Benguela Current Forage Fish Workshop
2 - 4 November 2020 – Online via GoToMeeting

Doc: BCFF Inf. 6
Date: 26 October 2020

Sandeel stocks and seabirds in the North Sea

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The North Sea has been one of the most heavily fished of the world's seas for over 150 years, but also supports a high abundance of seabirds, with between 2 and 4 million breeding pairs of seabirds around the North Sea (Dunnet *et al*. 1990; Mitchell *et al*. 2004). These include many seabirds that feed primarily on sandeels, in particular the lesser sandeel *Ammodytes marinus*, during the breeding season (Furness and Tasker 2000). Because of the particular ecology of sandeels, which spend most of the winter buried in the sea bed so are unavailable as food for most seabirds in winter (Rindorf *et al*. 2000; van Deurs *et al*. 2011), many of the seabirds that depend on sandeels when breeding migrate out of the North Sea after the breeding season or switch to other foods (Dunnet *et al*. 1990; Mitchell *et al*. 2004). Internationally important seabird populations of the North Sea rely heavily on sandeels, with breeding success and survival influenced by sandeel availability (Furness and Tasker 2000; Furness 2002; Frederiksen *et al.* 2004; Davis *et al*. 2005; Frederiksen *et al.* 2005; Wanless *et al.* 2005). Hence, the fate of North Sea seabird populations is closely linked to that of sandeels.

However, linking the demography of seabirds to sandeel abundance is complicated. Sandeels (adults and larvae) are a major prey of many predatory fish, so their abundance may be influenced by 'top-down' factors such as variation in abundance of large predatory fish and the strength of this interaction may vary around the North Sea depending on the spatial distributions of the main predatory fish (Frederiksen *et al*. 2007a). Sandeels are the target of an industrial reduction fishery converting small fish into fish meal (ICES 2010). Sandeels are sensitive to climate change, showing a relationship between recruitment and sea temperature (Arnott and Ruxton 2002; Macdonald *et al*. 2015; Carroll *et al*. in review), and showing impacts from bottom-up forcing of the ecosystem caused by climate affecting zooplankton communities (Wanless *et al*. 2004; Frederiksen *et al*. 2006; van Deurs *et al*. 2009; Frederiksen *et al*. 2013; van Deurs *et al*. 2015). Assessment of sandeel abundance has largely depended on commercial fishery catch data rather than on fishery-independent surveys (ICES 2010). Management of the sandeel fishery in the North Sea has historically treated the entire North Sea as only two management units, recognising that there is a smaller but discrete sandeel stock at Shetland in the northwestern corner of the North Sea, but treating the rest of the North Sea as a single unit for stock assessment (ICES 2010). Thus the spatial scale of foraging seabirds from breeding colonies does not map onto sandeel stock assessments in a convenient way. All of these issues complicate assessing the relationship between seabird populations and their sandeel prey base.

In addition, aspects of seabird ecology complicate the assessment. The importance of sandeels in seabird diets varies among species (Furness and Tasker 2000), varies within species in different parts of the North Sea (Furness and Tasker 2000; Bull *et al*. 2004), and varies among years (Lewis *et al*. 2001; Wanless *et al*. 2007; Anderson *et al*. 2014). Breeding success of seabirds is not only affected by sandeel abundance, but also by abundance of other alternative foods, by impacts of predators (Oro and Furness 2002; Mitchell *et al*. 2004), by disturbance at colonies (Mitchell *et al*. 2004), by temperature influences (Frederiksen *et al*. 2007b; Frederiksen *et al*. 2008a; Oswald *et al*. 2008; Oswald *et al*. 2011; Burthe *et al*. 2014; Russell *et al*. 2014), storminess (Newell *et al*. 2015) and wind (Taylor 1983; Furness and Bryant 1996). In addition, seabird species with different ecologies may have more or less 'spare' time in their breeding season daily activity budget and other mechanisms by which they can increase or decrease foraging effort to compensate to some extent for small changes in food abundance (Furness and Tasker 2000; Smout *et al*. 2013). Some seabirds may choose not to breed if food is scarce (Reed *et al*. 2015) and if, as seems likely, the birds that choose not to breed in a poor season are birds of low quality or low body condition, then the breeding success of those that remain in the breeding population may increase, while breeding numbers, but not the total population size, may decrease. Since monitoring of population size tends to be based on counting breeding birds at colonies, such responses to changes in food supply may give misleading impressions of population change (Davis *et al*. 2013; Miles *et al*. 2015). Stress and energy costs of breeding when food is in short supply may carry over into the migration behaviour (Bogdanova *et al*. 2011; Frederiksen *et al*. 2012; Schultner *et al*. 2014) and overwinter survival of adult seabirds, while variation in food abundance in wintering areas may carry over into breeding success of birds in their following breeding season and affect survival rates of birds from different colonies (Harris *et al*. 2000; Reynolds *et al*. 2011; Reiertsen *et al*. 2014; Szostek and Becker 2015).

An historical perspective indicates both the importance of top-down natural predation rates on sandeels by large predatory fish and commercial fishing targeting sandeels as factors influencing sandeel stock size, and therefore food availability to seabirds. Abundances of large predatory fish (such as cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, and whiting *Merlangius merlangus*) in the North Sea declined with heavy fishing effort in the 1890s, recovered briefly during the two world wars in 1914-18 and 1939-45, but declined again after 1945 (Daan *et al*. 1990). Heavy fishing on herring *Clupea harengus*, including harvest of immature fish for fish meal production, reduced the North Sea herring stock to very low levels in the 1970s (Daan *et al*. 1990). With reduction in herring abundance, pelagic fishing effort switched to North Sea mackerel *Scomber scombrus*, dramatically reducing that stock (Daan *et al*. 1990). There was then an increase in sandeel abundance which has been interpreted as a response to reduced predatory impact from large piscivorous fish such as cod, and reduced competition for zooplankton food due to the depletion of stocks of herring and mackerel (Sherman *et al*. 1981; Daan *et al*. 1990). The North Sea industrial fishery for fish meal production switched from targeting immature herring and mackerel to targeting sandeels. The fishery expanded rapidly in the 1970s, reaching peak landings of around 1 million tonnes of sandeels per year in the late 1990s (ICES 2015). Sandeels were harvested from suitable sand banks (Wright *et al*. 2000) at Shetland in the northwest North Sea, off southern Norway in the north-east North Sea, off Denmark in the east, off Scotland in the west, and from the Dogger Bank in the southern North Sea. The sandeel fishery was then the biggest single-species fishery in the region (Furness 2002; Reilly *et al.* 2014). Since the 1990s, sandeel landings have declined to around 100,000-400,000 tonnes per year, with Denmark taking the majority (ICES 2015). The most productive area is now the Dogger Bank (van der Kooij et al. 2008; ICES 2015), a shallow area in the southern North Sea, with the sandeel stocks currently depleted at Shetland, Norway and off Scotland and fishing for sandeel mostly closed in those areas (ICES 2010; ICES 2015). There is evidence that the North Sea sandeel fishery has still been exceeding levels that are sustainable for top predators in recent years (Cook *et al.* 2014).

From the 1970s to 2000s the sandeels in the North Sea were managed as two separate stocks or management units; a small discrete stock at Shetland, and the rest of the North Sea as a single management unit, or separated into ‘northern’ and ‘southern’ components of the North Sea. Because sandeel larvae drift with currents for a short period in spring (Heath *et al*. 2012) before settling into suitable seabed habitat (sandy sediments with a low silt content; Wright *et al*. 2000), and adult sandeels remain on the same area once settled, it was clear that there is only limited connectivity between sandeel sub-populations in different areas of the North Sea, but management only began to assess these discrete units separately after 2009 (Boulcott *et al*. 2007; Christensen *et al.* 2008; Jensen *et al*. 2011; ICES 2015). In particular, it has been difficult to relate the breeding success of seabirds at numerous colonies around the North Sea with the large single management unit of sandeels that encompasses most of the North Sea. Separation of stock assessment into smaller areas (Fig. 1) makes such analysis possible. Even so, there are spatial mis-matches between seabird breeding season, at sea distributions from colonies and the areas covered by sandeel stocks. However, Frederiksen *et al*. (2005) showed that black-legged kittiwake breeding success at different colonies around the North Sea showed strong correlations across years among colonies within the same general area, but showed independent trends between areas. The areas identified within which changes across years were coherent mapped onto areas that had been identified by studies of larval drift of sandeels, suggesting that the local stock dynamics of sandeels in different parts of the North Sea was driving variation in kittiwake breeding success.

In Shetland, a long time-series of breeding success of seabirds is available from the early 1970s for the island of Foula, a very large seabird colony to the west of Shetland. The Shetland sandeel stock is distributed over a wider area than seabirds forage from Foula, so the assumption has to be made that the Shetland stock density provides a proxy for the sandeel population density within the areas used by breeding seabirds from Foula. Given the large changes in sandeel abundance, this is probably reasonable, but it is an assumption that has not been possible to test. Breeding success of Arctic skuas (parasitic jaegers) *Stercorarius parasiticus* at Foula between 1976 and 2004 shows a strong correlation with sandeel stock abundance, a natural logarithm regression fitting significantly better than a linear regression, and sandeel stock abundance explaining 71.2% of the variance in breeding success (Fig. 2). Arctic skuas feed almost exclusively on sandeels at Shetland, stealing those from breeding Atlantic puffins *Fratercula arctica*, black-legged kittiwakes *Rissa tridactyla,* and Arctic terns *Sterna paradisaea.* Survival rates of adult Arctic skuas are also affected by sandeel abundance (Davis *et al*. 2005). Unfortunately, with the decline in sandeel abundance, closure of the fishery resulted in loss of the fishery-derived data required for stock assessment, and fishery-independent surveys were ended some years after closure of the fishery on the basis that the small stock biomass and lack of a commercial fishery did not justify expenditure of government money on stock assessment. Data on breeding success have been collected since 2004, but there are no data on sandeel abundance in that stock after 2004.

Breeding success of black-legged kittiwakes at Foula in the same years also show a strong relationship, better described by a logarithmic rather than linear relationship with sandeel stock biomass (Fig. 3), with 63.6% of variation in breeding success explained by sandeel abundance (see also Furness 2007; Cury *et al*. 2011). Kittiwakes breeding at Shetland feed almost exclusively on sandeels during the breeding season so this strong influence of sandeel abundance is no surprise. For the great skua *Stercorarius skua*, the relationship is also logarithmic rather than linear, but is more noisy, with 41.8% of the variance explained. This lower fit is likely to be due to the fact that great skuas will feed their chicks on fishery discards when sandeels are less abundant (Bicknell *et al*. 2013), so have the ability to switch diet and can breed successfully if discards are plentiful (Votier *et al*. 2004). Arctic tern breeding success at Foula shows a significant relationship with sandeel abundance, but is well-described by a linear function (which explains 52.4% of the variance in breeding success). The linear function suggests that sandeel abundance never reached such high levels as to provide higher prey density than needed by breeding terns. The high variation around the regression is influenced by the sensitivity of breeding terns to a range of environmental factors affecting breeding success, including variation in weather conditions and predation impacts among years. The clear relationships seen for these species at Foula can be seen for colonies in other parts of Shetland too (e.g. Hamer *et al*. 1993; Foster and Marrs 2012), although no other Shetland colonies provide such long time series of data. In contrast to these species, breeding success of some seabird species shows very little, or no, relationship with sandeel stock abundance. For example, northern gannet *Morus bassanus* breeding success at Shetland colonies has remained consistent and high throughout the study period. Gannets fed mainly on sandeels when sandeels were abundant at Shetland, but when the stock declined, gannets switched diet to herring, mackerel and discards, and showed no reduction in breeding success.

When a sandeel fishery operated off the Firth of Forth (east Scotland) in the 1990s, black-legged kittiwakes in the region showed reduced breeding success and survival (Rindorf *et al.* 2000; Frederiksen *et al.* 2004; Daunt *et al.* 2008; Frederiksen *et al*. 2008b). Frederiksen *et al*. (2004) showed that kittiwake breeding success at the Isle of May colony correlated with sea surface temperature in the area, but was significantly lower in years when sandeel fishing took place than it was in years without sandeel fishing (Fig. 6), indicating strong influences of both climate change and the sandeel fishery. A closed area encompassing much of Scotland's east coast was established in 2000: sandeel biomass initially rebounded, but has since continued to decline, likely due to worsening environmental conditions (Greenstreet *et al.* 2010a,b). However, the closure, which is still in place, did appear to benefit kittiwakes, known to be sensitive to sandeel availability (Furness and Tasker 2000; Frederiksen *et al.* 2004; Daunt *et al.* 2008).

Given that sandeel recruitment is reduced in warmer sea conditions (ICES 2010), it is somewhat counterintuitive that with recent climate change and clear bottom-up shifts in the North Sea ecosystem (Frederiksen *et al*. 2013), the largest and earliest decline in sandeel abundance occurred in the northern North Sea (Shetland), followed by declines in the Norwegian sector then off east Scotland, with the most robust stock being that on the Dogger Bank (ICES 2015; Carroll *et al*. in review). The Dogger Bank stock now supports the remaining fishery on sandeels, but with a much reduced quota. Near the Dogger Bank is the largest black-legged kittiwake colony in the North Sea, at Bempton Cliffs. Breeding success of that population has been monitored by RSPB who manage a reserve at Bempton that holds this very large colony of kittiwakes. The breeding success at that colony has been much higher than breeding success of kittiwakes at colonies in the northern North Sea, suggesting better foraging conditions for the birds at Bempton. Breeding adults from that colony have been tracked using GPS loggers, and the tracking study shows that they forage predominantly closer to the colony than the area where sandeel fishing takes place on the Dogger Bank, although there is some overlap between the fishery and kittiwakes. Analysis of kittiwake breeding success, however, shows a strong decrease in breeding success two years after high fishing mortality has been imposed on the Dogger Bank sandeel stock (Fig. 7). Further analysis of these time series and of climatic data has indicated that the Bempton kittiwake breeding success is affected both by climate change and by sandeel fishing intensity on the Dogger Bank stock (Carroll *et al*. in review).

In conclusion, while some seabirds are able to switch diet so are not strongly affected by changes in sandeel abundance, some species, such as kittiwake and Arctic skua are very sensitive to variations in sandeel stock biomass. In order to demonstrate these relationships, a long time-series of data is a prerequisite, but also the fish stock data needs to be for an area that is appropriate in relation to the area used by foraging breeding seabirds. Appropriate does not necessarily mean exactly the same area; studies in the North Sea show that clear relationships can be seen even when the fish stock assessment area is only partly overlapping with the foraging distribution of breeding seabirds. Ecological relationships can differ for many reasons, including differences in the relative importance of bottom-up versus top-down control. Seabirds may be able to buffer effects of reduction in food abundance through behavioural modifications or by skipping breeding in poor seasons, and relationships with prey abundance may not be evident over a wide range of prey abundances but only show when the prey abundance falls below a critical threshold (Cury *et al*. 2011; see also Fig. 4 as a good example of this).

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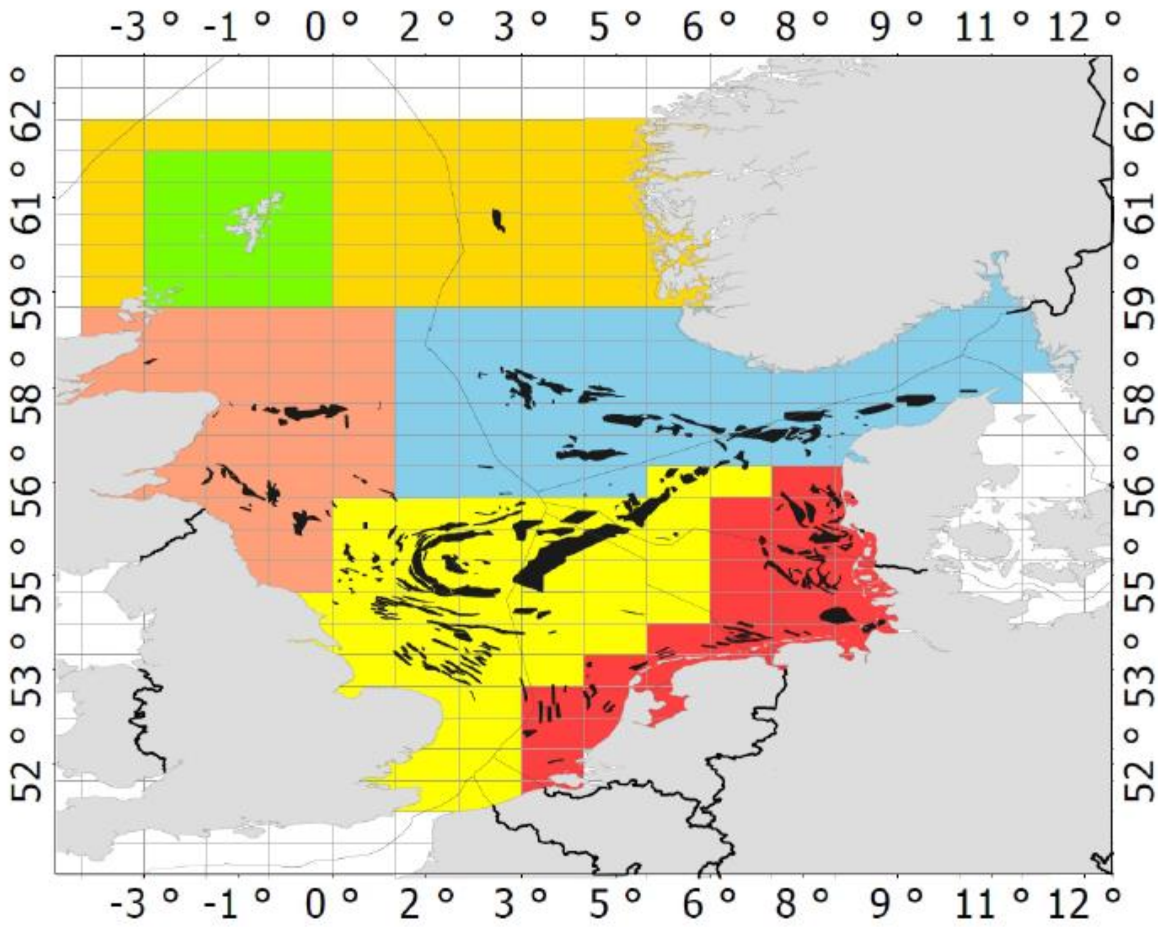

Figure 1. Sandeel assessment areas in the North Sea as used by ICES since 2009: Green='Shetland' (including Foula at 60N 2W, Pink='east Scotland' (including Isle of May at 56N 2W), Yellow='Dogger Bank' (including Bempton at 54N 0E). Before 2009, sandeels were assessed in two areas, 'Shetland' (green) and 'North Sea' (all coloured areas except green). The main fishing grounds are marked in black within each division. Sandeel fishing grounds in Shetland are too small in area to be identified in this way.

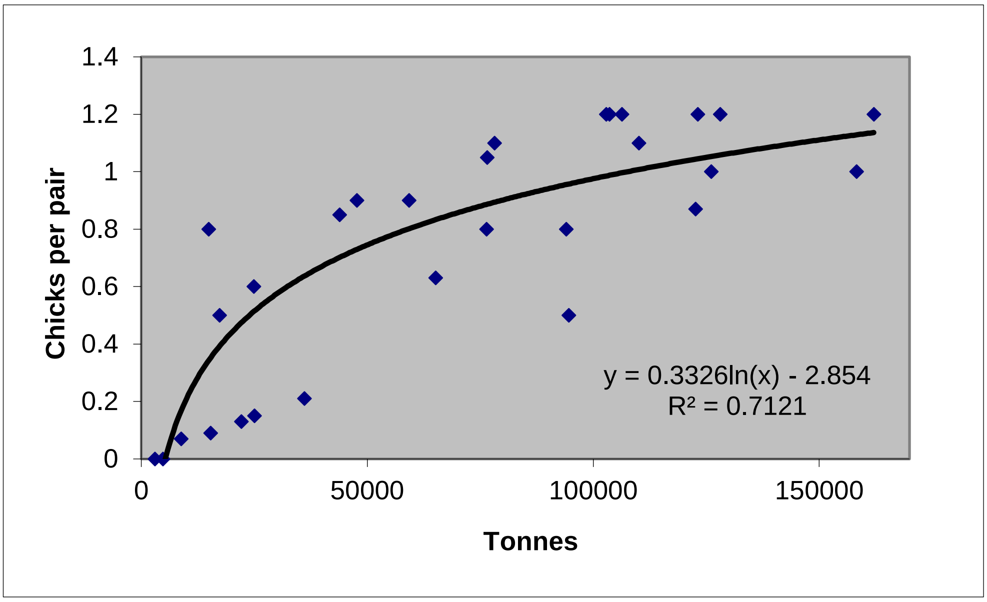

Figure 2. Breeding success of Arctic skua (parasitic jaeger) at Foula, Shetland, in relation to the Shetland sandeel total stock biomass for the years 1976 to 2004

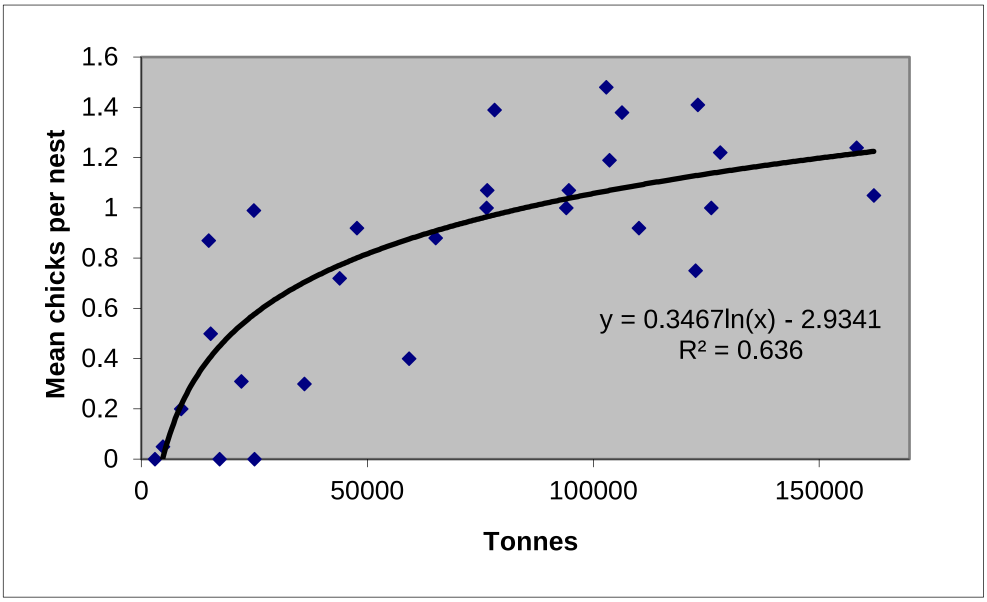

Figure 3. Breeding success of black-legged kittiwake at Foula, Shetland, in relation to the Shetland sandeel total stock biomass for the years 1976 to 2004

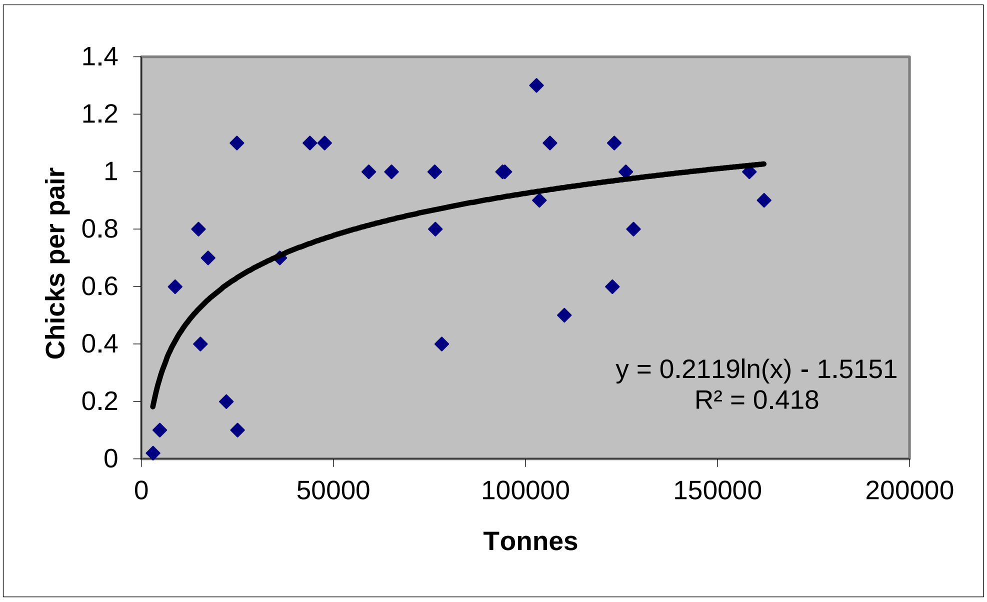

Figure 4. Breeding success of great skua at Foula, Shetland, in relation to the Shetland sandeel total stock biomass for the years 1976 to 2004

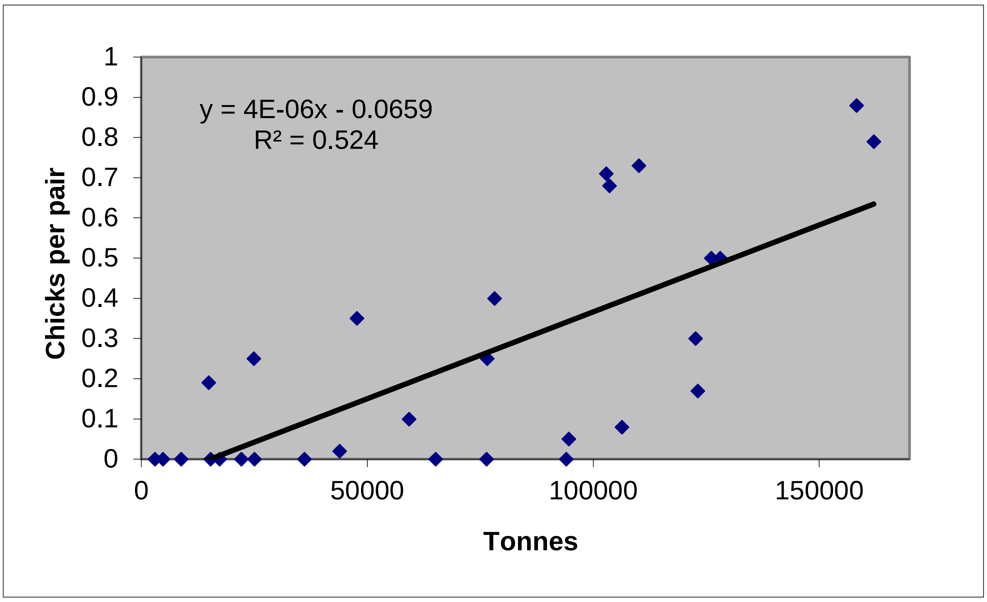

Figure 5. Breeding success of Arctic tern at Foula, Shetland, in relation to the Shetland sandeel total stock biomass for the years 1976 to 2004

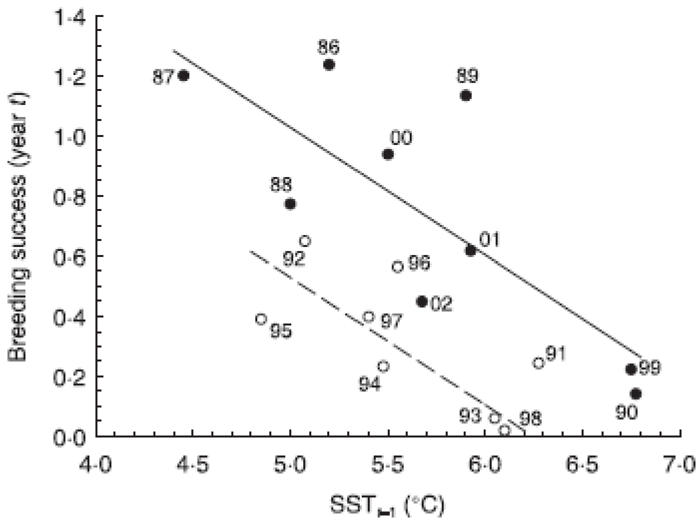

Figure 6. Black-legged kittiwake breeding success at the Isle of May, east Scotland, in relation to local Sea Surface Temperature in February-March of the previous year, and the presence (open circles and dashed line) or absence (black dots and solid line) of a sandeel fishery off east Scotland. From Frederiksen et al. (2004)

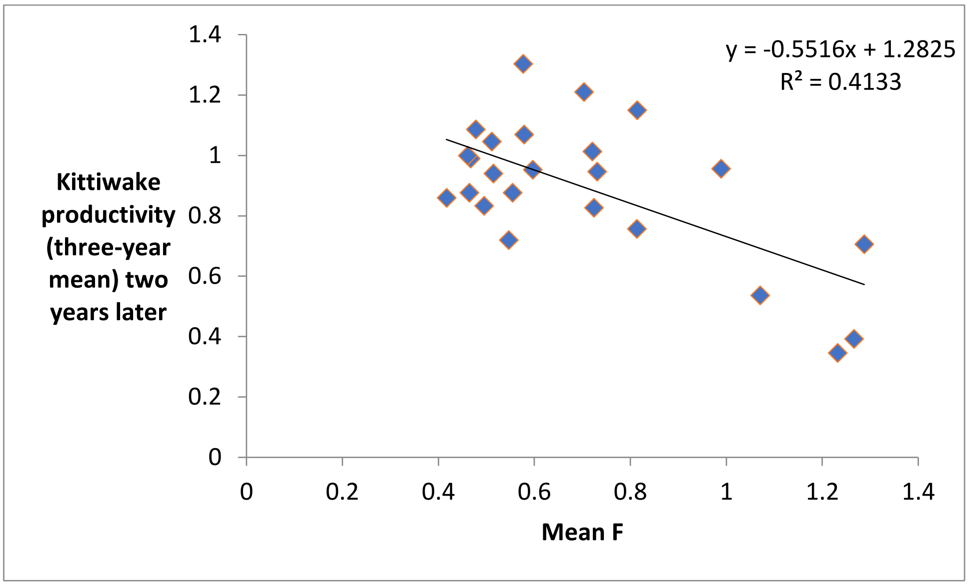

Figure 7. Breeding success (mean number of chicks per nest) of black-legged kittiwakes at Bempton (east England) (data from RSPB) in relation to fishing mortality of sandeels in the Dogger Bank stock two years previously (data from ICES stock assessments)