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Identifying drivers of change; did fisheries play a role in the spread of North Atlantic fulmars?

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Uncertainty over the role of top-down and bottom-up forces influencing marine top predator populations often constrains their use as indicators of marine ecosystem change. This chapter reviews historic and contemporary data to explore how different potential drivers have shaped abundance trends and distribution of the northern fulmar. Previously, debate on the causes underlying this classic example of range expansion has centred on alternative hypotheses; each championing single drivers of change. Instead, studies now suggest that fulmar populations have responded to multiple drivers, each with varying influence depending both upon the population parameters being investigated, and the scale at which these studies are made. These findings highlight how attempts to identify a single driver of change may be misplaced, and efforts should instead be made to understand how different drivers interact to influence the dynamics of these and other marine top predators.

Many marine top predators have shown dramatic changes in abundance over the last century, potentially providing useful clues to the state of the marine environment. However, in most cases, there is uncertainty over the drivers of observed abundance changes, constraining attempts to predict future trends or to incorporate such information into ecosystem management. Most fundamentally, it is often unclear whether changes are driven by top-down processes, or bottom-up influences on food supplies (eg. Springer et al., 2003; Trites & Donnelly, 2003). Furthermore, where evidence that bottom-up processes exist, changes in food availability could result from climate-driven regime shifts, or be a by-product of fisheries; either directly from discards, or indirectly due to fishery induced changes in prey community structure.

That there should be uncertainty over the drivers of change in top predator abundance is not surprising. Marine mammals and seabirds are long-lived species, living in environments where it is difficult to study the population ecology of both predators and their prey. Estimates of marine top predator abundance are generally based upon counts at breeding sites, providing only indices of population size that can be sensitive to variability in breeding success or population structure. Estimates are also often highly variable, and it may take many years to detect population trends.

Alongside broader-scale assessments of population trends, many finer scale studies have investigated variability in breeding numbers and the factors influencing key population parameters at particular colonies. This work has highlighted the role that both broad-scale ocean climate variation, and more local measures of food availability, may have on reproduction (e.g. Durant et al., 2003; Gjerdrum et al., 2003; Rindorf et al., 2000) and survival (Barbraud et al., 2000; Jones et al., 2002). In general, however, most studies have focussed on variation in reproductive parameters. Whilst reproductive success may be highly sensitive to changes in food availability and predation, uncertainty about other key population parameters (particularly dispersal and juvenile survival) make it difficult to assess longer-term population consequences.

Therefore, to what extent can we generalise from these finer-scale studies to understand broader-scale changes in population dynamics? For example, do the environmental variables that influence reproductive output at particular colonies have similar effects on survival or dispersal rates? And even where there is a good understanding of the driving forces underlying population changes at specific colonies, are similar factors shaping colony dynamics in other parts of the species range?

Population changes in the North Atlantic fulmar

The North Atlantic fulmar (*Fulmarus glacialis*) provides one of the best-known examples of an increasing marine top predator population (Box 1). Because this species was absent from mainland coasts of the United Kingdom, the broader-scale pattern of expansion and population increase during the 20th century was extremely well documented. At the same time, finer-scale studies have investigated factors influencing key population parameters at particular colonies (Hatch, 1991; Ollason & Dunnet, 1978; Thompson & Ollason, 2001). Throughout the expansion, there has been intense debate about underlying causes of these changes, particularly in relation to the potential influence of commercial fisheries (Box 2). As such, this provides an interesting case study where inferences can be integrated from both broad-scale and fine-scale ecological studies of this species. More recently, fulmar populations in European waters have stabilised (Mitchell et al., 2004), and investigations of earlier trends may provide useful insights into current management issues involving both fulmars and other marine top predators.

Investigating driving forces underlying historical changes in abundance and distribution.

Obtaining data to understand ecological changes that may have occurred decades earlier presents enormous challenges. Indeed, in many cases it may prove impossible to test hypotheses put forward to explain historical changes in abundance. Nevertheless, there have been a number of recent studies that have provided new insights into this long-standing debate. Furthermore, they highlight the potential of other work that could help understand both historical and contemporary changes in the dynamics of these populations.

Foraging ecology and diet composition.

It has been strongly argued, and is now widely believed, that the spread of fulmars was driven largely by increases in food availability from whaling and commercial fisheries (Fisher, 1952). At the time, little was known about fulmar diet and feeding ecology but, over the last decade, there has been more research in this area. Fulmars often scavenge around fishing boats, but wider-scale studies indicate that their distribution is more closely related to hydrographic features than to fisheries (Camphuysen & Garthe, 1997; Skov & Durinck, 2000). Similarly, comparisons of diet across their range suggest that fishery-derived offal and discards can form an important part of the diet in some areas, but that birds at many other colonies tend to forage on pelagic crustaceans and small fish (Furness & Todd, 1984; Hamer et al., 1997; Phillips et al., 1999). Nevertheless, while these prey appear to be taken directly, their availability may also have increased indirectly as a result of fishing pressure (Pauly et al., 1998). More generally, this work has shown that fulmars are extremely catholic in their diet, and that diet composition can differ markedly between years at a single site (Phillips et al., 1999). Such inter-annual variation makes assessments of longer-term trends difficult to evaluate, and further highlights that seasonal variation in diet is likely. The predominance of breeding season studies may therefore bias our understanding of the overall diet of these birds. A third approach has been to develop bio-energetic models, to assess whether current levels of discarding could support the

energetic requirements of different seabird populations. Even in heavily fished areas such as the North Sea, fewer than 50% of fulmars could be fully supported by fishery waste (Camphuysen & Garthe, 1997). Together, these studies suggest that fulmars are not, at least currently, heavily dependent upon fishery waste. Nevertheless the availability of discards may be important to these birds at times, or in areas, where natural prey are more limiting (Mitchell et al., 2004); probably during the winter (when natural prey are less available), and during the early chick-rearing period (when adults are constrained to shorter foraging trips).

Individually-based studies of reproductive success and survival

Long-term individually based studies have underpinned many finer-scale studies of marine top predator population ecology (Wooller et al., 1992). One of the longest running of these studies has been of a colour-ringed population of fulmars at a small colony on Eynhallow, Orkney (Dunnet, 1991). Since 1950, studies have described the continued increase of this population, and provided estimates of reproductive and survival rates. More recently, these data were used to explore the relative influence of large-scale climate variation and local measures of fisheries activity on this population. Inter-annual variability in reproductive success and the proportion of each cohort that recruited back to the natal colony were both related to indices of climate variation, but not to available data on fisheries (Thompson & Ollason, 2001). However, while reproductive success was most closely related to variations in the winter North Atlantic Oscillation (wNAO), recruitment was strongly and negatively related to northern hemisphere temperature anomalies (NHT). Thus, contrary to earlier assumptions (see Box 2), these data suggest that warmer conditions may improve some measures of productivity, even in this arctic species. More generally, the differential effects of these two variables meant that annual estimates of reproductive success and cohort recruitment rates did not co-vary (Fig 2). Causal links between these large-scale climate variables and reproduction and recruitment remain unclear, but the wNAO and NHT seem likely to either be influencing different prey stocks or impact birds at different times of year. Fulmars do not recruit until they are at least 7 years old, and these bottom-up effects on reproduction and recruitment therefore had a lagged effect on short-term variability in de-trended estimates of colony size (Thompson & Ollason, 2001). Together, these data highlight that natural variations in ocean climate have influenced the local dynamics of this colony, but this does not necessarily mean that other factors are not involved. Indeed, these analyses showed that there remains a strong, unexplained, linear increase in colony size, which earlier work suggests must have been driven by immigration from other areas (Ollason & Dunnet, 1983).

Use of proxies to explore historical ecological change

One of the key constraints when interpreting recent data on diet composition, is that these patterns may not be representative of earlier critical periods during the fulmar's expansion. Even the retrospective analysis of long-term individual-based data is restricted to the later phases of the expansion, and there is limited information on relevant environmental co-variates. Attempts to understand historical patterns of ecological changes have therefore often drawn upon a wide variety of indirect proxies of abundance, diet or environmental changes that may have driven such changes. In other systems, these have included economic records of catches (Allen & Keay, 2001), analyses of hair and fish scales in seabed sediments (Hodgson et al., 1998; O'Connell & Tunnicliffe, 2001) and an increasing array of molecular and biochemical techniques for understanding variation in abundance (Roman & Palumbi, 2003), dispersal and feeding ecology (Hobson, 1993, 1999; Smith et al., 1997). Such studies provide useful new insights into the nature of the fulmar's spread, and highlight the potential for similar approaches to extend these findings in the future.

The first of these insights involve paleoecological studies, where Montevecchi and Hufthammer (1990) described the distribution of fulmar bones from archaeological sites in Norway. They found evidence of fulmars at 26 sites, extending through northern and southern Norway. Most recovered bones were dated at between 1 - 4,000 years before present, with a peak in the period 1-2,000 years ago. The recent colonisation of Norway in 1920 therefore appears to have been a re-colonisation, and clearly shows that recent changes in distribution did not necessarily depend upon man-made changes in food supplies. Records of fulmars at Scottish archaeological sites are also scattered through the literature. Fisher & Waterston (1941) briefly mention, but then ignore, that fulmar bones were found in a midden from the west of Scotland, and more recent studies have recorded fulmars from excavations dating from the Neolithic to the early medieval (Serjeantson, 1988). Further review of archaeological data from other parts of the fulmar's contemporary range, together with carbon dating of the Scottish specimens would provide valuable insights into their historical distribution. In addition, stable isotope analyses of such specimens can also provide information on changes in diet composition. Using more recent museum samples, Thompson et al. (1995) found reductions in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in contemporary feathers compared with those from skins collected between 1850 and 1950. The difference in $\delta^{15}\text{N}$ was modest, representing a reduction of 25-33% of a trophic level, but is consistent with a decreasing tendency for fulmars to feed upon offal from toothed whales or large fish. However, contemporary samples were taken in a single year and may not fully reflect the full breadth of contemporary diet, suggesting that further work on more recent, and older, samples would be worthwhile.

Secondly, recent molecular analyses investigated the relationship between fulmars from five more recently established colonies, and the possible source colonies of St Kilda and Iceland (Burg et al., 2003). Many early writers had argued in favour of one or other of these sites as the most likely source colony (Fisher, 1952; Gordon, 1936), but mitochondrial DNA analyses provided evidence that these birds had recruited from both St Kilda and Iceland. Furthermore there were high levels of haplotype diversity at all sites, suggesting that founding events tended to involve many unrelated birds.

Did fisheries play a role in the spread of North Atlantic fulmars?

These studies suggest that, whilst fisheries waste has proved an important source of food for fulmars in certain areas, it was clearly not the sole cause underlying the population's expansion. Instead it seems much more likely that the population was responding to multiple driving forces, leaving us with the challenge of determining the relative importance of different drivers. While this is beyond the scope of this paper, examination of the process by which explanations for the spread were developed and interpreted provides some general lessons for evaluating this and similar issues in the future.

One clear feature of criticisms of alternative hypotheses was that they were often constrained by the limited information available on seabird life-history patterns at that time. Perhaps most obviously, complex descriptions of the spatial pattern of spread were based on the assumption that successful breeders produced young that recruited to nearby colonies at just one or two years old (Fisher, 1952). Similarly, lack of knowledge about age at maturity and longevity meant that the sensitivity of population trends to variations in reproduction and adult survival were not fully appreciated (Fisher & Waterston, 1941). There remains uncertainty over the detailed ecology of many species involved in current fisheries interactions, and we should be careful not to dismiss hypotheses simply because they lie outside our current understanding of the system.

Secondly, issues of scale heavily influenced perceptions of the importance of fisheries. At a fine scale, large feeding flocks of fulmars around whale carcasses and trawlers appeared to provide convincing support for the importance of these artificial prey supplies. Only when larger scale studies have been conducted has it become clear that attraction to vessels is a relatively local process (Skov & Durinck, 2000). Indeed, our perception of the rapid rise in abundance is itself biased because most studies have been carried out at a local scale in newly colonised parts of the UK. Broader scale assessments of population increases are less dramatic (see Box 1), and may not be so very different to those observed in other seabirds in the region (Mitchell et al., 2004). Another aspect of scale that links to our understanding of life-history, is that driving forces acting upon reproduction or early survival will have lagged effects on measures of population abundance. Particularly given the low power of many marine monitoring programmes, this means that we may need to look well back into the past to identify drivers of recently detected changes.

The lack of opportunities to directly test alternative hypotheses appears to have encouraged the champions of different hypotheses to become increasingly entrenched in their opinions (Box 2). The dismissal of some hypotheses now seems premature, as several arguments used against these ideas are much less convincing in the light of current ecological understanding. Fisher & Waterston's (1941) assessment of the impact of hunting on populations in both Iceland and St Kilda was based on the assumption that only young birds were taken. However, other sources indicate that harvests were of both adults and young, and there would also be additional losses from egg harvesting. When Martin Martin visited St Kilda in 1697, he estimated that the people of St Kilda had given their party 16,000 seabird eggs during their stay, while his description of the delicate taste of the adult fulmars highlights the existence of a mixed harvest (cited in: Gordon, 1936). Given the sensitivity of populations of long-lived vertebrates to changes in adult mortality, slight changes in the ratio of adults to young in reported harvest levels (for example in response to a known decline in the market for the oil and down during the late 19th century (Harman, 1997) could have had important impacts on population growth rates. Alternative hypotheses clearly need to be kept under review; particularly where there may be opportunities to develop new techniques to explore some of these old questions.

Even if changes in top-down processes did not influence the early stages of the expansion, reductions in hunting after the 1930's must have contributed to the faster increases during the next few decades (see Box 1). With an estimated 20,000 birds per year currently caught by Norwegian long-liners (Dunn & Steel, 2001), it would be timely to assess the role that this may play in the current levelling of European populations. Several different factors are also likely to have contributed to bottom-up influences on food supply. Whaling and fisheries may have played a part, directly or indirectly, but there have been other important responses of plankton communities to ocean climate variation (Beaugrand et al., 2002). In some cases, there may be co-variation in responses of different population parameters to each of these factors, but there is also evidence that different parameters may be responding to different driving forces (Fig 2). Modelling frameworks exist to explore such issues (eg. Jenouvrier et al., 2003), but there remain important challenges when parameterising models. In particular, few detailed studies have estimated reproduction and survival rates, and caution is required when scaling up from local studies to explore impacts across the population's range. Similarly, data on dispersal rates between different colonies remain elusive, but are crucial to any attempts to model changes beyond the colony scale. If these problems can be overcome, these tools provide exciting, but challenging, opportunities for modelling how these different factors could influence historical and future population trends.

Box 1: Population expansion of northern fulmars

The northern fulmar is currently one of the most numerous seabirds in the Northern Hemisphere, with an estimated population of 5-7 million pairs (Mitchell et al., 2004). Arctic populations appear to have remained relatively stable, but boreal populations have expanded greatly over the last 400 years. In the 17th century, the boreal population was believed to occur at just two sites: St Kilda in the Outer Hebrides and Grimsey off northern Iceland. The subsequent spread through Europe has been documented by Fisher (1952), and more detailed data on the expansion of UK colonies are available through a series of national surveys organised through the British Trust for Ornithology (Fisher, 1966) and later the Seabird Group and the Joint Nature Conservation Committee (Cramp et al., 1974; Lloyd et al., 1991; Mitchell et al., 2004). During the 19th and 20th century, fulmars spread from Grimsey to the coast of mainland Iceland, and colonised the Faroe Islands between 1816 and 1839. By 1878 they were breeding on Foula in Shetland, and they subsequently spread south through the UK and Ireland during the 20th century. Norway was colonised in about 1920, and fulmars have since colonised France and Germany. In the western Atlantic, the spread has not been so dramatic, but new colonies were established in Newfoundland, Labrador and southwest Greenland (Brown, 1970; Stenhouse & Montevecchi, 1999).

The current estimate of the UK breeding population is around 538,000 (Fig 1). Following a rapid increase in the first half of the 20th century, UK population growth has slowed. Typically, the rapid growth of the UK population has been illustrated using data that exclude the largest population on St Kilda (Fig 1a). Data from St Kilda are sparse and uncertain, but if one assumes that numbers remained relatively stable at 21,000 up to 1939, as proposed by Fisher and Waterston's (1941), Fig 1b provides a more representative picture of the rate of expansion of the British and Irish population. Notably, the period in which the rate of increase is fastest occurs later (1925-1975) when one considers population dynamics at this larger spatial scale.

Box 2: What caused the spread of fulmars; a historical perspective.

Recent reviews of the causes underlying the fulmars' expansion focus on three competing hypotheses that were prevalent during the 1950's and 1960's. The first, and most widely cited, is Fisher's (1952) suggestion that fulmars responded to increases in food availability following the expansion of whaling and commercial fisheries. A second hypothesis, proposed by Salomonsen (1965), and later supported by Brown (1970), argued that fulmars had instead responded to natural changes in food availability, co-occurring with a period of warming in the temperate North-Atlantic. Finally, Wynne-Edwards (1962) suggested that the spread resulted from natural evolution following a genetically or culturally-based change in dispersal behaviour. One notable feature about all three of these ideas is that the authors provide only the most anecdotal of evidence in support of their own hypothesis. Instead, they each focused on presenting arguments against the alternative hypotheses of the day. Wynne-Edwards (1962) highlighted that neither the timing nor the geographical pattern of new breeding colonies showed any close correlation with major developments in whaling or trawling. For example, in the early phase of the expansion, there was no evidence of an increase around Greenland and the Davis Strait, despite much of the 18th and 19th century whaling occurring in these areas. Similarly, during the later expansion period, there was a tendency for colonies to form on the west coasts of the UK and Ireland rather than on the coasts around the more heavily fished southern North Sea. Both Wynne-Edwards (1962) and Fisher (1952) were, however, unanimous in their dismissal of any role of climate change. In both cases ruling this possibility out because a period of warming could not have driven a population increase in a species that has a predominantly arctic distribution (but see Fig 2).

The common feature of these hypotheses is that they all relate the expansion to the fulmars' exploitation of new food resources. Yet this focus on different bottom up processes neglects decades of earlier debate on the potential role of top down processes. Fulmars were regularly taken by island communities around Iceland, the Faroes and St Kilda, providing important supplies of oil, down and meat. Between 1900 and 1940, Icelandic government statistics recorded annual catches of 20-60,000. Estimates of Faroese catches in the 1930's were even higher at 80,000 per annum in the 1930's, and those from St Kilda were in the region 6-10,000 until the islanders were evacuated in 1934 (Fisher 1952). Based on such figures, several authors argued that the fulmars' expansion into other parts of the UK could have resulted from a decrease in human predation. This, in turn, was believed to have followed the introduction of regular supply ships that reduced the St Kildan's dependence upon their seabird harvest. Fisher & Waterston (1941) argued that this was an unlikely cause of the spread particularly because they found no clear evidence that the St Kildans had reduced their take of birds during the early phase of expansion. By the time that Fisher wrote his 1952 monograph, that belief became almost evangelical, and the "St Kilda theory of the fulmar's spread is stated, if only to be demolished". Detailed data on changes in the numbers of birds killed before the 1930's remain unavailable, though there may be potential to explore variations in harvest through more detailed analyses of estate records (see Harman, 1997). What is certain, however, is that harvests on St Kilda, Iceland and the Faroes had all reduced dramatically by the end of the 1930's. St Kilda was evacuated, and legislation in Iceland and the Faroes banned the harvest of young fulmars following their identification as a source of psittacosis infection (Fisher, 1952).

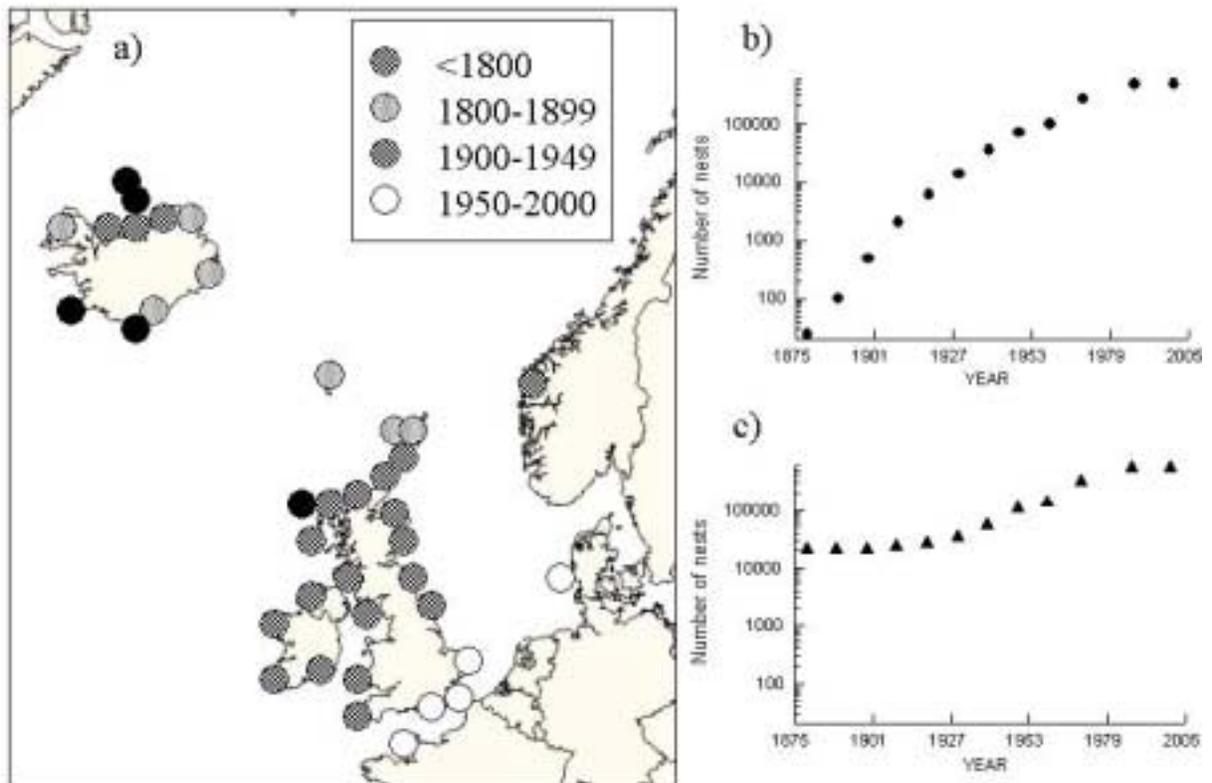


Fig. 1. Changes in the distribution and abundance of northern fulmars. (a) Schematic distribution of boreal populations, illustrating the timing of their range expansion. (b) Changes in the number of apparently occupied nest sites at newly colonised breeding sites in Britain and Ireland. Data from (Cramp et al., 1974; Fisher, 1966; Fisher & Waterston, 1941; Mitchell et al., 2004). (c) Changes in the number of apparently occupied nest sites at all breeding sites in Britain and Ireland, including St Kilda. Data sources as for Fig 1b, with an assumed stable population of 21,000 on St Kilda between 1875 and 1939 (see Fisher & Waterston, 1941).

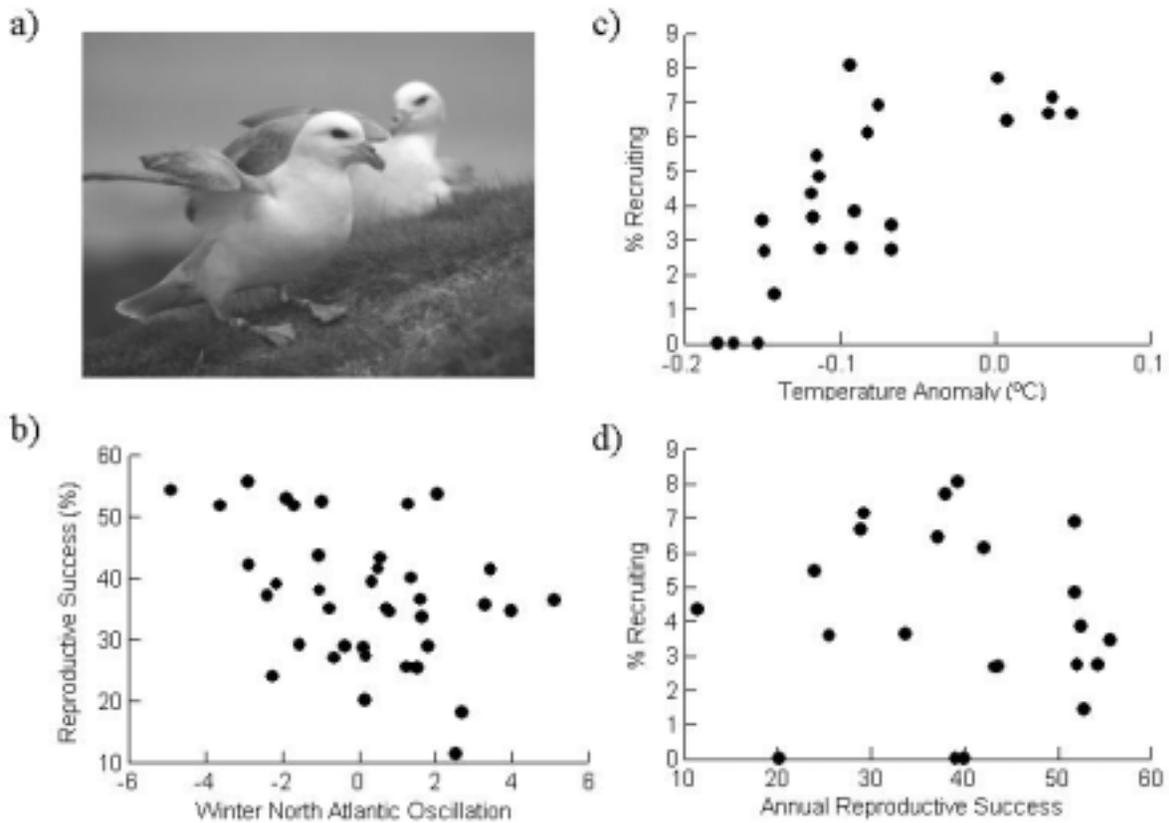


Fig 2. Studies of individually marked fulmars on Eynhallow (a) have shown that reproductive success and recruitment are influenced by climate variation. (b) Reproductive success is positively related to the winter North Atlantic Oscillation index. (c) Cohort recruitment rates are positively related to northern hemisphere temperature anomalies. (d) Cohorts experiencing higher reproductive success do not necessarily exhibit higher levels of recruitment. Figs b and c redrawn from (Thompson & Ollason, 2001).

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