CLIMATE DRIVEN TROPHIC CASCADES AFFECTING SEABIRDS AROUND THE BRITISH ISLES

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Abstract

After flourishing during the second half of the twentieth century, many North Sea seabird populations are now in decline. Much evidence is accumulating that climate change is driving these negative trends in growth rate. Climate driven changes in the physical environment may affect seabirds both directly and indirectly. Direct impacts such as increasingly common extreme weather events will result in negative physiological responses. However, climate effects on seabirds are more likely to be indirect, and mediated by prey quality and availability. Mounting evidence suggests that climate impacts on lower trophic levels are altering the pathway of energy to seabirds. While the basis for changes in primary production are complex and uncertain, climate driven changes in sandeels, and *Calanus finmarchicus*, key prey species in adjacent trophic levels, appear to be causing a reduction in breeding success and growth rate in several British seabird species.

Introduction

Numbers of many species of seabirds around the UK increased between 1970 and 2000 (**Figure 1**). However, since the Seabird 2000 census (Mitchell et al. 2004), some of the species have started to decline e.g. Atlantic puffin *Fratercula arctica* (Harris & Wanless 2011), northern fulmar *Fulmarus glacialis* and Great Cormorant *Phalacrocorax carbo*. Others have continued to increase, for example the common guillemot *Uria aalge,* razorbill *Alca torda,* and especially the northern gannet *Morus bassanus*. In Scotland, northern gannets

are possibly the only species to increase in the past decade (Wanless & Harris 2012), and are continuing to form new colonies (Wanless et al. 2005a).

Most surface-feeding seabird species in the northern North Sea have suffered breeding failure since 2003. In Shetland, similar declines in breeding success happened earlier during the 1980s. Large pursuit diving species have not been so affected (Heubeck 1989, Okill 1989). Consequences of such declines in breeding success only become apparent in the population numbers after a considerable time lag as these year-classes of birds mature and join the breeding population (Frederiksen et al. 2004, Mavor et al. 2005, 2006, 2007, Reed et al. 2006).

The overall trends in seabird breeding numbers over recent decades mask some marked regional variations (**Figure 2**). Significant increases were observed in the breeding numbers of e.g. guillemots, in England and Wales; however the trend was reversed for those breeding in Scotland. Within any one year, some species have bred successfully, and others have not. For a given species, some regions have produced successful breeding and others not. In some cases, a lack of consistency has even been found among species inhabiting the same region (Wanless & Harris 2012).

Climate change is considered to be playing a significant role in the declines in seabird breeding numbers (Russell et al. 2014). In particular, sea surface temperatures (SST) in UK coastal waters, which have been rising between 0.1 and 0.5°C decade $^{-1}$ for the past 30 years (Dye et al. 2013), have shown a strong negative relationship with the demographic rates of several seabird species. For example, the productivity of northern fulmar and black-legged kittiwake *Rissa tridactyla* on the Scottish east coast shows a negative relationship with SST (Burthe et al. 2014). Furthermore, survival rates of kittiwakes, European shags

Phalacrocorax aristotelis (Burthe et al. 2014), Atlantic puffins, guillemots, and razorbills (Lahoz-Monfort et al. 2011) are also strongly negatively correlated with SST.

The physical environmental changes which accompany climate change may affect seabirds in a variety of direct and indirect ways. Direct effects include incidences of extreme weather events causing mass mortalities and damage to nests in breeding colonies (Frederiksen et al. 2008a, Wanless & Harris 2012). Physiological responses to higher temperatures can be expected to cause changes in vital rates for population dynamics (Oswald et al. 2008, 2011). Population dynamics of long-lived seabird species are especially sensitive to adult survival (Lebreton & Clobert 1991, Saether & Bakke 2000, Ratcliffe et al. 2002, Furness 2003). Indeed, reduced overwinter survival rates for breeding Atlantic puffins on the Isle of May in 2006-2007 and 2007-2008, combined with an increase in immature mortality (Harris et al. 2013), was sufficient to explain a 30% reduction in breeding population between 2003 and 2008 (Harris & Wanless 2011). Synchrony in guillemot survival rates from different colonies around Britain, that share overwintering areas, provides further evidence that climate could be the key determinant of mortality (Reynolds et al. 2011).

In contrast, indirect effects may be mediated through prey quality and availability (Wanless et al. 2005b, Burthe et al. 2012), affecting growth rates and breeding success. These are referred to as bottom-up cascading trophic effects (Carpenter et al. 1985, Pace et al. 1999, Polis et al. 2000, Heath et al. 2014). The aim of this paper is to review and synthesize the evidence for these climate-driven trophic cascade effects on seabirds in waters around the British Isles. In particular the hypothesis that increasing climate-driven changes in phytoplankton and zooplankton have led to a decline since 2000 in the abundance of small planktivorous fish, especially sandeels, and hence to the observed changes in seabird breeding success, frequency of breeding, and increased age of first breeding (**Figure 3**). We

approach the matter by addressing the coupling between successive trophic levels in the food web, beginning with the connection between seabirds and fish and working towards lower levels.

Connections between seabirds and fish

The majority of open-sea bird species around Britain are essentially piscivorous. The prey items brought back to breeding sites by the 26 major seabird species was analysed during the Seabird 2000 survey (1998-2002) (**Table 1**) and found to consist mostly of sandeels (mainly *Ammodytes marinus*), small clupeoid fish or zooplankton. Prey were either self-caught or stolen from other birds (Furness 1987, Davis et al. 2005). Exceptions were scavenging species such as northern fulmars and gulls which feed opportunistically and rely partly on discarded fish and offal from vessels (Camphuysen & Garthe 1997, Furness 2003), and some of the diving species whose diet includes a proportion of seabed organisms (Furness et al. 2012).

There is abundant evidence that fish communities are being affected by climate change. Geographical shifts in the distribution of many shelf-sea fish communities around the British Isles have been well documented. Broadly speaking, these changes can be viewed as a response to warming sea temperatures, so as to maintain individuals in a preferred temperature range (Hedger et al. 2004, Perry et al. 2005, Poulard & Blanchard 2005, Desaunay et al. 2006, Heath 2007, Dulvy et al. 2008). In some areas, this is manifested as a poleward shift in distribution or a move into deeper water. However, local topography and hydrography may limit the extent of such shifts.

Poleward shifts in distribution lead to decreases in abundance at the southern edge of the geographic range of a species, and increases at the northern edge (in the northern hemisphere). Temperature-associated species-level changes in abundance which may be accounted for in this way have been identified in 39 of 50 of the most common species in the North Sea (Simpson et al. 2011). Catches of warm-water species, i.e. anchovy *E. Encrasicolus*, sardine *Sardina pilchardus*, and striped red mullet *Mullus surmuletus*, all increased in the North Sea, coinciding with increased temperatures after 1995 (ICES 2007). Moreover, statistical modelling shows northward movements for Atlantic horse mackerel *Trachurus trachurus*, European anchovy, European sprat *Sprattus sprattus*, Pollack *Pollachius pollachius*, Common sole *Solea solea*, Saithe *Pollachius virens* and Turbot *Scophthalmus maximus* between the 1960s and the period 2000-2005 (Lenior et al. 2011). Northward movements for these species, with the exception of Pollack, are predicted to increase substantially under projected IPCC changes in SST (IPCC 2007). Some fish species now inhabit areas where they were absent prior to the 1980s. Examples include anchovy and sardine (Beare et al. 2004a), striped red mullet (Beare et al. 2004b) and bluemouth *Helicolenus dactylopterus* (Mamie et al. 2007).

Although many of the fish species mentioned above are not directly preyed up on by seabirds, their responses to climate change may be significant to understanding the impacts on birds because they are potential competitors for the main food of piscivorous birds – the common sandeel *A. marinus*. This species is currently at the southern edge of its latitudinal range around the British Isles (Fishbase 2014), but unlike most other fish species, sandeels are not free to move into deeper waters in response to warming sea temperatures because they are tightly associated with sandy sediments of rather narrow range of grain size composition (Wright et al. 2000, Holland et al. 2005, Greenstreet et al. 2010a). In addition, sandeel stock display a complex spatial population structure which may further limit their capacity to adjust

their distribution in response to warming. For example, the North Sea stock is composed of seven distinct populations, each exhibiting different population dynamics (Boulcott et al. 2007, ICES 2010, 2013, Boulcott & Wright 2011). Since 2000, some sandeel populations have undergone a decrease in abundance in parts of the northern North Sea, primarily Shetland and the north-western North Sea (**Figure 4**), but not in the southern North Sea. The drivers behind patterns of decline in sandeels are complex and may include a combination of climate and fishing impacts.

The decrease in stocks of sandeels in the north-western North Sea since the late 1990's has occurred despite a substantial reduction in fishing activity, suggesting a strong environmental effect. Although larval abundance, and by inference spawning stock biomass, decreased after 2001, recruitment was maintained due to an increasing larval survival rate (Heath et al. 2012). The number of sandeels less than age one around the time of seabird breeding therefore would not have changed dramatically over time, yet the number of older sandeels continued to decline.

Two main factors have been proposed as responsible for the decline in sandeel abundance. Data from chick-feeding Atlantic puffins and Continuous Plankton Recorder samples indicate that the size-at-date of sandeels less than age 1, hereafter referred to as '0-group', has declined substantially since 1973. However, it is unclear what the exact cause of this decline might be (Wanless et al. 2004). A decline in 0-group size-at-date is presumably due to changes in hatch or spawning dates, or changes in growth rate (Frederiksen et al. 2011). However, there is no evidence of trends in hatch dates on the Scottish east coast (Heath et al. 2012a), so the proximate cause for the decline in 0-group size-at-date must be a change in growth rates.

Alternatively, it is noted that sandeels undergo an overwinter fasting period between late summer and the spawning period in January, during which they remain buried in the seabed in order to evade predation. Individuals show significant weight loss during this period (Boulcott et al. 2007, Boulcott & Wright 2008), and it is speculated that increased temperature will increase this rate of loss due to elevated metabolism. The energy reserves required to sustain the animals through the winter fast must be accumulated the previous summer, so unless warming is accompanied by increased scope for summer feeding, which does not appear to be the case (Wanless et al. 2004, Boulcott et al. 2007), then the net effect is likely to be reduced overwinter survival (Van Deurs et al. 2011). The recruiting age class in the population, entering its first winter, may be particularly vulnerable to overwintering mortality. Fish older than age 1 usually enter the overwintering period in August and remain buried in the sediment until April the following year emerging only to spawn in January (Winslade 1974). However, many young-of-the-year sandeels may not begin to overwinter until December (Macer 1966, Reeves 1994, Kvist et al. 2001) suggesting that they require extra time to accumulate the necessary energy reserves.

Overwintering mortality may also have played a role in declining sandeel abundances around the Shetland Isles, because sandeels growth rates are much slower at Shetland than elsewhere around Britain (Wright & Bailey 1993, Bergstad et al. 2002). However, recruitment failure appears to be the more likely cause and increased predation by fish that consume sandeel larvae could explain the decline in this region (Frederiksen et al. 2007). Herring *Clupea harengus* are known to feed on larval sandeels (Hardy 1924, Last 1989), and stocks of herring have increased from 100,000 tonnes in the late 1970s to 2 million tonnes in 2004 (ICES 2004), in approximately inverse relationship with sandeel abundance around Shetland. Such a mirror-image pattern may indicate a top-down effect of herring predation on sandeel in the northern North Sea. There are precedents for such a phenomenon elsewhere,

for example herring predation has been implicated in the recruitment variability of Barents Sea capelin *Mallotus villosus* (Gjøsæter & Bogstad 1998). However, counter-evidence is that although adult herring biomass has been high since 2000, survival and growth rate of herring larvae has declined (Payne et al. 2009, 2013), which might suggest a common environmental factor affecting both sandeels and herring. Other possible reasons for recruitment failures of the northern sandeel populations are changes in the dispersal patterns of larvae from spawning to settlement sites (Proctor et al. 1998, Christensen et al. 2009), or changes in the phenology of the spring plankton bloom in relation to burial and spawning times of the sandeels (Greenstreet et al. 2006, Scott et al. 2006).

Data from other regions support the idea that a variety of factors may be causing the climate-related changes in sandeel abundances. Recruitment is strongly inversely related to winter temperatures for the sandeel stocks in the central North Sea, especially around Dogger Bank (Arnott & Ruxton 2002), though the causal mechanism is not known (ICES 2013). In contrast, there is little evidence of direct climate impacts on southern stocks, although changes in growth rates in the southern North Sea have been linked to fluctuations in zooplankton abundance (van Deurs et al. 2014).

Turning to the effects of changes in fish abundance and community composition on seabird populations, the evidence is strikingly clear. Sandeels constitute a significant proportion of the diet for many North Sea seabirds during the breeding season (Wanless et al. 1998, Furness & Tasker 2000, Furness 2002, Frederiksen et al. 2004, Sandvik et al. 2005, Lahoz-Monfort et al. 2011). Between 1991 and 2011 on the Isle of May sandeels comprised approximately 75% of the diet of European shag, kittiwake and Atlantic puffins (Newell et al. 2013). Some seabirds, such as kittiwakes and Arctic skuas *Stercorarius parasiticus*, are highly sensitive to fluctuations in sandeel abundance while others, such as the northern gannet, appear less affected (Furness & Tasker 2000). The most sensitive seabirds are those

with high foraging costs, little ability to dive below the sea surface, little 'spare' time in their daily activity budget, short foraging range from the breeding site, and little ability to switch diet (Furness & Tasker 2000). The well documented declines in breeding productivity of kittiwakes, shags, and Atlantic puffins (Lahoz-Monfort et al. 2013), are highly correlated with the availability of sandeels, especially the older age classes of sandeel (Pinaud & Weimerskirch 2002, Frederiksen et al. 2006, 2013).

In addition to inter-species variation in the importance of sandeel in the seabird diet, there are also strong regional variations. In northern UK waters sandeels are the only significant prey for seabirds. For example, sandeels have been the only common high-lipid schooling fish around Shetland in recent decades. Breeding success of most seabirds is therefore strongly related to sandeel abundance in that region (Hamer et al. 1993, Davis et al. 2005). Seabirds off south-east Scotland have access to other fish prey, e.g. young herring and sprat (Bull et al. 2004, Harris et al. 2004, Wilson et al. 2004), but sandeels are still the main prey (Wanless et al. 1998). However, in south-western British waters there are higher abundances of alternative prey such as sprat and juvenile herring, so the linkage to sandeel availability is correspondingly weaker. However, it cannot be ruled out that climate change could result in the growth of sprat or juvenile herring populations in northern waters. In fact, a pronounced increase in abundance of European sprat in the North Sea between 2000 and 2005 can be explained by increases in temperature (Lenior et al. 2011). During this time guillemots at Fair Isle, between Orkney and Shetland, underwent a dietary shift (Heubeck 2009), consuming more gadoids and sprat, and fewer sandeels, than previously. Moreover, records on guillemot chick diet composition from the Isle of May in the Firth of Forth indicate that sprat have accounted for the majority of chick diet since 2000 (Anderson et al. 2014). While this is probably a response to lack of sandeels, it is possible that guillemot diet partially reflects their preference for sprat. Indeed, sprat might actually represent a higher

quality prey resource than sandeels (Smout et al. 2013). For example in 2000 the guillemots at the Firth of Forth switched to sprat even though they were two orders of magnitude less abundant than sandeels (Greenstreet et al. 2010b).

In the north-western North Sea, other potential effects on seabirds arise from the apparent changes in growth rates of sandeels since the 1970's. The decline in size-at-date of the recruiting 0-group stages leads to a mismatch between the timing of seabird breeding and availability of adequate prey. The weight-specific energy content of sandeel is related to their body size, so slower growth rates mean declining calorific content of prey fed to chicks on a given day of the year (Wanless et al. 2004, Burthe et al. 2012). Interestingly, there has been a trend towards later breeding in several species (Burthe et al. 2012), partially mitigating the decline in prey length. Nevertheless, guillemots, shags, kittiwakes, Atlantic puffins and razorbills chicks have all suffered net reductions in energy value because of this decline in sandeel length (Burthe et al. 2012).

In addition to effects on seabird chicks, a lack of 0-group sandeel availability and quality can affect adult seabird mortality, which is particularly influenced by prey availability during the breeding season. This is because seabirds must attain a sufficient level of body energy to meet breeding costs (Oro & Furness 2002, Ratcliffe et al. 2002). In Shetland, sandeel abundance is related to adult survival of various species, in particular Kittiwake and Great Skua *Catharacta skua* (Oro & Furness 2002, Ratcliffe et al. 2002).

Other fish species responding to climate change, may have indirect effects in birds by interfering with the relationship between sandeels and seabirds. This interference may take the form of competition for sandeels as prey (Greenstreet et al. 2010b), or presenting as an abundant but less nutritious alternative prey. The much-reported influx of snake pipefish *Entelurus aequoreus* into European waters in 2003 (Lindley et al. 2006, Harris et al. 2008, Kloppmann & Ulleweit 2007, van Damme & Couperus 2008) represents an example of the

latter. Trawl survey records show catches of snake pipefish began to increase in 2003 off north-west Scotland, and had covered the entire North Sea by 2007 (**Figure 5)**. Catches declined sharply in 2009. A simultaneous population explosion and subsequent contraction happened in the Barents Sea (Høines et al. 2009). It is unclear why snake pipefish numbers increased. However, Continuous Plankton Recorder samples show that high numbers of larval and juvenile stages extended as far west as the Mid-Atlantic Ridge, and may have coincided with a rise in sea temperatures between January and September, when the eggs are developing and the larvae are growing in the plankton (Kirby et al. 2006). Alternatively, a shift in zooplankton species composition may have helped facilitate the explosion of pipefish numbers (van Damme & Couperus 2008).

In 2003, snake pipefish began to appear in the diet of several seabird species (Anderson et al. 2014, Harris et al. 2007). We do not know if seabirds mistook pipefish for their usual prey, or whether they were capturing them because sandeels and clupeoid fish were in short supply. In either case, the pipefish represented a poor quality resource; low in lipid, bony and difficult to digest (Harris et al. 2008). Previous work has shown that most seabird colonies have less successful breeding years when chicks are fed on prey with lower than average energy content (Wanless et al. 2005b).

Connections between fish and zooplankton

The principal role of zooplankton in the food web is as a vector for transferring primary production to fish. Sandeels, are likely to be bottom-up limited by zooplankton abundance (Frederiksen et al. 2006). In particular, the crucial larval stage, is more likely to be affected by bottom-up effects through the plankton (Pitois et al. 2012).

During the 1980s the North Sea ecosystem underwent a regime shift that resulted in pronounced changes to the fish and plankton community composition (Beaugrand 2004). These changes have been ascribed to increased sea temperature (Beaugrand et al. 2002, Perry et al. 2005). Moreover, recent decades have seen pronounced northward shifts in the range of calanoid copepods (Reid et al. 1998, 2001, Beaugrand et al. 2002, Drinkwater et al. 2003, Reygondeau & Beaugrand 2011). The mean rate of northward movement for some north-eastern North Atlantic species assemblages between 1958 and 2005 has been estimated at roughly 23 km yr^{-1} (Beaugrand et al. 2009). During this time, the critical threshold separating boreal and temperate zooplankton systems has moved forward by 22 km yr^{-1} (Beaugrand et al. 2008).

The calanoid copepod, *Calanus finmarchicus*, is currently vital in the diet of sandeel larvae as larval survival depends specifically on the abundance of *C. finmarchicus*, not overall *Calanus* spp., or *C. helgolandicus* (van Deurs et al. 2009). However, despite being previously dominant in the North Sea, *C. finmarchicus*, has declined in biomass by 70% since the 1960s. Species with warmer-water affinities (e.g. *C. helgolandicus*) are moving northward to replace this species but these species are not as numerically abundant or nutritionally beneficial (lower lipid contents) to higher trophic levels. Moreover, recent temperature increases have reduced the size of zooplankton. Declines in sandeel length have been linked with these changes (van Deurs et al. 2014). A time series of sandeel length at age in the southern North Sea shows a decrease in the late 1980s, around the time when the mean size of calanoid copepods decreased by a factor of two (Beaugrand et al. 2003). This decrease in copepod size was an effect of the regime shift that took place in the North Sea in the late 80s, caused by a switch in the NAO index from a negative to positive phase (Reid et al. 2001, Beaugrand et al. 2002, 2003, Beaugrand & Reid 2003, Beaugrand 2004).

Despite the documentation of changes in species distribution, there is little clear evidence of changes in overall zooplankton production in the North Sea. Trends in zooplankton production on the Scottish east coast do not reflect the pattern of decline in sandeels (Heath et al. 2012, O'Brien et al. 2013). Apart from changes in zooplankton abundance, changes in seasonality (van Deurs et al 2009), size (Beaugrand et al. 2003) and lipid content of zooplankton (Wanless et al 2005b, Beaugrand et al 2009) could all affect sandeel populations. Zooplankton community production is exceptionally difficult to estimate, even by direct experimental measurements, and certainly from just data on species abundances.

Northward shifts of plankton species are expected to continue with increasing sea temperatures (Reygondeau & Beaugrand 2011). How these changes will affect higher trophic levels remains unclear. However, it is thought that the retreat of *C. finmarchicus* will be damaging to sandeel populations (van Deurs et al. 2009), and ultimately seabirds (Frederiksen et al. 2013). A recent niche model study (Frederiksen et al. 2013) showed that the breeding success of kittiwakes and Atlantic puffins on the Isle of May is significantly related to environmental suitability for *C. finmarchicus* (van Deurs et al. 2009). Therefore, it may become increasingly difficult for several boreal seabird species to maintain adequate breeding success as this *Calanus* species continues its retreat.

The future of sandeels in the North Sea will rest on whether a suitable replacement prey can be found with the most viable candidate being *C. helgolandicus*. However, *C. finmarchicus* abundance peaks in spring (Bonnet et al. 2005) concurrently with mean larval hatch date (Heath et al. 2012), whereas *C. helgolandicus* abundance peaks in autumn (Bonnet et al. 2005). Therefore, a mismatch between larval emergence and prey availability may occur if *C. helgolandicus* becomes the dominate prey species for sandeels.

Geographical shifts in plankton species can be related to environmental changes (Beaugrand & Helaouët 2008). We can have reasonable confidence in such predictions for different climate change scenarios, subject to the assumption that the underlying processes governing the ecological niche will remain constant in the future (Davis et al. 1998, Pearson & Dawson 2003). In addition, we can be quite confident that the zooplankton diversity in UK waters will increase with continued warming (Beaugrand et al. 2008), with a progressive shift towards smaller-sized plankton. Moreover, we can speculate that a shift towards smaller zooplankton may lead to reductions in trophic transfer efficiency due to increased food chain length.

Ocean modeling predicts a reduction in zooplankton biomass in the North Sea over the next century (Chust et al. 2014). These changes are thought to arrive via bottom up amplification of negative climate-driven impacts on phytoplankton (Chust et al. 2014). Therefore, it is important to understand how climate change may affect zooplankton indirectly through changes in primary production.

Connections between zooplankton and phytoplankton

The production of zooplankton, fish and higher trophic levels in the marine ecosystem must ultimately be related to primary production, and the efficiency of transfer between trophic levels (Aebischer et al. 1990, Schwartzlose et al. 1999, Chavez et al. 2003). Hence, comparing across ecosystems in the north-western Atlantic, there is a positive correlation between long-term average chlorophyll concentration and fishery yield (Frank et al. 2005). In the case of sandeels, it is clear that primary production drives stock biomass in some ecosystems (Eliasen et al. 2011). However, within individual ecosystems the relationships over time between primary production and fisheries yield varies depending on a range of

factors affecting the transfer of energy up the food web and the intensity of exploitation of the fish stocks.

Overall phytoplankton biomass in the North Sea has increased in recent decades (Edwards et al. 2001); and there has been a concurrent increase in smaller flagellates that are promoted by warmer and more stratified conditions (Edwards & Richardson 2004). Over the whole north-east Atlantic, there has been an increase in phytoplankton biomass with increasing temperatures in cooler regions, but a decrease in phytoplankton biomass in warmer regions (Barton et al. 2003). However, nutrient concentrations are likely to limit any positive response to warming (O'Brien et al. 2012).

Over multi-decadal periods in the North Atlantic, changes in phytoplankton species and communities have been associated with temperature trends and variations in the NAO index (Beaugrand & Reid 2003). These changes have included the occurrence of sub-tropical species in temperate waters, changes in overall phytoplankton biomass and seasonality, changes in the ecosystem functioning and productivity of the North Atlantic (Beaugrand 2004, Edwards et al. 2001).

Unfortunately it is only possible to speculate on how climate change may indirectly impact zooplankton through changes in phytoplankton. For example, we can speculate that climate driven changes in phytoplankton and zooplankton phenology (Edwards & Richardson 2004) may reduce prey availability for zooplankton. The key point is clear evidence that changes in climate have already impacted phytoplankton, resulting in zooplankton changes, remains thin.

Discussion

There is much evidence to suggest climate-driven trophic cascades have already affected seabirds in the waters around the British Isles. Whilst the basis for changes being driven by primary production are complex and uncertain, there is growing evidence of direct climate impacts on zooplankton and the immediate prey of seabirds. The key route of energy transfer to many of the main seabird species is through *C. finmarchicus* and *A. marinus*. Climate change is disrupting this pathway of energy transfer and appears to be causing a decline in breeding success and survival of several important UK seabirds, primarily those in northern areas e.g. Scottish east coast.

In the short term we can predict with reasonable confidence that the recent succession of poor breeding years will propagate through seabird populations to cause a decline in breeding numbers. Beyond this, changes will depend on the balance between breeding success, maturation rate and adult survival. The future patterns of seabird breeding maturation and survival may depend critically on the scope for feeding on alternative prey, if sandeel stocks do not recover over time with continued warming. However, the strength of resilience to food shortages may vary among species. For example, kittiwakes are sensitive to reductions in sandeel availability (Furness & Tasker 2000) while adult guillemots seem able to maintain provisioning of their chicks despite fluctuating abundances of key prey (Smout et al. 2013). Inter species variation in sensitivity to reductions in sandeel abundance may explain why climate effects appear to be species-specific (Lahoz-Monfort et al. 2011), assuming that sandeel abundance is negatively correlated with climate indices. Winter NAO and SST are contributing to synchrony, as well as desynchrony in survival rates of auks off the Scottish east coast (Lahoz-Monfort et al. 2011).

Continued decline in sandeel quality and abundance may cause the North Sea seabird community to become increasingly dominated by species least reliant on sandeels (Furness and Tasker 2000). An example of this may be the northern gannet, which has prospered in recent decades (Wanless et al. 2005a, Murray et al. in press). These birds are very insensitive to reductions in sandeel availability, owing in part to their high ability to switch diet (Furness and Tasker 2000). Northern gannets are also the largest seabirds in the North Atlantic. Therefore, a trend towards a seabird community dominated by larger seabirds contrasts strongly with observed trends in prey length in lower trophic levels.

The regional pattern of decline in seabird numbers is strikingly similar to the decline in sandeel populations. Regional differences in the strength of bottom-up regulation may provide an explanation. In the Irish Sea, Celtic Sea and the English Channel, there appears to be little evidence of bottom-up regulation (Lauria et al. 2013). However, bottom-up effects have been found to exist in the north-western North Sea (Frederiksen et al. 2006), which could be diagnostic of different oceanographic conditions (Lauria et al. 2013). Climate change impacts on lower trophic levels may therefore affect seabird numbers in the northern North Sea but have little effect on seabirds in southern areas.

While the predicted short-term increase in sprat abundance around Britain in response to warming (Lenior et al. 2011) may mitigate a shortage of sandeels, they probably do not represent a long-term solution for seabirds. Sprat are predicted to disappear from these waters by the end of this century, with the distribution shifting to the Barents Sea (Lenior et al. 2011). In fact, warm-water mid-trophic fish such as anchovies (Lenoir et al. 2011) will likely be performing the role in the ecosystem vacated by sandeels and sprat. Although these fish could potentially fill the void left by sprat and sandeels in seabird diets, whether or not there will be a smooth transition in prey is unknown. Consistent recruitment failure of herring (Payne et al. 2009, 2013) places in doubt the viability of this species as alternative prey for

seabirds. Many seabirds are able to prey on piscivorous demersal fish like whiting *Merlangius merlangus*, but these have a very low energy density and the body condition of chicks is much poorer in years where whiting are the main prey (Harris 1980).

In the case of seabirds that feed opportunistically by scavenging at fishing vessels (especially great skuas, northern fulmars, great black-backed gulls *Larus marinus*) part of the impact on their breeding success may be due to reduced amounts of fishery discards and offal in recent years (Votier et al. 2004, 2007, Käkelä et al. 2005, 2007, Furness 2006, 2007). Although these seabirds prefer to feed by on sandeels, they turn to fishery offal and discards as an alternative food, and in the last few years there have been large reductions in amounts of discards and offal provided to seabirds all around Britain at a time when sandeels have also declined. Great skuas have attempted to mitigate this situation by increasingly killing other seabirds, but have also suffered breeding failures due to food shortage, part of which results from the fact that great skuas will kill chicks of neighbouring skua pairs. The depredations on other seabirds will also reduce their breeding success, as the chances of chicks surviving if a parent has been killed during the breeding season will be much reduced. Although gannets mainly feed on pelagic fish in summer, discards at fishing vessels makes up a significant component of the diet in winter. A trend for gannets to be moving further south in winter than they did previously may be related to reductions in discarding (Kubetzki et al. 2009).

In 2014, the EU common fisheries policy was reformed to include a complete ban on fishing discards. A ban on discards of pelagic species will be enforced in January 2015, with the ban extending to the most valuable demersal species (cod, hake and sole) in 2016, and all total allowable catch species in 2019 (European Commission, 2013). This will almost certainly have a major impact on many seabird populations throughout Europe that are, at the moment,

reliant on discards. Species native to the north-east Atlantic that are currently extensively exploiting fishery discards are kittiwakes, herring gulls *Larus argentatus*, the lesser black-backed gull *Larus fuscus*, the great black-backed gull, the great skua, the northern fulmar and the northern gannet (Bicknell et al. 2013). We can speculate that the cessation in discards could slow the sustained growth in gannet populations.

Evidence suggests that anthropogenic and climate impacts on seabirds could be additive (Frederiksen et al. 2004, Votier et al. 2005). On the Scottish east coast, the species most vulnerable to these combined threats are northern fulmars, kittiwakes, and shags (Burthe et al. 2014). The vital rates (e.g. growth, maturation and survival rates) of these species have been decreasing with rising temperature, most likely through changes in prey e.g. sandeels. To ameliorate any declines in these demographic parameters, efforts to safeguard vital seabird prey around important colonies, such as the Isle of May, could be put in place. The most notable case is the sandeel fishery closure off the east coast of Scotland in 2000. Established with the aim of avoiding depletion of the sandeel stock, a substantial area covering approximately 21,000km^2 was closed to sandeel fisheries (Frederiksen et al. 2008b, Greenstreet et al. 2010b). However, closing off the area to fishing has not been sufficient to ensure high sandeel abundance (**Figure 4**). Recent measures have been enforced to protect seabird adjacent marine habitats. In 2009, 31 of Scotland's seabird breeding colony Special Protection Areas (SPAs) were extended (http://www.snh.org.uk/about/directives/ab-dir15j.asp), however, the marine areas protected are extremely small (<5 km) and therefore may not effectively safeguard seabird prey. This is especially true for sandeel feeding seabirds because of the patchiness of sandeel habitat. Moreover, many seabirds have foraging ranges that span many tens of kilometres (Thaxter et al. 2012). In addition to protecting sandeel prey in the vicinity of seabird colonies, measures to protect sources of sandeel larvae

that are exported to these areas can also be put in place. Recently marine protected areas in north-west Orkney and Turbot bank have been established with the aim of protecting sandeel larvae (http://jncc.defra.gov.uk/page-6484, http://jncc.defra.gov.uk/page-6490). These location were chosen as they are thought to be important sources of newly hatched sandeel larvae (Wright & Bailey 1996) which, through dispersal, support populations afar. It is possible that MPAs may lead to increased abundance outwith the MPA caused by larval spillover (Christensen et al. (2009). However, the extent of spillover will obviously depend on availability of suitable habitat.

Conclusions

We summarize our key findings from this review as follows:

- Climate-driven trophic cascades are already affecting seabirds in UK waters.
- There appears to be marked inter-species variation in sensitivity to climate change.

- Strong regional differences exist in climate effects on seabirds, possibly due to spatial variation in prey affecting the strength of bottom-up effects.

- Winter temperature appears to be having a negative impact on sandeel populations in the north-western North Sea. These populations are characterised by low growth rates so metabolic costs of overwintering should increase with rising temperatures.

- A reduction in mean copepod size may explain a long term decline in sandeel size-at-date. This ongoing reduction in sandeel size-at-date is causing a mismatch between seabird peak energy requirements and adequate sandeel prey.

- *C. finmarchicus* is a key prey species of sandeel so we should expect further deleterious impacts on sandeels in future in response to the ongoing northward shift of this *Calanus* species. This will have the effect of a reduction in seabird breeding success.

- There is no evidence of indirect climate impacts on zooplankton through changes in phytoplankton. Therefore, any indirect climate impacts on seabirds may be restricted to changes in fish prey or zooplankton.

- Future patterns of sandeel-dependent seabird breeding maturation and survival will depend critically on the scope for feeding on alternative prey.

- An increase in sprat abundance should temporarily mitigate the impact of a shortage of sandeels for some seabirds. However, existing modelling indicates that they may not represent a long-term solution.

- Declines in sandeel quality and abundance could cause the North Sea seabird community to become increasingly dominated by larger species.

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TABLE 1

Table 1. Names and life history characteristics of seabird species regularly breeding in the British Isles, which are included in the JNCC's Seabird Monitoring Programme, and the Seabird Colony Register. All except the Red-throated diver were included in the Seabird 2000 census or Seabird Colony Register. Source: JNCC, http://www.jncc.gov.uk/page-3201 General diet description taken from (Robinson 2005). Data on seabird clutch size is taken from Snow & Perrins (1998) and Harrison (1975) unless stated otherwise. Lifespan is calculated as $\lambda = \mu - 1/\ln(\varphi)$,where λ=lifespan, μ=age at first breeding & φ=adult survival rate (Robinson 2005).

Common name	Scientific name	General Diet	Clutch size (no. eggs)	Age at first breeding (years)	Adult survival rate (year^{-1})	Lifespan (years)
Red-throated diver*	*Gavia stellata* *	Primarily fish, captured by seizing in bill, also frogs, large invertebrates.	2	3 (Okill 1994)	0.840 (Hemmingsson & Eriksson 2002)	9
Northern Fulmar	*Fulmarus glacialis*	Crustaceans, squid, fish, offal, carrion mostly from surface.	1	9 (Dunnet & Ollason 1978a)	0.972 (Dunnet & Ollason 1978b)	44
Manx Shearwater	*Puffinus puffinus*	Mostly small fish and squid, also small crustaceans and offal from surface or diving.	1	5 (Thompson 1987)	0.905 (Brooke 1990)	15
European Storm-petrel	*Hydrobates pelagicus*	Mainly surface plankton, small fish,	1	4-5 (Scott 1970)	0.870 (Cramp et al.	11-12

Leach's Storm-petrel	*Oceanodroma leucorhoa*	Mainly surface plankton, small fish, feeds from water surface without alighting.	1	4-5 (Huntington & Burtt 1972)	0.880 (Furness 1984)	12-13
		feeds from water surface without alighting.			1977-94)	
Northern Gannet	*Morus bassanus*	Fish (up to 30cm), usually plunging from heights of 10-40m.	1	5 (Alerstam 1990)	0.919 (Wanless et al. 2006)	17
Great Cormorant	*Phalacrocorax carbo*	Fish, mostly by diving from surface.	3-4	2-4 (Cramp 1977)	0.880 (Frederiksen &	10-12

					Bregnba lle 2000)	
European Shag	*Phalacrocora x aristotelis*	Fish, mostly by diving from surface.	*3*	3 (Potts et al. 1980)	0.878 (Harris et al. 1994)	11
Arctic Skua	*Stercorarius parasiticus*	Summer: mostly birds, small mammals, insects; Winter: fish, mostly by piracy from other birds.	2 (Furness 1987)	4 (Lloyd et al. 1991)	0.886 (O'Dona ld 1983)	12
Great Skua	*Catharacta skua*	Mostly fish, obtained from sea, scavenging or by piracy.	2 (Furness 1987)	7 (Klomp & Furness 1991)	0.888 (Ratcliff e et al. 2002)	15
Mediterranean Gull	*Larus melanocephal us*	Summer: insects; Winter: marine	3	*NA*	*NA*	*NA*

		fish and molluscs.				
Black-headed Gull	*Larus ridibundus*	Opportunist, insects, earthworms, also plant material and scraps.	2-3	2-5 (Clobert et al. 1994)	0.900 (Prévot-Julliard et al. 1998)	11-14
Mew Gull	*Larus canus*	Invertebrates, some fish, preference for foraging on ground.	3	3-4 (Cramp & Simmons 1983)	0.860 (Buckcicinski & Buckcicinska 2003)	10-11
Lesser Black-backed Gull	*Larus fuscus*	Omnivorous, often feeds at rubbish dumps	3	4-5 (Harris 1970)	0.913 (Wanless et al.	15-16

		or on shoals of fish.			1996)	
[Herring Gull](#)	*Larus argentatus*	Omnivorous, but mostly animal material, also scavenges and pirates food.	3	4-5 (Chabrzyk & Coulson 1976)	0.880 (Wanless et al. 1996)	12-13
[Great Black-backed Gull](#)	*Larus marinus*	Omnivorous, but mostly animals including other seabirds, also scavenges and pirates food.	2-3	4-5 (Cramp & Simmons 1983)	*NA*	*NA*
[Black-legged Kittiwake](#)	*Rissa tridactyla*	Mainly marine invertebrates and fish.	2	3-4 (Coulson & White 1959)	0.882 (Harris et al. 2000a)	11-12
[Sandwich Tern](#)	*Sterna sandvicensis*	Fish, mostly plunge-diving.	1-2	3 (Snow & Perrins 1998)	0.898 (Robinson 2010)	12
[Roseate Tern](#)	*Sterna*	Fish, mostly	1-2	3-4	0.855 (	9-10

	dougallii	plunge-diving.		(Spendelow 1991)	Ratcliffe et al. 2008)	
[Common Tern](#)	*Sterna hirundo*	Mostly fish, also crustaceans in some areas, mostly by plunge-diving.	2-3	3-4 (Nisbet et al. 1984)	0.900 (Becker & Ludwigs 2004)	12-13
[Arctic Tern](#)	*Sterna paradisaea*	Fish, crustaceans and insects.	1-2	4 (Coulson & Horobin 1976)	0.900 (Balmer & Peach 1997)	13
[Little Tern](#)	*Sterna albifrons*	Small fish and invertebrates, often hovers before plunge-diving.	2-3	3 (Massey et al 1992)	0.899 (Tavecchia et al. 2006)	12
[Common emot](#)	*Uria aalge*	Mostly fish, usually taken from depths up	1	*5* (Olsson et al.	0.946 (Harris et al.	23

		to 60m.		2000)	2000b)	
Razorbill	*Alca torda*	Fish, some invertebrates.	1	4-5 (Lloyd 1976)	0.900 (Chapdelaine 1997)	13-14
Black Guillemot	*Cepphus grille*	Mostly fish, also crustaceans especially in the Arctic.	1-2	3-4 (Ewins 1988)	0.870 (Frederiksen & Petersen 1999)	10-11
Atlantic Puffin	*Fratercula arctica*	Mostly fish, also crustaceans especially in the Arctic.	1	4-6 (Harris 1983, Johnsgard 1987)	0.924 (Harris et al. 1997)	17-19

FIGURE 1

Changes in the numbers of breeding seabirds in the United Kingdom 1969-2002 (JNCC 2014). Percentage changes refer to coastal-nesting seabirds only –inland colonies were not surveyed during the Operation Seafarer (1969-70) (Cramp et al. 1974) and the Seabird Colony Register Census (SCR) (1985-88)(Lloyd et al. 1991). Manx Shearwater, Leach's Storm petrel and European Storm-petrel are omitted as they were not surveyed during the Operation Seafarer (1969-70) and the SCR Census (1985-88). Survey methods for Black Guillemots during Operation Seafarer (1969-70) were not comparable with Seabird 2000 (1998-2002). Change from 2000-2012 (i.e. over the period since the last national census) is estimated from trends derived from the Seabirds Monitoring Programme sample of colonies; this analysis is only available for species with sufficient data to accurately estimate trends. *change between censuses in 1984-5 and 2004-5.
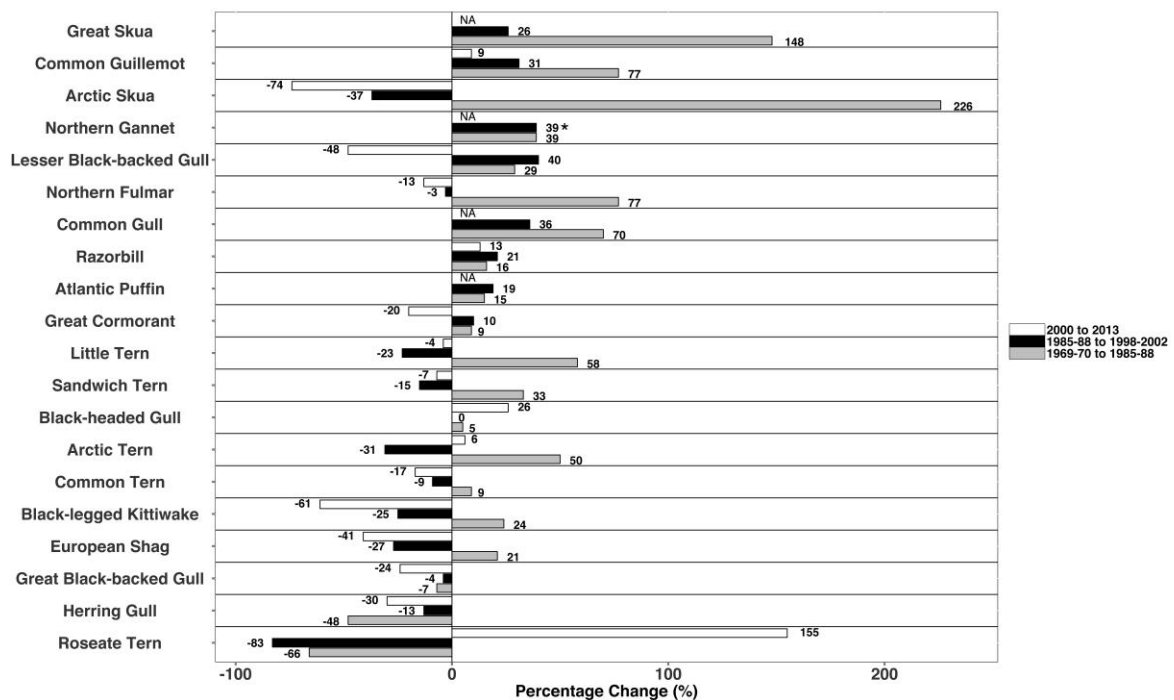
FIGURE 2
Changes in the numbers of breeding seabirds in Scotland, England and Wales during the period 2000-2013 (JNCC 2014). Change from 2000-2013 (i.e. over the period since the last national census) is estimated from trends derived from the Seabirds Monitoring Programme sample of colonies; this analysis is only available for species with sufficient data to accurately estimate trends (JNCC 2014).
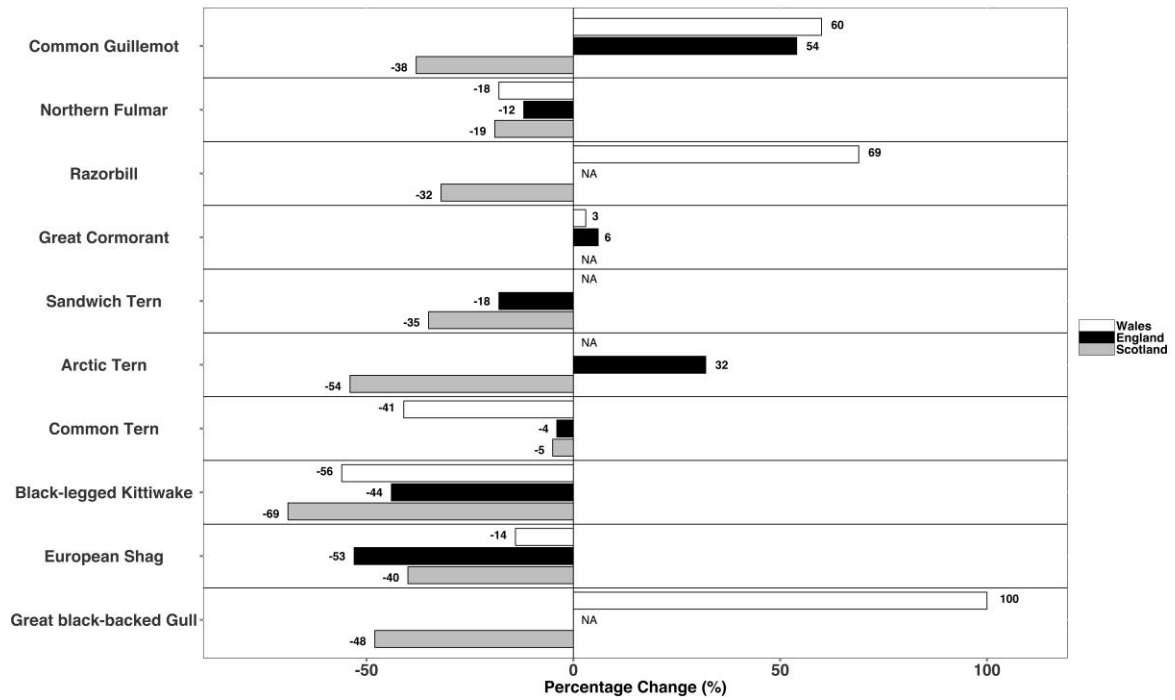
FIGURE 3

From Friederikson et al. (2007). Simplified diagram of some documented and probable trophic and climatic controls in the North Sea pelagic ecosystem. 1: bottom-up control of zooplankton by phytoplankton (Richardson & Schoeman 2004); 2: bottom-up control of sandeel larvae by zooplankton (Frederiksen et al. 2006); 3: bottom-up control of seabird breeding success by sandeels (Hamer et al. 1993, Frederiksen et al. 2006); 4: top-down control of zooplankton by herring predation (Arrhenius 1997); 5: bottom-up control of herring by zooplankton (Corten 2001, Beaugrand 2004); 6: top-down control of sandeels by herring predation (Friederikson et al. 2007); 7: top-down control of herring by human fisheries (Jennings et al. 2001); 8: local top-down control of sandeels by human fisheries (Rindorf et al. 2000); 9: climatic control of herring recruitment (Sætre et al. 2002); 10 and 11: climatic control of phytoplankton and zooplankton (Edwards & Richardson 2004, Hays et al. 2005); 12: climatic control of sandeel recruitment (not known if direct) (Arnott & Ruxton 2002).
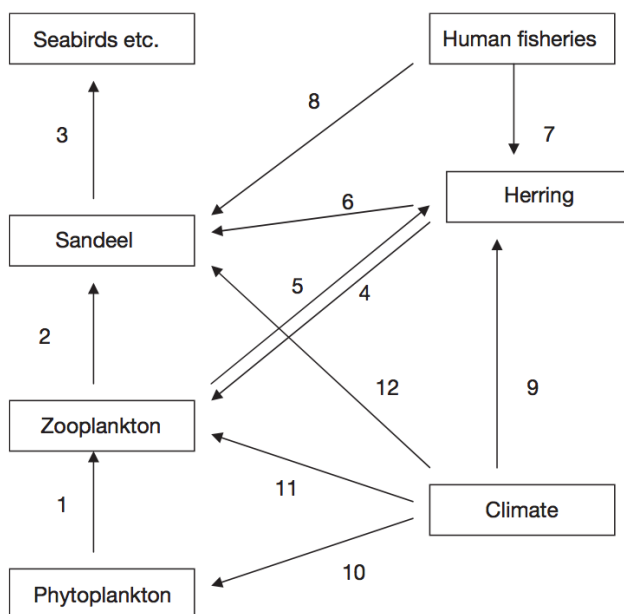
FIGURE 4

Catch per unit effort of sandeel larvae off the Firth of Forth (bars) and abundance of early larvae (3-7 days old) at Stonehaven (symbols and lines). CPUE data from 1990 to 2000 was derived from analysis of vessel log-books from the Danish sandeel fishery. CPUE Data from 2000 onwards is taken from a supervised monitoring fishery. CPUE data for 2006 and 2007 is taken from H. Jensen, Danish Institute for Fisheries Research. Larval abundance was measured at Stonehaven (between 56° 57.83 N and 002° 06.74 W) and is taken from Heath et al. (2012). The dotted line delineates the fishery closure.
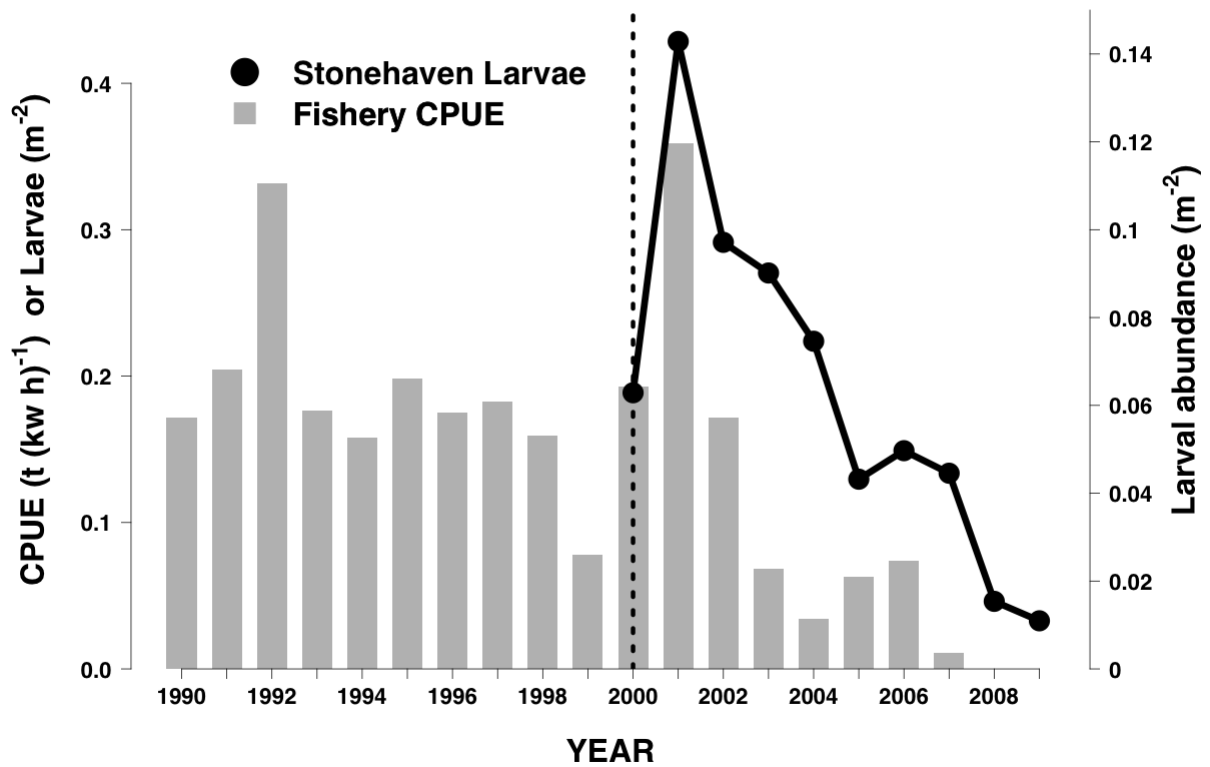
FIGURE 5

4-year aggregated mean (log10) abundance of snake pipefish caught by commercial trawlers, for the periods 1997-2000 (top left), 2001-2004 (top right), 2005-2008 (bottom-left) and 2009-2012 (bottom right). Trawl survey data extracted from ICES DATRAS. The domain of interest lies between 49° 45' N and 61°45' N, and 10° 30' W and 12° 30' E. World borders were downloaded from http://thematicmapping.org/downloads/world_borders.php.