef, it is possible that offshore wind farms may be beneficial for marine communities due to the exclusion of fishing pressure within the wind farm area, thereby inducing an MPA-effect (van Deurs et al., 2012; Ashley et al., 2014). Although this was not detected in the study by van Deurs et al. (2012), this may be due to the low levels of sandeel fishing in the control area.

During consultation of the proposed offshore wind farm at Dogger Bank Creyke Beck, JNCC and Natural England raised concerns regarding the potential negative impacts on sandeels of physical disturbance to the seabed, alteration of the substrate and suspended sediment (Brown and May Marine, 2014). However, the risks of adverse impacts of the development were assessed as being minor, and it was stated that only 1.8% of preferred sandeel habitat in the area would be impacted under a “worst case scenario” (Brown and May Marine, 2014).

Summary

Lesser sandeels (*Ammodytes marinus*) are found in offshore waters of the North Sea and associate with coarse-grained sand into which they tend to bury at night and during the winter. They are important prey for many seabirds, fish and mammals and form the largest single-species fishery in the North Sea. The high habitat specificity, low dispersal of adults and shoaling behaviour in the spring and summer renders lesser sandeels vulnerable to local depletion. Spatial and temporal variation in population dynamics are driven by a range of factors, including oceanic currents influencing larval dispersal, density-dependent effects driving competition and predation, regional variation in hatching date and growth rate, and the abundance and availability of plankton prey at critical life stages. A decline in sandeel abundance in recent years is likely to have been caused primarily by a climate-driven reduction in the abundance of the preferred prey, *Calanus finmarchicus*, in the North Atlantic including the North Sea. Although large-scale climate change may be the predominant cause of the sandeel decline, reducing sandeel fishery mortality can allow populations to recover following years of high recruitment. Sea temperatures are predicted to continue rising, causing further declines in the availability of *C. finmarchicus*, reduced reproductive potential of sandeels due to higher metabolic costs and possible problems of hypoxia in sandy sediments occupied by burying sandeels.

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