Interaction between top-down and bottom-up control in marine food webs

Christopher Philip Lynam[a], Marcos Llope[b,c], Christian Möllmann[d], Pierre Helaouët[e], Georgia Anne Bayliss-Brown[f], and Nils C. Stenseth[c,g,h,1]

[a]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft, Suffolk NR33 0HT, United Kingdom; [b]Instituto Español de Oceanografía, Centro Oceanográfico de Cádiz, E-11006 Cádiz, Andalusia, Spain; [c]Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, NO-0316 Oslo, Norway; [d]Institute of Hydrobiology and Fisheries Sciences, University of Hamburg, 22767 Hamburg, Germany; [e]Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom; [f]AquaTT, Dublin 8, Ireland; [g]Flødevigen Marine Research Station, Institute of Marine Research, NO-4817 His, Norway; and [h]Centre for Coastal Research, University of Agder, 4604 Kristiansand, Norway

Climate change and resource exploitation have been shown to modify the importance of bottom-up and top-down forces in ecosystems. However, the resulting pattern of trophic control in complex food webs is an emergent property of the system and thus unintuitive. We develop a statistical nondeterministic model, capable of modeling complex patterns of trophic control for the heavily impacted North Sea ecosystem. The model is driven solely by fishing mortality and climatic variables and based on time-series data covering >40 y for six plankton and eight fish groups along with one bird group (>20 y). Simulations show the outstanding importance of top-down exploitation pressure for the dynamics of fish populations. Whereas fishing effects on predators indirectly altered plankton abundance, bottom-up climatic processes dominate plankton dynamics. Importantly, we show planktivorous fish to have a central role in the North Sea food web initiating complex cascading effects across and between trophic levels. Our linked model integrates bottom-up and top-down effects and is able to simulate complex long-term changes in ecosystem components under a combination of stressor scenarios. Our results suggest that in marine ecosystems, pathways for bottom-up and top-down forces are not necessarily mutually exclusive and together can lead to the emergence of complex patterns of control.

trophic control | ecosystem modeling | marine food web functioning | wasp-waist | regime shifts

T he question of whether food webs are resource- (bottom-up) or predation- (top-down) controlled is one of the most fundamental research questions in ecology (1–3). Marine ecosystems, originally thought to be mainly steered by bottom-up control, have recently been shown to exhibit periods of top-down control due to the extraction of large predators through fishing (4–7) or climate oscillations (8). Furthermore, experimental evidence shows climate warming may exert a host of indirect effects on aquatic food webs mediated through shifts in the magnitudes of top-down and bottom-up forcing (9, 10). However, for large marine ecosystems that are not amenable to experimentation studies, investigations of how interactions in their complex food webs mediate the influence of both top-down (e.g., fishing) and bottom-up (e.g., climate change) control are lacking or are based on aggregated species complexes. We model an extensive historical dataset for the North Sea (over 45 y) at the lowest possible resolution (often species) to determine key interactions between species and estimate their responses to pressures. The model reveals both simple (direct) and complex (indirect) pathways linking plankton to seabirds and can highlight the wider effects of climate change and potential actions by fishery managers.

The North Sea is one of the most anthropogenically impacted marine ecosystem and is thought to be fundamentally driven from the bottom-up through climatic (temperature-related) influences on plankton, planktivorous fish, and the pelagic stages of demersal fish (11–13). Some studies, however, have suggested that top-down effects, such as predation by sprat on zooplankton, are equally important in what is termed a "wasp-waist" system (14). For demersal piscivorous fish species like cod and whiting, the importance of fishing activity and predator–prey interactions has also been clearly demonstrated (15). Seabirds are also important predators and they are considered sensitive to change in the abundance of planktivorous fish, particularly sandeel and juvenile clupeids, i.e., sprat (14, 16, 17).

We tested how interactions between key species in the complex North Sea system mediate the effects of the dominant external stressors of climate and fishing on long-term trends in their abundance. To address this question, an advanced statistical modeling approach (18, 19) was developed incorporating the interactions between three phytoplankton measures (abundance of diatoms and dinoflagellates and a greenness index), three zooplankton groups (the large copepods *Calanus finmarchicus* and *Calanus helgolandicus* as well as an assemblage of small copepod species), four forage fish species (herring, sprat, sandeel, and Norway pout), four piscivorous fish species (cod, haddock, whiting, and saithe), and one seabird group. The model incorporates direct and indirect responses of these groups to

Significance

Whether environmental conditions, harvesting, or predation pressure primarily regulate an ecosystem is still a question of much debate in marine ecology. Using a wealth of historical records, we describe how climate and fishing interact in a complex marine ecosystem. Through an integrative evidence-based approach, we demonstrate that indirect effects are key to understanding the system. Planktivorous forage fish provide an important role in the system, linking bottom-up and top-down processes such that fishing can indirectly impact the plankton and environmental effects can cascade up to impact demersal fish and predatory seabirds. Cascading trophic interactions can be mediated by opposing bottom-up and top-down forces; this combination has the potential to avert regime wide shifts in community structure and functioning.

Fig. 1. Diagrammatic representation of the significant interactions modeled between functional groups and drivers. Thresholds in the relationships are indicated by colored lines dependent on whether the threshold variable is the AMO (red) or diatom abundance (green). Lines point from predictor to response and are labeled with "+" if the relationship is positive, "−" if negative, and, in one case, with a "v" where the relationship curves up at both extremities of the data range. Thick solid lines are relationships without lag, thin lines with a single year lag (as required between fishing mortalities and spawning stock biomass terms), and dashed lines if a 2-y lag was modeled (as expected for recruitment effects to become evident in the biomass of fish). Individual models are shown in *SI Appendix,* Fig. S1, and goodness of fit shown in *SI Appendix,* Fig. S2.

fishing mortality and temperature based on long time series (1964–2010; seabird data 1989–2010). The dominant signals were modeled using Generalized Additive Models in fully additive (GAM) and also a threshold (tGAM) formulation (18, 19) that allows for changes in the relationship between a response term and an explanatory variable as a function of another variable. The models were used to hindcast the data and to conduct simulations under scenarios of external forcing based only on the initial conditions of each food web component. We demonstrate that our approach allows for the partitioning of the effects of climate change and fishing in a complex food web given the historical patterns arising from bottom-up and top-down processes.

Results

Our modeling simulations show that high system complexity can arise from strong connectivity between even a limited number of groups (Fig. 1). Controlling forces that arise from environmental conditions, predation, and/or harvesting can lead to wider effects on the system through indirect interactions that can be detected through nondeterministic modeling (Figs. 2–4). Bottom-up and top-down effects do not necessarily operate through mutually exclusive pathways, and cascading trophic interactions can be mediated by opposing forces with the potential to avert regimewide shifts in community structure and functioning. The multitude of cascading effects (Fig. 1) illustrates the difficulty of anticipating the outcome

that a change in external drivers, such as fishing or climate change, would have on an ecosystem component (Fig. 3). Bottom-up processes, forced by temperature, have dominated change in the abundance of planktonic groups since the 1960s. In contrast, top-down impacts of fishing have dominated changes in the biomass of commercially exploited fish. Planktivorous forage fish provide a key role in the system linking bottom-up and top-down processes such that fishing can indirectly impact the plankton, and temperature effects can cascade up through the web of interactions to impact demersal fish and predatory seabirds.

In general, GAM formulations were sufficient to identify sensible linkages between the time series (including both linear terms and simple smooth terms between response and predictors, *SI Appendix,* Table S1), which reflect pathways between variables that agree with studies reported in the scientific literature. Threshold formulations (tGAMS) were preferred for plankton groups only and linked to climate forcing: i.e., diatoms were linked to both local sea-surface temperature (SST) and predation pressure (by *C. helgolandicus* and small copepods) by thresholds based on the Atlantic Multidecadal Oscillation (AMO). Additionally, predation pressure on small copepods by sandeels was mediated by a threshold relationship dependent on diatom abundance. Because the abundance of diatoms is dependent on temperature, this threshold relationship between small copepods and sandeels is linked indirectly to temperature. Thus, sandeel can impact small

copepod abundance only if small copepods themselves are limited by a period of low diatom abundance during a cold regime.

For phytoplankton and the majority of fish (all except for sandeel and sprat) the most important term was the response term for previous years (*SI Appendix*, Table S1). For fish, this lagged term can be considered to represent population dependency, whereas for phytoplankton it can be interpreted as the effect of typically similar environmental conditions from year to year that are not explicitly included in the model. Phytoplankton groups were the most important predictors of zooplankton groups. Although zooplankton groups were linked to half of the eight fish species presented (Fig. 1), none of these links formed the dominant, or even second-most dominant, predictive signal for fish. So, bottom-up effects of climate acting through the plankton were weak for four fish species (sandeel, herring, sprat, haddock) and not evident for the remainder. Fishing mortality (F) was the most important predictor of sandeel biomass and, after the population delay term, also for herring biomass (*SI Appendix*, Table S1). For other fish species, interactions with fish were most important after inherent population dependency: The cod model was the exception to this rule because SST was highly important as a predictor but interactions with other species were not.

The direct impact of fishing mortality upon a fish stock is represented in the interaction web (Fig. 1) by the type of vessel that dominates the catch of each species; these impacts are all negative. Pathways for indirect effects of climate and fishing can be identified through the cascade of links: fishing on sandeels and warming SSTs have knock-on detrimental effects for whiting, haddock, and the breeding success of seabirds. Similarly, fishing of herring (the dominant planktivore in the North Sea) can be seen to have a cascading effect on many other fish species and thus on zooplankton groups and diatoms; a decrease in herring biomass is expected to have a direct negative effect on haddock but positive effects on Norway pout, sprat, and *C. finmarchicus*, leading to
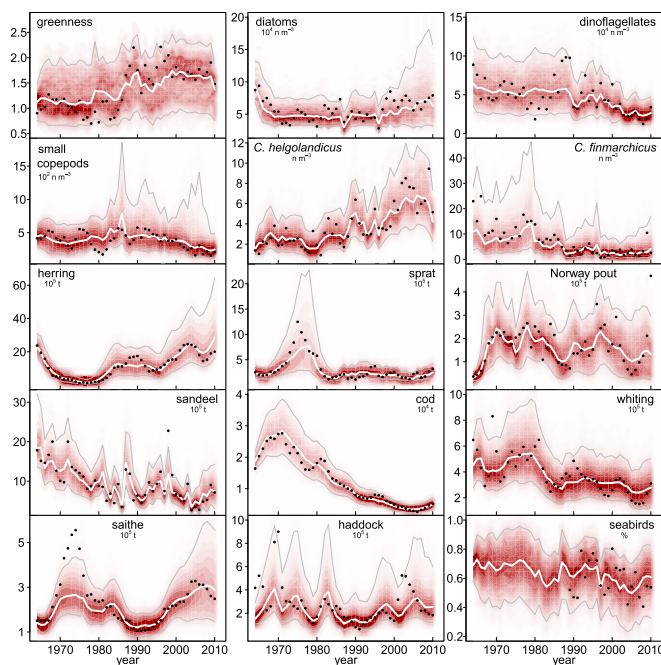
Fig. 2. Simulations to 2010 based solely on predictions from initial conditions in 1964 and the time series of SST and fishing mortality to 2010 (*SI Appendix*, Fig. S3). The best estimates (median values) of the simulations are shown by the white lines and the 95% confidence bands by the gray lines: red shading indicates the annual probability density of simulated values (dark red, high likelihood). Data used for calibration are shown by points.
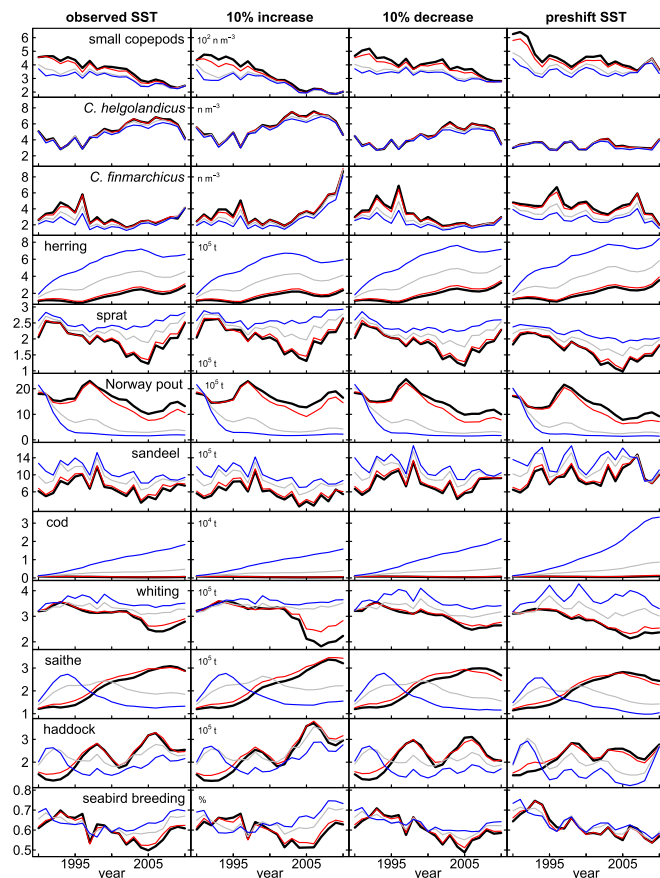
Fig. 3. Sensitivity of the interaction web to fishing levels under four climate scenarios (see *SI Appendix*, Fig. S3). The lines result from the median of 999 simulations and show change in zooplankton abundance, fish biomass, and seabird breeding success (y axis) over time (x axis) as a function of fishing mortality (F, by color) and differing SST scenarios (by column). Heavy black lines are from simulations based on the observed F. Colors of thin lines relate to F multiplier applied for all stocks: red, 10% decrease in F; gray, 50% decrease in F; blue, 80% decrease in F. The first column shows the effect of changing F with observed SST driving the model, second column with a 10% increase in observed SST, the third column with a 10% decrease in observed SST, and the fourth column with SST replicating observed variability about the mean in the period 1964–1984. The x axis starts in 1990.

increases in saithe and whiting but decreases in *C. helgolandicus*. Potentially, these changes then lead to decreases in sandeel and thus increases (dependent on a high abundance of diatoms) in small copepods, which would serve to increase the depleted herring biomass through improved recruitment. As a result of the increase in small copepods, additional decreases in diatoms (dependent on a high phase of the AMO) are expected to cause a decrease in *C. finmarchicus* which counteracts the effect of a decrease in predation by herring. A decrease in herring biomass could lead to a decrease in haddock, but this is similarly offset by the indirect effects of decreased predation by herring on *C. finmarchicus* (a prey for haddock) and through a cascade of interactions initiated through decreased competition of herring with sprat, which operates through diatoms, *C. finmarchicus*, and *C. helgolandicus*. The multitude of cascading effects illustrates the high complexity and strong connectivity in the system and highlights the difficulty of anticipating the outcome that a change in external drivers, such as fishing or climate change, would have on a particular component.

The North Sea experienced a series of abrupt stepwise changes in the late 1980s, particularly affecting the plankton community

(20, 21) and recruitment of several fish species (22). These changes, associated with warming temperatures, are often described as a regime shift. We used our model to simulate what would have happened if temperatures had not risen since the mid-1980s (the "preshift SST scenario"). Furthermore, we tested scenarios whereby the increases in SST experienced were either 10% greater or lesser in the warm period from 1990 onward. Our results show that sandeel, cod, and herring would have benefited to the detriment of Norway pout, sprat, whiting, and saithe (Fig. 3). By contrasting the preshift SST scenario against the predictions with observed SST (Fig. 3 and *SI Appendix*, Figs. S4 and S5), it is evident that cold temperatures lead to a decrease in *C. helgolandicus* and, thus, sprat. The small copepods group increases as temperatures decrease, following an increase in dinoflagellates, resulting in an increase in herring and contributing to increases in sandeel, decreases in Norway pout, and reinforcing the decrease in sprats. Sandeel and cod respond to increased temperatures with decreases as expected given the direct links of these groups to SST (Figs. 1 and 3 and *SI Appendix, Fig. S1*). Whereas whiting should benefit from an increase in sandeel, the effect is offset by the decrease in sprat (Fig. 3 and *SI Appendix, Fig. S4*): notably though, this compensation due to low sprat biomass was not evident once fishing pressure was removed and whiting increased during the cold scenario (Fig. 3 and *SI Appendix, Fig. S5*). In the colder scenarios, and in response to increases in *C. finmarchicus* and sandeel, seabird breeding success also increased. Although Norway pout, sprat, and saithe may benefit from changes in the plankton during the warmer postshift temperatures, the temporal trends in biomass observed are attributable partly to fishing mortality, which had been successfully managed downward since the high values of the 1980s (*SI Appendix, Fig. S3*), and partly to interactions with the dominant planktivore, herring (Fig. 1). Without fishing mortality constraining the biomass of herring, this stock would increase to the detriment of sprat, Norway pout, and, thus, saithe (Fig. 3, blue lines, and *SI Appendix, Fig. S5*).

Despite climate effects, fishing mortality has been the greatest driver of change in the biomass of commercial fish stocks since 1964 and, through ecosystem interactions, has likely depressed the breeding success of seabirds since 2000 (Fig. 3 and *SI Appendix, Table S1*). For most fish species, their biomass responded directly to fishing mortality with the exception of whiting and Norway pout, which responded indirectly to effects of fishing on their prey (sandeel and sprat) and predators (herring), respectively. Although there are linkages between the zooplankton and fish species (Fig. 1), predation effects do not appear strong enough to significantly change the trajectories of the biomass time series for zooplankton groups even if fishing mortality was reduced greatly (Fig. 3). These simulations of fishing effects suggest that the top-down effects on the zooplankton are not dominant processes structuring the plankton community.

Whereas the biomasses of each fish species, other than whiting, respond directly to fishing mortality, climate was only linked directly to cod and sandeel. Nevertheless, numerous indirect fishing and climate effects emerged from the model simulations. Indirect fishing effects were shown most clearly by the response of Norway pout and saithe biomass to changes in fishing mortality on herring (Fig. 4). The biomass of saithe is high when the abundance of its prey, Norway pout, is also high. However, reducing fishing mortality on planktivorous fish (including both Norway pout and herring) simultaneously leads to a decrease in Norway pout and, thus, saithe (Fig. 4). This counterintuitive finding is a result of the interaction term between herring and Norway pout. Herring biomass increases during periods of low fishing mortality, but as it does so predation on Norway pout increases, as does potential competition between the species. Despite the same percentage decrease in fishing mortality on Norway pout as on herring, Norway pout biomass decreases and this has a knock-on effect for piscivorous saithe. In this case, the cascade can be attributed to top-down effects but indirect interactions are also implied.

Whereas both saithe and whiting are relatively remote from climate effects in the model (Fig. 1), whiting do respond to temperature changes due to a clear response by their prey species: sprats and sandeels (Fig. 3). However, the biomass of whiting does not respond in a simple way to changes in the biomass of these prey species due to indirect fishing impacts (Fig. 3 and *SI Appendix*, Figs. S4 and S5). As the fishing mortality on sandeels is decreased, the biomass of whiting should increase. However, the increase in whiting feeds back through the interaction web as a significant negative effect on sandeel biomass, representing a clear food web response in this instance. As temperatures increase, the biomass of sandeel and thus predatory whiting should decrease as a direct response to temperature. However, not only do sandeel respond directly to climate impacts, but both sandeel and sprat also respond to temperature influences on their plankton prey. The indirect climate effect on sandeel is through bottom-up effects via dinoflagellates and small copepods, whereas sprats are linked by a pathway from temperature through their prey, *C. helgolandicus*. Thus, a cooler climate indicates an increase in sandeels (from both the direct and indirect pathway, Fig. 1), but a decrease in sprat due to a decrease in *C. helgolandicus*. The response of whiting to climate is thus dependent on two prey species that have contrasting responses to temperature and are fished by different fleets. Thus, whiting can benefit from both increases and decreases in temperature dependent on the fishing mortalities imposed (Fig. 3). The effect is clearer when contrasting the difference between the biomass of whiting simulated under observed conditions and under preshift temperatures (Fig. 3). If observed fishing mortalities are used to drive the model, then whiting appear to have benefited from the observed warming in SST due to increases in sprat (Fig. 3), but should temperatures increase a further 10% beyond observations (Fig. 3) these increases in sprat would be negated by larger decreases in sandeel biomass. However, if all fishing mortalities were reduced to zero, whiting would benefit most under cold conditions (preshift SST) due to increases in sandeel (Fig. 3 and *SI Appendix, Fig. S5*).

In the recent warm period, between 2000 and 2010, a pattern of high diatom and low dinoflagellate abundance has been evident (Fig. 2). This period was accompanied by high abundance of *C. helgolandicus* but low abundance of *C. finmarchicus* and the small copepod group. Of the four planktivorous fish modeled with significant direct links to plankton, herring increased in biomass since 2000 despite low abundance of its significant prey group: small copepods. Other planktivorous fish species (sandeel and sprat) remained at low levels. Whereas sprat should benefit from the high abundance of *C. helgolandicus*, the biomass of sprat has not increased in the model due to the low fishing mortality on herring (*SI Appendix*, Figs. S1 and S3). Nevertheless, the increase in SST and decrease in *C. finmarchicus* have had a negative effect on the recruitment of some commercial fish (in particular cod, sandeel, and to a lesser extent haddock).

Sprats and sandeel are important prey species for seabirds foraging in the North Sea. The average breeding success of seabirds is linked to climate change through temperature effects on plankton and forage fish species (Fig. 1). As fishing mortality on sprat and sandeel is reduced, the average breeding success of seabirds should increase. Generally, colder conditions under observed fishing mortalities would appear beneficial to seabirds, albeit with some variability, due to an increase in secondary production (small copepods and *C. finmarchicus*) and sandeels (*SI Appendix, Fig. S4*). If fishing mortalities are reduced or removed completely from the simulations, then the modeled breeding success of seabirds would benefit, under current warm conditions, due to an increase in diatoms and sprats, particularly post-2005 (*SI Appendix, Fig. S5*). Therefore, further increases in temperature could benefit seabirds if low fishing mortality was imposed on sprat and sandeel (Fig. 3).

ENVIRONMENTAL SCIENCES
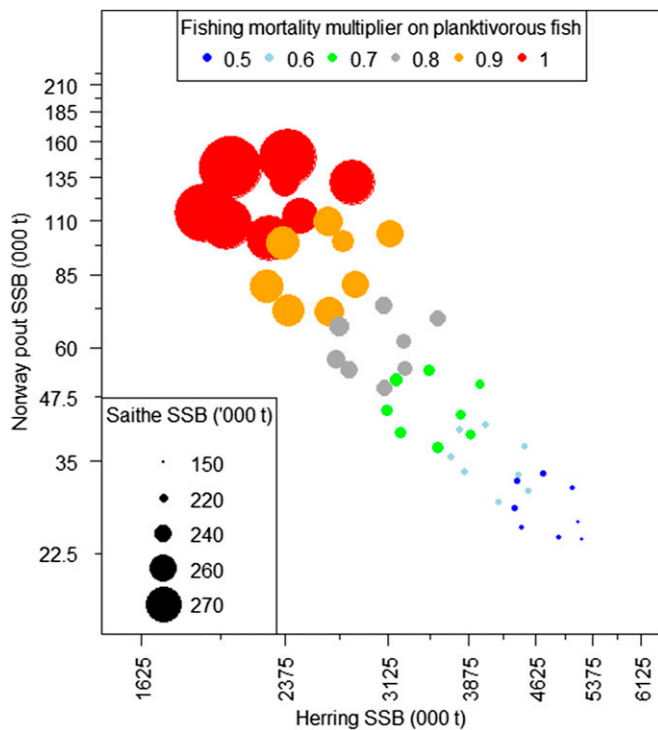
Fig. 4. Indirect effects on piscivorous saithe through fishing on prey species. The recovery of herring biomass (along the x axis) follows a decrease in fishing mortality (see color scale) on all planktivorous fish (herring, sprat, sandeel, and Norway pout). Despite the decreases in fishing mortality, there is a decrease in the biomass of Norway pout (along the y axis) due to the interaction in the model between herring and Norway pout. The change in the biomass of Norway pout cascades to a decrease in the biomass of the predatory demersal species: saithe, where bubble size is proportional to saithe biomass.

Discussion

Our study combines more than four decades of monitoring data in a statistical model to demonstrate that both bottom-up and top-down effects are regulating processes in the North Sea ecosystem (Fig. 1). The simulations indicate that bottom-up processes, forced by temperature, dominate change in the abundance of planktonic groups, whereas top-down impacts of fishing have dominated change in the biomass of commercially exploited fish. Some species are directly affected by both fishing and temperature (such as cod and sandeel). Interestingly, long indirect pathways occur that exemplify the complexity of the interaction web. For instance, sandeel, herring, sprat, and haddock are influenced by indirect temperature effects through a cascade of interactions in the plankton, whereas whiting, zooplankton groups, and diatoms are indirectly influenced by fishing mortality.

Some interactions between fish can be interpreted as predatory effects on prey and others as competition, whereas others may simply be useful statistical correlations that can be used to model the system as proxies for missing components. For example, as herring increase, both Norway pout and sprat decrease (Fig. 1): Herring is known to be a predator of Norway pout larvae (23) and sprat larvae (24), whereas small herring are competitors with sprat (25). Similarly, whiting are important predators of sandeel (26). Examples of potential cannibalism are present in lagged relationships including haddock (27) and Norway pout, whereby a high biomass of 2-y-old fish serves to counter the effect of the positive population dependence (i.e., 1-y lag term). An alternative explanation of these lagged relationships is that of skipped spawning events, as has been observed for Norway pout (28), which would take some time to be detected in the adult population. Additional predatory effects are likely hidden from the model; for example,

whereas large herring may consume juvenile cod, juvenile cod may also consume fish eggs and larvae, and such relationships within subcomponents of each species could provide additional feedback mechanisms that would act to stabilize simulations from the web.

Our results reveal the key role of planktivorous fish species in the system linking bottom-up and top-down processes, known as wasp-waist control (14). In addition, interactions between planktivores, such as herring, sprat, and Norway pout, can strengthen the relative flows to top predators, such as whiting, saithe, or seabirds. Importantly, these complex interactions lead to counterintuitive temporal patterns (29) demonstrated by the increase in saithe due to increased fishing mortality on planktivorous fish (Fig. 4). Therefore, despite the relative separation of top-down and bottom-up effects toward lower and upper trophic levels, respectively, the outcome of a given external intervention is the net effect of a number of cascading interactions.

The study demonstrates that bottom-up effects are dominant in structuring the zooplankton community. However, bottom-up control of the fish community (acting through sandeel, sprat, herring, and haddock) has been weak because the bottom-up influence of zooplankton has been limited by the strong impact of fishing in the period 1964–2010. As a result, the hypothesized "regime shift" in the North Sea during the mid-1980s (30, 31) is not shown in the spawning stock biomass of exploited fish. The regime shift is clearly apparent in the phytoplankton greenness index (with a step increase) and the relative abundance of the two *Calanus* species (increase in *C. helgolandicus* relative to *C. finmarchicus*) (Fig. 2). This should have led to an increase in sprat relative to haddock (Fig. 1); however, interactions between these two fish species with herring following management action to recover the herring stock has overwhelmed this effect (Fig. 3 and *SI Appendix*, Fig. S4). Clearly bottom-up processes can potentially lead to regime shifts, but in this case the changes were limited to the lower trophic levels due to top-down control from fishing effects on higher trophic levels. Although the relationships described here are considered key interactions in the study period, they are not necessarily permanent. A fundamental change in the system may occur following a sustained period of low fishing pressure potentially exacerbated by further effects of climate change (e.g., acidification). For example, a recovery by cod may lead to stronger predation on forage fish, which combined with further reductions in planktonic abundance could have ramifications for seabirds.

The breeding success of seabirds was related not only to the biomass of fish prey (sprat and sandeel), but also to the abundance of zooplankton. The 2-y lag in the seabird–zooplankton relationship may reflect the production of fish groups that are prey for birds but not included in the model. Alternatively, the relationship may represent that there is a high spawning success of fish when zooplankton abundance is high and that these small fish are consumed by seabirds. Fauchald et al. (14) found a significant relationship between the abundance of seabirds at sea and herring catches (dominated by juvenile fish) in the International Bottom Trawl Survey. Thus, our relationship between seabird breeding success and zooplankton may be a proxy for a link between seabirds foraging on herring juveniles. Fauchald et al. (14) suggested that the North Sea system demonstrates some characteristics of a wasp-waist ecosystem (32), whereby a single species dominates the intermediate trophic level. They suggest that herring regulate the abundance of seabirds through bottom-up control. They also suggest that herring regulate the abundance of krill, whereas sprat can regulate the abundance of *C. helgolandicus*. Whereas we model the same relationship between sprat and *C. helgolandicus*, we find that the impact of sprat is much smaller than that of temperature and interactions among the plankton.

Our empirical modeling approach demonstrated how fishing and warming alter the dynamics of a highly impacted marine ecosystem through species interactions. Not only has this occurred via direct effects of the external stressors, but also through indirect effects mediated by shifts in the relative importance of top-down and

bottom-up forcing. To make predictions from the model more re-liable as we move from the fitted data, further improvements such as including carrying capacity limits based on other studies could be included in the model. Taken together with energetic modeling approaches, such models can provide useful insight in key processes and support the ecosystem approach to management (33). A fruitful approach would be to fully embed the statistical relationships identified here within a theoretical model framework, i.e., use the interaction web as an emulator for a more complex model, as is commonly done in climate science, and consider within an ensemble modeling approach (34).

Materials and Methods

Our empirically based modeling followed a three step approach: (*i*) fitting separate statistical models for each component, (*ii*) combining relationship from (*i*) to build an interaction web, and (*iii*) simulating scenarios of change to test the sensitivity of the interaction web to change in pressures (temperature and fishing mortality). The main drivers of climate change included in the model were SST and the AMO. Plankton abundance was extracted from the Continuous Plankton Recorder database and functional groups were created

based on prior knowledge (35, 36). The fish species data (i.e., time series of spawning stock biomass and fishing mortality) were obtained from the International Council for the Exploration of the Sea assessment reports. The productivity of seabirds, i.e., number of chicks fledged per adult pair, for 300 colonies along North Sea coasts, was calculated for 19 species combined from the UK national seabird monitoring program. Data are available at www. repositorio.ieo.es/e-ieo/handle/10508/10771.

Our study uses GAMs (37) and tGAMS (38). See *SI Appendix, Materials and Methods* for details and further diagnostics. All models were fitted in R (Version 2.5.1) (39) and required the mgcv package (40, 41). Threshold nonadditive formulations of GAMs were built using the tgam library for this version of R by Kung-Sik Chan (tGAMs, ref. 38).

1. Heath MR, Speirs DC, Steele JH (2014) Understanding patterns and processes in models of trophic cascades. *Ecol Lett* 17(1):101–114.
2. Vinueza LR, Menge BA, Ruiz D, Palacios DM (2014) Oceanographic and climatic variation drive top-down/bottom-up coupling in the Galápagos intertidal meta-ecosystem. *Ecol Monogr* 84:411–434.
3. Wollrab S, Diehl S, De Roos AM (2012) Simple rules describe bottom-up and top-down control in food webs with alternative energy pathways. *Ecol Lett* 15(9):935–946.
4. Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. *J Anim Ecol* 78(4):699–714.
5. Boyce DG, Frank KT, Worm B, Leggett WC (2015) Spatial patterns and predictors of trophic control in marine ecosystems. *Ecol Lett* 18(10):1001–1011.
6. Frank KT, Petrie B, Shackell NL (2007) The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol Evol* 22(5):236–242.
7. Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84:162–173.
8. Litzow MA, Ciannelli L (2007) Oscillating trophic control induces community re-organization in a marine ecosystem. *Ecol Lett* 10(12):1124–1134.
9. O'Connor MI, Piehler MF, Leech DM, Anton A, Bruno JF (2009) Warming and resource availability shift food web structure and metabolism. *PLoS Biol* 7(8):e1000178.
10. Shurin JB, Clasen JL, Greig HS, Kratina P, Thompson PL (2012) Warming shifts top-down and bottom-up control of pond food web structure and function. *Philos Trans R Soc Lond B Biol Sci* 367(1605):3008–3017.
11. Beaugrand G, Luczak C, Edwards M (2009) Rapid biogeographical plankton shifts in the North Atlantic Ocean. *Glob Change Biol* 15:1790–1803.
12. Kirby RR, Beaugrand G (2009) Trophic amplification of climate warming. *Proc Biol Sci* 276(1676):4095–4103.
13. Olsen EM, et al. (2011) Spawning stock and recruitment in North Sea cod shaped by food and climate. *Proc Biol Sci* 278(1705):504–510.
14. Fauchald P, Skov H, Skern-Mauritzen M, Johns D, Tveraa T (2011) Wasp-waist interactions in the North Sea ecosystem. *PLoS One* 6(7):e22729.
15. Mackinson S, Deas B, Beveridge D, Casey J (2009) Mixed-fishery or Ecosystem conundrum? Multi-species considerations inform thinking on long-term management of North Sea demersal stocks. *Can J Fish Aquat Sci* 66:1107–1129.
16. Engelhard GH, et al. (2014) Forage fish, their fisheries, and their predators: who drives whom? *ICES J Mar Sci* 71:90–104.
17. Anderson HB, Evans PGH, Potts JM, Harris MP, Wanless S (2014) The diet of Common Guillemot *Uria aalge* chicks provides evidence of changing prey communities in the North Sea. *Ibis* 156:23–34.
18. Llope M, et al. (2011) Overfishing of top predators eroded the resilience of the Black Sea system regardless of the climate and anthropogenic conditions. *Glob Change Biol* 17:1251–1265.
19. Blenckner T, et al. (2015) Climate and fishing steer ecosystem regeneration to uncertain economic futures. *Proc Biol Sci* 282(1803):20142809.
20. Reid PC, Edwards M, Hunt HG, Warner AJ (1998) Phytoplankton change in the North Atlantic. *Nature* 391:546.
21. Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430(7002):881–884.

22. Beaugrand G (2004) The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Prog Oceanogr* 60:245–262.
23. Huse G, Salthaug A, Skogen MD (2008) Indications of a negative impact of herring on recruitment of Norway pout. *ICES J Mar Sci* 65:906–911.
24. Karaseva EM, Patokina FA, Kalinina NA (2013) Fish eggs and larvae in the diet of herring *Clupea harengus membras* Linnaeus, 1758 and the sprat *Sprattus sprattus balticus* (Schneider, 1904) (Clupeidae) in the Southeastern Baltic Sea. *Russ J Mar Biol* 39:350–356.
25. Casini M, Cardinale M, Arrhenius F (2004) Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern Baltic Sea. *ICES J Mar Sci* 61:1267–1277.
26. Engelhard GH, et al. (2008) Fishing mortality versus natural predation on diurnally migrating sandeels *Ammodytes marinus*. *Mar Ecol Prog Ser* 369:213–227.
27. Bromley PJ, Watson T, Hislop JRG (1997) Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea. *ICES J Mar Sci* 54:846–853.
28. Jørgensen C, Ernande B, Fiksen Ø, Dieckmann U (2006) The logic of skipped spawning in fish. *Can J Fish Aquat Sci* 63:200–211.
29. Pikitch EK, et al. (2014) The global contribution of forage fish to marine fisheries and ecosystems. *Fish Fish* 15:43–64.
30. Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. *Fish Oceanogr* 12:270–283.
31. Beaugrand G, Edwards M, Brander K, Luczak C, Ibanez F (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecol Lett* 11(11):1157–1168.
32. Cury P, et al. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES J Mar Sci* 57:603–618.
33. Plagányi ÉE, et al. (2014) Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish Fish* 15:1–22.
34. Castruccio S, et al. (2014) Statistical emulation of climate model projections based on precomputed GCM runs. *J Clim* 27:1829–1844.
35. Edwards M, Beaugrand G, Reid PC, Rowden AA, Jones MB (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar Ecol Prog Ser* 239:1–10.
36. Batten SD, et al. (2003) CPR sampling: The technical background, materials, and methods, consistency and comparability. *Prog Oceanogr* 58:193–215.
37. Hastie TJ, Tibshirani RJ (1990) *Generalized Additive Models* (Chapman and Hall, New York), p 352.
38. Ciannelli L, Chan KS, Bailey KM, Stenseth NC (2004) Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology* 85:3418–3427.
39. R Development Core Team (2007) *R: Foundation for Statistical Computing* (R Development Core Team, Vienna).
40. Wood SN (2000) Modelling and smoothing parameter estimation with multiple Quadratic Penalties. *J R Stat Soc B* 62:413–428.
41. Wood SN (2006) *Generalized Additive Models: An Introduction with R* (Chapman & Hall CRC, New York), p 410.

ENVIRONMENTAL SCIENCES

Interaction between top-down and bottom-up control in marine food webs - Supplementary information

Christopher Philip Lynam, Marcos Llope, Pierre Helaouët, Christian Möllmann, Georgia Bayliss-Brown, Nils Chr. Stenseth

The SI is structured in four parts.

Part I contains additional methods and discussion on the study.

Part II contains the supporting charts for the simulation results to distinguish fishing and climate effects on the system.

> Figure S1a – Individual models partial plots (9 models).
> Figure S1b – Individual models partial plots (6 models).
> Figure S2 – Taylor diagram summarising the goodness of fit.
> Figure S3 – Time-series used to drive simulations and test for model sensitivity.
> Figure S4 – Climate scenarios with no change in observed fishing effects: i.e. contrasting the warm climate and new planktonic regime with simulations for the same period whereby the temperature had not risen.
> Figure S5 – Climate scenarios with zero fishing from 1985: The scenarios here are the same as in Figure S4. However, by removing the modelled effect of fishing from the simulations we explore the greatest possible response to the climatic stimulated planktonic regime shift.

Part III collates diagnostic plots for each modelled component.

> Table S1 – Final individual models for each ecosystem component and summary statistics.
> Table S2 – tGAM/GAM selection.
>
> Figure S6 – Predictions from the individual models (observations and climate covariates).
> Figure S7 – Individual models residuals plots
> Figure S8 – tGAMs (diatoms and small copepods).

Part IV is a simple list of colonies used to inform the seabird breeding success index.

Part I - supplementary data, methods, results and discussion

Data

Climate. For sea surface temperature (SST) we used annual temperature anomalies relative to the 1961-2005 climatology from the Hadley Centre SST dataset (UK Met Office) averaged over the North Sea (HadSST2, www.metoffice.gov.uk/hadobs/hadsst2). To characterise the low-frequency phase of variability in the temperature signal we used the Atlantic Multi-decadal Oscillation (AMO). The AMO index was used due to the fact that it has been linked to multi-decadal changes in plankton abundance and fish biomass in the North Sea (42, 43). AMO data can be found at www.esrl.noaa.gov/psd/data/timeseries/AMO/. Time series are shown in Fig. S3.

Plankton. Plankton have been collected by the Continuous Plankton Recorder (CPR) survey in the North Sea on a routine monthly basis since 1946. The CPR is a high-speed plankton sampler that is towed, at a constant depth of approximately 6.5m, behind merchant ships voluntarily (44). The methods of CPR sampling and analysis have remained consistent throughout the time series (36). Three phytoplankton groups were determined: greenness, a proxy for chlorophyll concentration (36), diatom abundance and dinoflagellate abundance. Three zooplankton groups were chosen to represent both the resident assemblage and those that regularly invade (11): small copepod species that reside in the North Sea (*Temora*, *Acartia*, *Paracalanus*, *Pseudocalanus*); southern warm-water indicator species (*Calanus helgolandicus*); and, northern cold-water indicator species (*Calanus finmarchicus*). Mean monthly abundances were calculated, for all six functional groups, following the standard procedures outlined in Batten *et al.* (36). Annual values were then taken as the average over all months (*sensu* Colebrook (45)) and since standard CPR samples are assumed to filter a volume of 3 m^3 of seawater the final annual abundances are given as values per 3 m^3. Time series shown in Fig. S3.

Fish. The North Sea fish community was represented by eight commercially important species: herring (*Clupea harengus*), sprat (*Sprattus sprattus*), Norway pout (*Trisopterus esmarkii*), sandeel (*Ammodytes marinus*), cod (*Gadus morhua*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*), for which multi-decadal time-series data on spawning stock biomass and fishing mortality (instantaneous fishing mortality rates, *F*) were available (ICES stock assessment, (46)). Sandeel and whiting data were obtained from the output of a Stochastic Multi-Species (SMS) model (47) stock assessments since sandeel stock assessments are now made for sub-stocks of the North Sea separately and current whiting stock assessment data begin at 1990. The fish community includes planktivorous forage fish that can be either considered generally pelagic (herring,

2

sprat) or pelagic/demersal (sandeel and Norway pout) in addition to demersal piscivores (cod, haddock, whiting and saithe). Time series shown in Fig. S3.

Seabirds. For the seabird breeding success index, data were available from 1986-2011, but only data from 1989 were used due to limited number of records prior to this. For example, there were no data for Common gull (*Larus canus*) in the period 1986-1988. See Part IV for a list of colonies used to inform the index.

Methods

Model selection for both GAMs and tGAMs (Table S1), was based on a combined forward and backward step-wise approach, removing covariates with a P-value ≥ 0.05 and attempting to minimize the generalized cross validation (GCV) criterion i.e. avoid over-fitting the data (40). The pure step-wise approach was tempered by expert knowledge taking into account the origin of the data and the expected relationships between components. The residuals of the models were checked in order to verify that they were not correlated over time and followed a normal and homoscedastic distribution in all cases as required for regression modelling (Fig. S7).

If no simple GAM was found to be sufficient to model a particular component, GAMs with thresholds (tGAMs) were then considered. The inclusion of a threshold variable dramatically increases the set of potential models available so, given the general agreement in the literature of the fundamental role played by the AMO in guiding marine ecosystems of the North Atlantic (e.g. 42), we attempted to use the AMO as the threshold variable in the first instance in each case. The threshold level of the covariate is chosen by minimizing the GCV score over the range of the covariate (see 38). To statistically compare threshold models (tGAMs) with fully additive models (GAMs) it is necessary to account for the additional parameter used for the threshold search. Following Ciannelli et al (38), we used genuine CV to compare between tGAM and GAM models i.e. average squared leave-one-out prediction errors (Table S2). Once models were fitted for each group, the deviance explained by each regression was investigated as a simple measure of the quality of the fit. The deviance was partitioned across the explanatory variables in order to explore whether internal population processes or trophic interactions were more important to each group (Fig. S1).

The empirically-based model of a complex web of interactions includes expert judgement where appropriate. For example, the biomass data for the fish groups came from age-structured stock assessment models. Therefore, both the time-lagged species biomass and the fishing mortality term were included in the GAMs, before we attempted to include plankton, climate or other fish biomass data in the set of predictors. Since spawning stock biomass values are considered to represent the value at the start of the year, the response to fishing mortality was generally lagged by 1 year. Relationships between groups were only retained if significant, but, regardless of significance, relationships were rejected if they were considered unrealistic. For example, an inverse relationship between a zooplankton group and a planktivorous fish would not be included in the fish model, since one would expect the fish to increase as the prey increase, rather the relationship would be included in the zooplankton group model and considered a predation effect by the fish. In this way, we construct a model built on significant and sensible relationships. Data on the North Atlantic Oscillation, modelled inflow and salinity were considered but rejected in an attempt to create a simple model focussed on key pathways alone.

Since descriptive relationships may not be the most suitable for predictions, relationships were considered robust only if the final simulations of all variables from their initial conditions managed to recreate the time-series closely. The quality of the simulations for each modelled component was assessed through Taylor diagrams (48), which summarise the goodness of fit (correlation and standard deviation relative to the data, Fig. S1). All models have Gaussian errors, the deviance explained is equal to the variance explained (unadjusted).

This model then allows simulation of the interplay between bottom-up and top-down effects arising from temperature change and fishing impacts and modified by the interactions between species (including predator-prey interactions, competition and relationships that emerge as proxies for other effects).

Simulations from the interaction web
A key feature of this modelling framework is that groups are linked across trophic levels where possible to allow for subsequent model simulations of the interaction web (18, 19). The interaction web is compartmentalised into 15 components across four trophic levels: primary producers (three phytoplankton groups), primary consumers (three zooplankton groups), secondary consumers (four species of planktivorous fish), and top predators (four species of largely piscivorous fish and one seabird group). The fitted models (Table S1, Fig. S1) were used to simulate from the initial conditions once the various sub-models for each functional group were selected. Climate forcing (i.e. SST averaged over the North Sea and AMO) and time-series of fishing mortality by species were used as the drivers for the model. In this way, predictions for components were used in a linked manner to predict other

components such that the entire system is forecast according to the interactions emerging from the individual models. Uncertainty was added to the model-states by sampling, with replacement, an entire vector of errors (from a randomly sampled year) from the model residuals in order to preserve the contemporaneous correlation of errors. 999 Monte Carlo simulations were run from which the median and the 95% prediction bands were calculated (Fig. 2).

Alternative climate and fishing scenarios were explored to investigate model sensitivity (Figs. S4-5). To evaluate the response of the interaction web to stress from temperature change and fishing pressure, a range of simulations were carried out: fishing mortality was decreased by 10%, 50% and 80% of observed values; simultaneously temperature was either unchanged, altered by +/-10%, or maintained throughout the time-series in the cool range experienced during the period 1964-1984 (before the observed global increases in temperature). For the latter simulations, the annual temperatures post 1984 were replaced by values drawn at random from 1964-1984 temperature observations.

Supplementary results and discussion
Evidence for bottom-up and top-down processes structuring the system
Bottom-up: Climate forcing showed strong direct relationships with the lower trophic levels of the interaction web: all phytoplankton groups and the two *Calanus* species were linked directly to SST. The remaining zooplankton group, small copepods, do show a response to climate but it is driven by change in the phytoplankton community as signalled by change in the dinoflagellate component (Table S1, Fig. S1a). Two fish species (sandeel and cod) also respond directly to sea surface temperature (Fig. S1b) and since all other fish species can be linked by trophic interactions to the plankton and thus climate (Fig. 1) there is considerable evidence for bottom-up control from the interaction web alone. The demersal piscivore, whiting is shown to be statistically dependent on the zooplankton-linked species, sprat and sandeels. Similarly, the breeding success of seabirds foraging in the North Sea was related to the biomass of sprat and sandeel, and also directly related to the abundance of zooplankton, with a two-year lag: notably this latter relationship formed a greater proportion of the deviance explained in breeding success than the fish groups together (Fig. 1, Fig. S1b). Seabird breeding success would appear to respond to bottom-up forcing but given the interactions between bird prey (sandeel, sprat) and both whiting and herring, there is potential for top-down effects to indirectly impact of seabirds. The top predators saithe and cod were relatively remote from the lower trophic levels. For saithe, predation on Norway pout and potentially haddock appears particularly important, while for cod direct climate impacts were strong. In fact, a peculiarity of the cod sub-model was that SST and fishing mortality explained so much of the deviance in the cod data that no links to other groups were possible.

5

Top-down: Fishing mortality impacted directly on seven of the eight fish stocks. Whiting (Fig. S1b) were the exception to this result but, since this species responds exclusively to the biomass of commercially fished sandeel and sprat, anthropogenic impacts on whiting are also strong. In general, the impacts of fishing and interactions between fish in the model emerge as stronger direct influences on fish biomass than zooplankton abundance, as is clearly the case for demersal piscivores (Table S1), suggesting top-down control is stronger than bottom-up effects. Plankton and fish were coupled in the model but not strongly. Haddock and three species of planktivorous fish (sandeel, sprat and herring, but not Norway pout) were linked statistically and directly to zooplankton (as illustrated in Fig. 1). However, in each of these species, the total deviance explained by fishing mortality was greater. In the case of two of the species (sprat and haddock), the deviance explained by fish interactions was even greater than the proportion explained by fishing mortality, emphasising the importance of herring and sandeels in the system (Table S1, Fig. S1b).

Bottom-up top-down integration: While evidence supporting bottom-up and top-down effects can be drawn from the interaction web (above), the relative importance of each can not be identified clearly from an examination of the fit of the models alone due to the cascading effect of indirect effects. A greater understanding of such interactions based on these models can be drawn through simulations.

For example, a doubling of sprat biomass during the period 2000-2005, assuming an 80% decrease in fishing mortality but no change in temperature, led to a small (10%) decrease in *C. helgolandicus* abundance. Greater increases of 3 to 5 times the herring biomass, in the period 2000-2005 assuming a similar reduction (80%) in fishing mortality, resulted in a larger percentage decrease (30%) in *C. finmarchicus* abundance, but this effect was partially negated if fishing mortality on sandeel was reduced in addition (overall decrease of 20%, Fig. S4). The small copepods group was no more sensitive to predation pressure by sandeel: a 16% decrease in small copepods was modelled as a result of an 80% increase in sandeel biomass following an 80% reduction in fishing mortality. This minor impact of sandeels on small copepods ultimately has a slight negative effect on herring biomass, but the herring stock is more sensitive to changes in fishing mortality upon it than change in its zooplankton prey.

This study shows that it is possible to simulate the dynamics of eight stocks without specifying stock-recruit relationships. Forecasts from such a model will become less reliable if recruitment processes become more important in the system as may be expected once the full effect of management measures (including the discard ban) toward maximum sustainable yield are realised in the system. Fauchald (49) suggests that in addition to temperature, the abundance of *C. finmarchicus* prey and

6

predation on cod larvae by herring are all important factors influencing cod recruitment. We find that the biomass trajectory of cod period could be almost fully explained by temperature and fishing mortality alone, which suggests that variability due to fluctuations in recruitment of cod during the model period were either small or limited due to issues such as the discarding problem of undersized fish.

Although many of the linkages identified here, such as the negative effects of fishing or the predation by whiting on sandeels, can be interpreted as representing underlying causal mechanisms, this is not the case universally. For example, there is a negative relationship between the abundance of *Calanus helgolandicus* and dinoflagellates: both groups also respond to temperature effects directly and their separate trends mirror each other such that it is conceivable that the zooplankton species can be an indicator of structural change within the phytoplankton community as a result of temperature change. Regardless on the interpretation, the study does not and cannot prove causation and the web shown in Fig. 1 must be considered as a summary of key statistical interactions and not a food web.

Supporting References

42. Edwards M, Beaugrand G, Helaouët P, Alheit J, Coombs S (2013) Marine Ecosystem Response to the Atlantic Multidecadal Oscillation. *PLoS ONE* 8(2): e57212
43. Harris V, Edwards M, Olhede SC (2014) Multidecadal Atlantic climate variability and its impact on marine pelagic communities. *J Marine Syst* 133:55-69
44. Hays GC (1994) Mesh selection and filtration efficiency of the Continuous Plankton Recorder. *J Plankton Res* 16:403-412
45. Colebrook JM (1975) The Continuous Plankton Recorder survey: automatic data processing methods. *B Mar Ecol* 8:123-142
46. ICES (2012) *Report of the ICES Advisory Committee 2012*. ICES Advice, 2012
47. ICES (2011) *Report of the Working Group on Multispecies Assessment Methods (WGSAM)*, Woods Hole, USA. ICES CM 2011/SSGSUE:10
48. Taylor KE (2001) Summarizing multiple aspects of model performance in a single diagram. *J Geophys Res* 106: 7183-7192
49. Fauchald P (2010) Predator-prey reversal: A possible mechanism for ecosystem hysteresis in the North Sea? *Ecology* 91:2191-2197

Part II - supporting charts and simulation results

Supporting Figure legends

Fig. S1a and S1b. Partial plots. Fitted splines, showing the partial effect of each predictor (x-axis) on the response variable.

Fig. S2. Taylor diagram. Goodness of fit (correlation as shown by the arc, standard deviation of the fit normalized relative to the data and root mean square) for the median of the set of simulations (black lines in Fig. 2) for each ecosystem component (48).

Fig. S3. Time-series used to drive simulations and test for model sensitivity. Climate scenarios: left, where black lines show observed AMO (top) and SST (bottom) anomalies, red lines indicate and 10% increase in each, blue lines a 10% decrease and grey lines show a 'preshift' scenario with SST 1985-2010 replicating observed variability about the mean in the period 1964-1984. Fishing mortalities (F): middle and right, where black lines are estimates of F from ICES assessments, red and green lines indicate F time series with a 10% and 25% decrease respectively.

Fig. S4. Climate scenarios with observed fishing effects. Median of 999 simulations showing change in zooplankton abundance, fish biomass and seabird breeding success with observed fishing mortality implemented for differing SST scenarios: the black lines are based on observed SST; red lines are based on observed SST for 1964-1984 while for the period 1985 onward SST values are taken from a scenario drawn from the temperature range during 1964-1984 (see Fig. S3).

Fig. S5. Climate scenarios with zero fishing from 1985. Median of 999 simulations showing change in zooplankton abundance, fish biomass and seabird breeding success with zero fishing mortality imposed post 1984 for differing SST scenarios: the black lines are based on observed SST; red lines are based on observed SST for 1964-1984 while for the period 1985 onward SST values are taken from a scenario drawn from the temperature range during 1964-1984 (see Fig. S3).
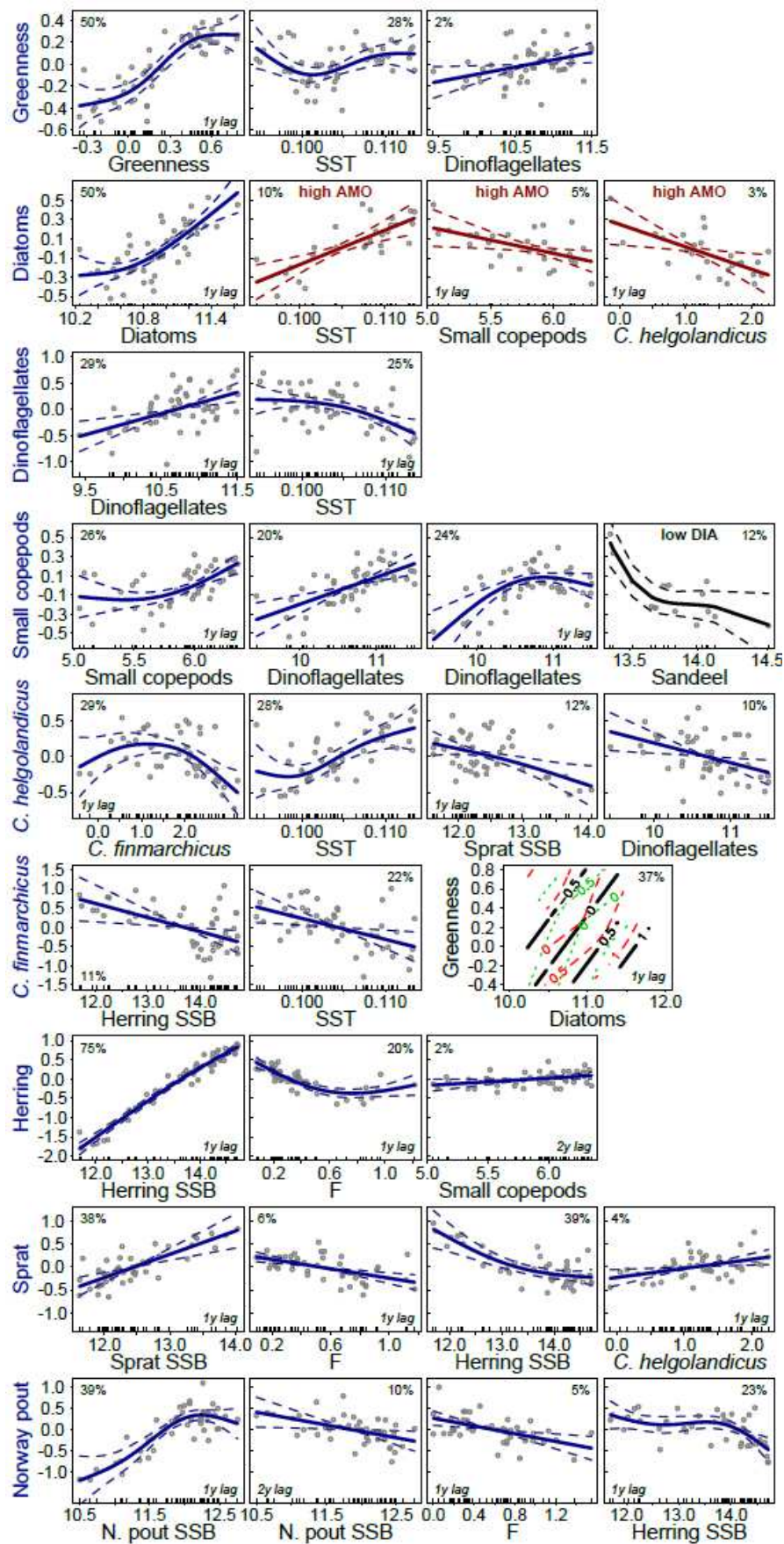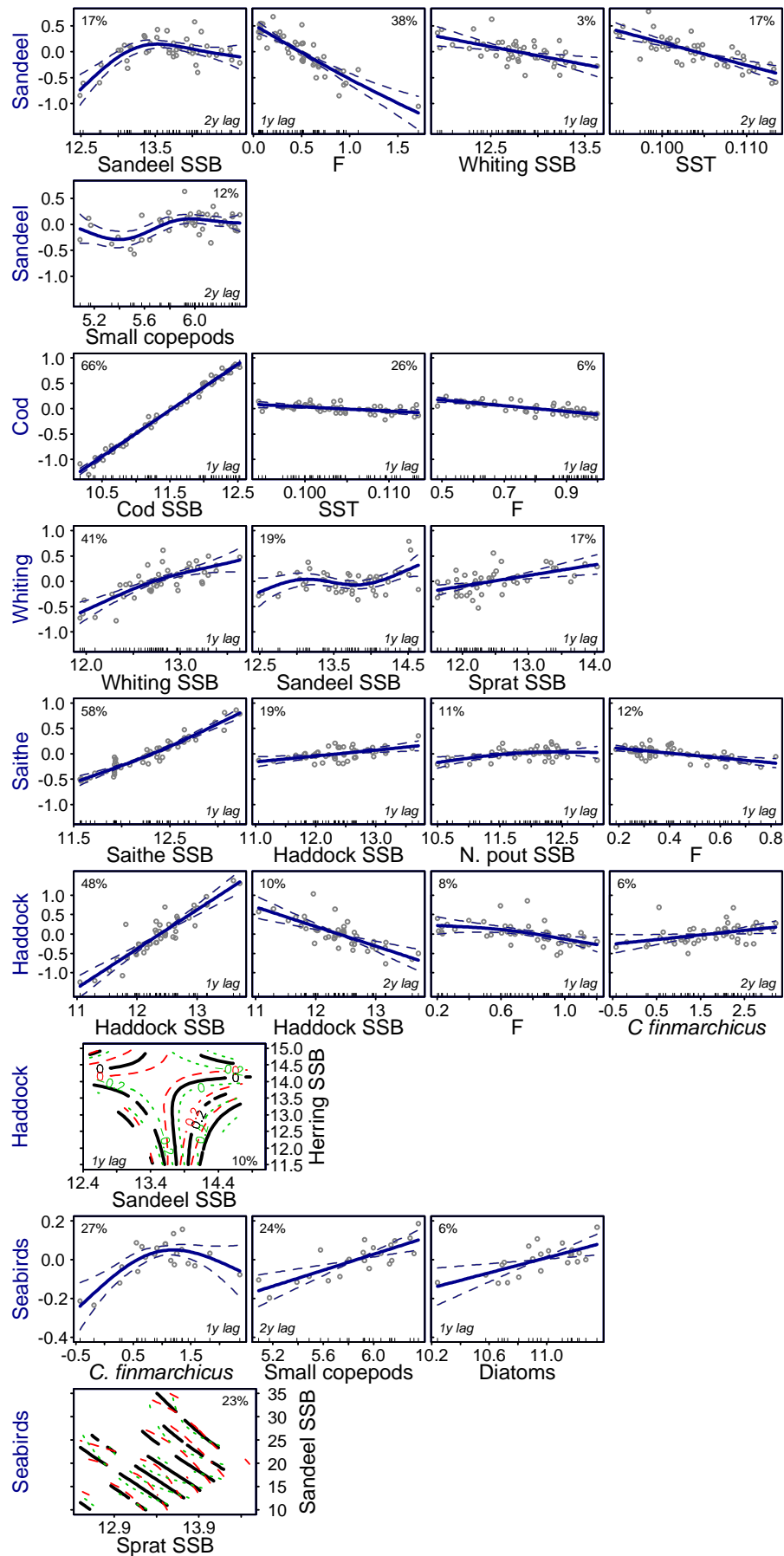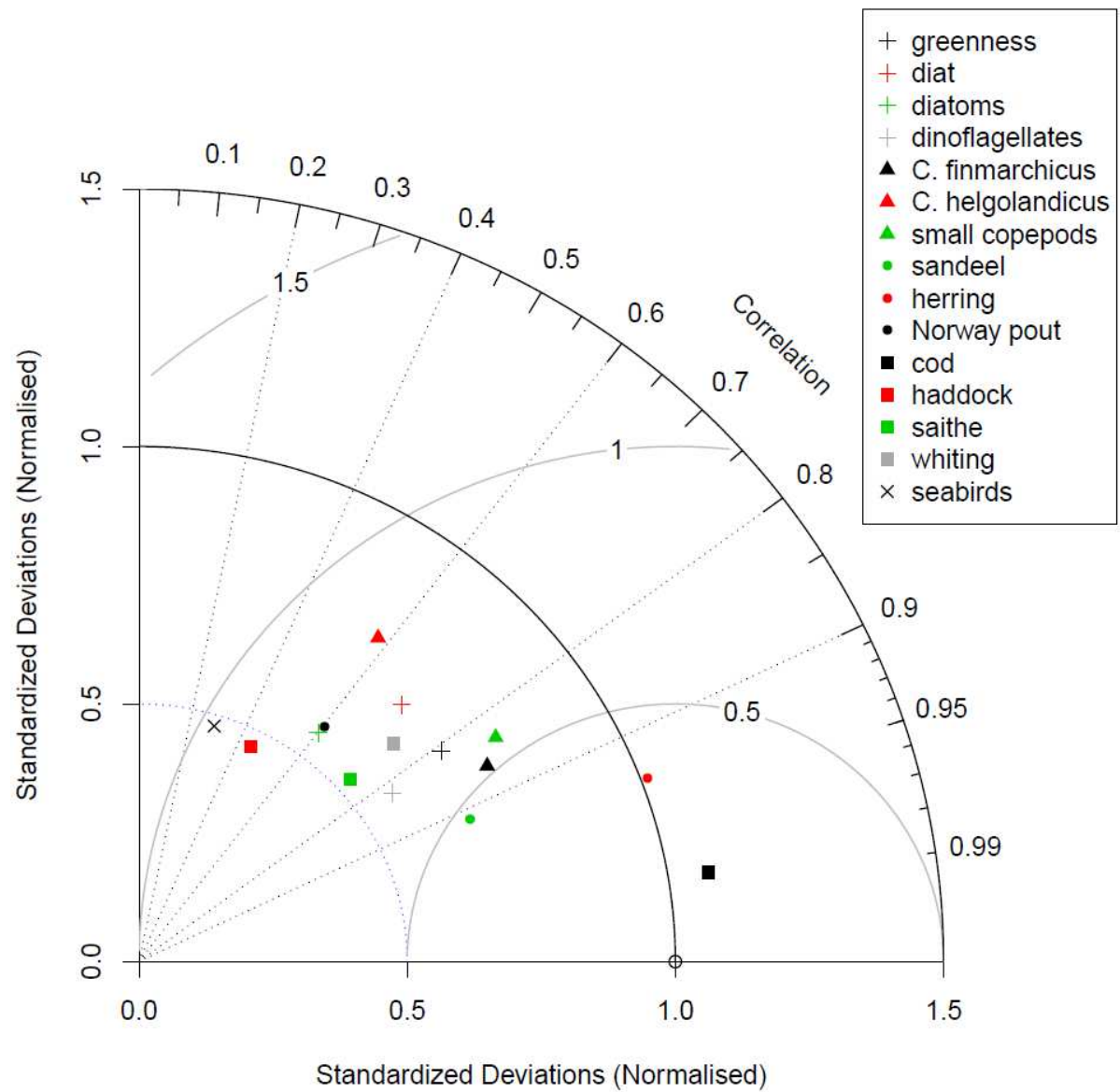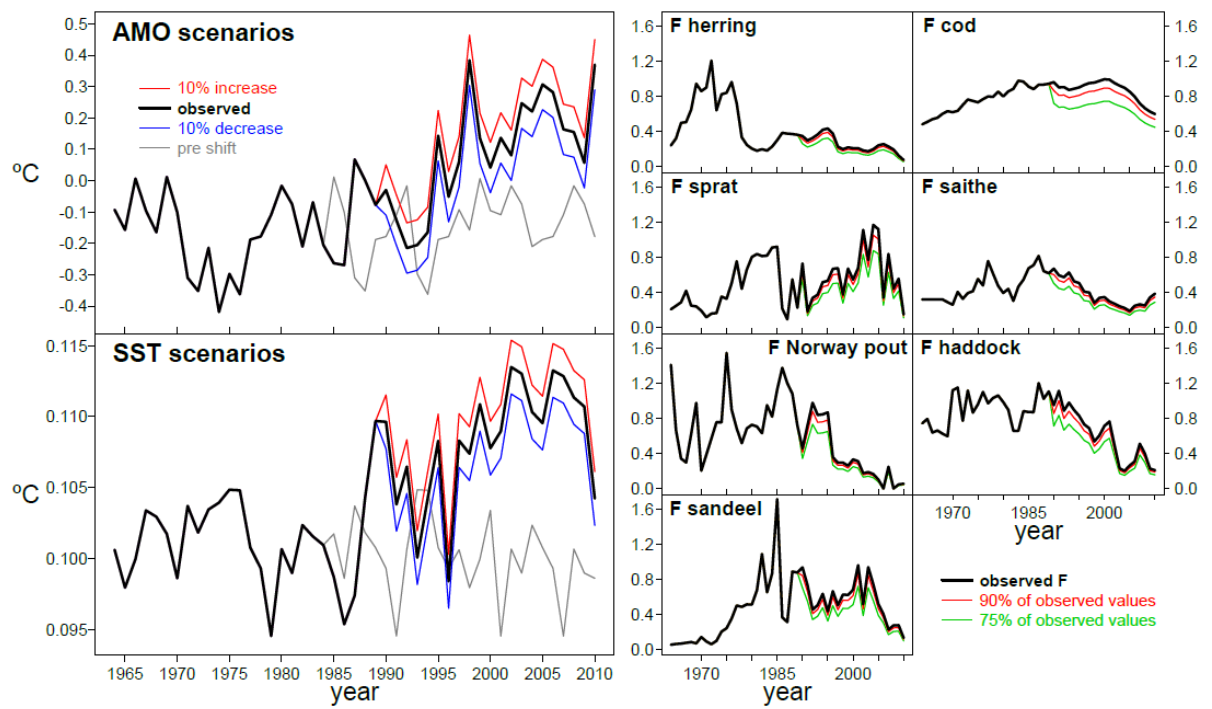
Figure S1a

9

Figure S1b

Figure S2

Figure S3

Figure S4

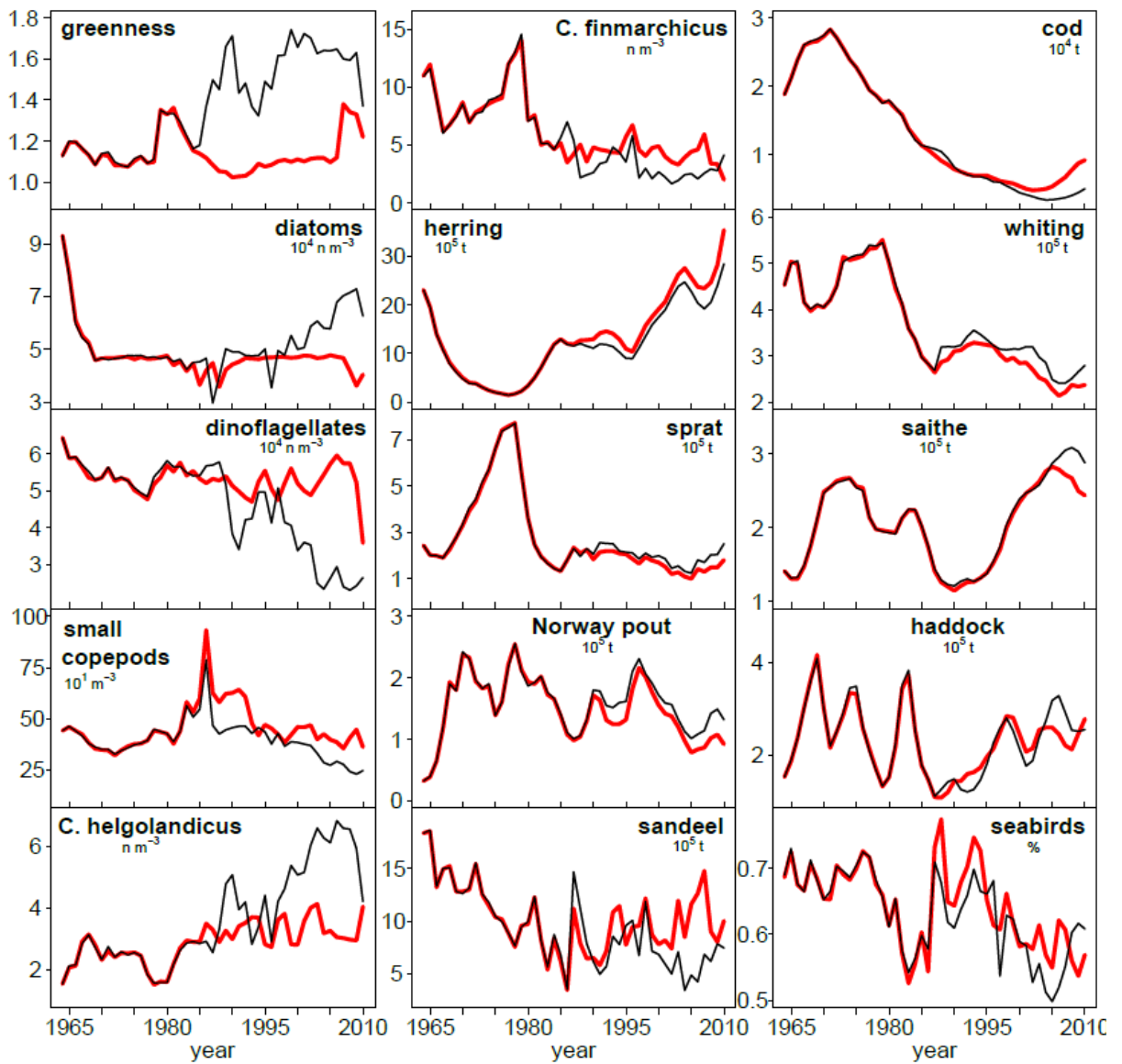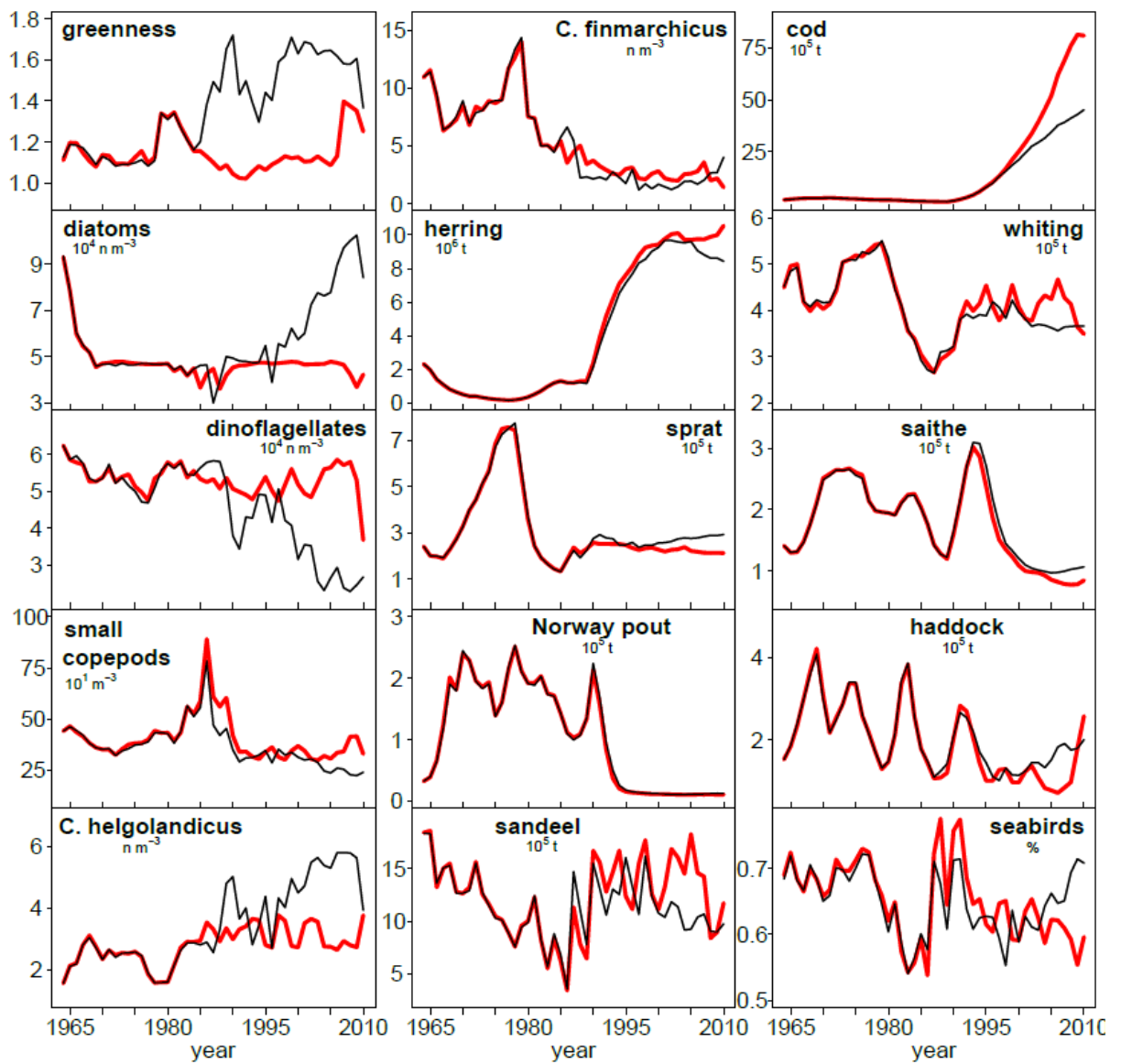Figure S5

Part III - diagnostic tables and plots

Supporting Tables

Table S1. Final models (GAM or tGAM) for each ecosystem component and summary statistics: proportion of deviance explained by the model and GCV. Of 15 models, 13 are simple GAMs while 2 include thresholds (tGAMS): those for diatoms and small copepods, and 3 included interactions: those for *Calanus finmarchicus*, haddock and seabirds. All terms are significant (P <0.05) and the estimated degrees of freedom (edf) for each smooth term is shown which represents the complexity of the smoother. Where no edf is given the value is 1 i.e. a linear term. When (1-year or 2-year) lags were included these are indicated by '_1' or '_2' (respectively) after the covariate's name. Acronyms are used as follows: Greenness (GRE), diatoms (DIA), dinoflagellates (DIN), *Calanus helgolandicus* (HEL), *Calanus finmarchicus* (FIN), small copepods (COP), sandeel (SAN), herring (HER), sprat (SPR), Norway pout (NPO), haddock (HAD), saithe (SAI), whiting (WHI), cod (COD), seabirds (BIR), fishing mortality (F), sea surface temperature (SST) and Atlantic Multi-decadal Oscillation (AMO). See also Fig. S1a, S1b for partial plots and deviance partitioned among predictors (which is shown inside the corresponding partial plots panels), Fig. S6 for residuals, Fig S7 for predictions, as well as Fig. 1 in main text.

Response variable	**Formula**, where smooth terms (GAM) are represented by s and shown in curly brackets if the term only applies above/below a threshold value for a specific variable (r)	**GCV**	**% deviance** All terms
GRE	s(GRE_1, edf=3.21) +s(SST, edf=2.70) + DIN	0.0284	80
DIA	s(DIA_1, 2.18) + *If* (AMO >= r) { s(SST, 1.33) +s(COP_1, 1.33) +s(HEL_1, 1.33) }	0.0402	68
DIN	DIN_1 +s(SST_1, 1.91)	0.1175	54
COP	DIN +s(DIN_1, 1.94) +s(COP_1, 1.86) +*If* (DIA <= r){ s(SAN, 3.80) }	0.0346	83
HEL	s(SST, 2.72) + s(FIN_1, 2.47) +DIN +s(SPR_1, 1.31)	0.0997	79
FIN	SST +HER + s(DIA_1, GRE_1, 2)	0.3069	70
HER	s(*F*_1, 1.96) +s(HER_1, 1.87) +COP_2	0.0328	97
SPR	*F*_1 +SPR_1 +HEL_1 +s(HER, 2.07)	0.0611	87
NPO	*F*_1 +s(HER_1, 2.76) +s(NOP_1, 2.81) +NOP_2	0.0992	76
SAN	s(F_1, 1.41) + s(SAN_2, 2.78) +SST_2 +s(COP_2, 3.58) +WHI_1	0.0549	87
HAD	s(*F*_1, 1.63) +HAD_1 +HAD_2 +FIN_2 +s(SAN_1,HER_1, 3.52)	0.0757	83
SAI	*F*_1 +s(SAI_1, 1.91) +s(NOP_1, 1.89) +HAD_1	0.0129	95
WHI	s(WHI_1, 1.90) +SPR_1 +s(SAN_1, 3.28)	0.0490	77
COD	*F*_1 + COD_1 + SST_1	0.0063	99
BIR	DIA_1 +COP_2 +s(FIN_1, edf=2.31) +s(SAN,SPR, 2.17)	0.0066	79

Table S2. tGAM-GAM comparison through genuine cross validation (gCV) following Ciannelli *et al.* (38). For small copepods the tGAM performed better than its fully additive equivalent. For diatoms the two scores are near equal but do favour the simple model. However, since the various explanatory variables in the simple model other than the population dependence term are not significant the simple model was rejected. With the modelling framework adopted here, simulations require adjacent trophic levels to be linked.

	gCV	
model	GAM	tGAM
Diatoms	0.2344	0.2367
Small copepods	0.2525	0.2214

Part II – Figure legends

Fig. S6. Residuals. Rows correspond to each of the individual GAM/tGAM models. First column shows the autocorrelation within the residuals to look for significant correlation over year (correlations are not significant if they lie within the dashed blue lines). Second column assess the homocedasticity. Third and fourth columns assess the normality.

Fig. S7. Predictions, predictors and observations. Predictions from the various models, climate variables (SST, AMO) and fishing mortality (F). Plots of fitted values (red) against observed abundances of plankton (counts per volume), biomass of fish (10^4 or 10^5 tonnes) and breeding success of seabirds (percentage).

Fig. S8. tGAMs. Left column: Time series showing those points where the associated AMO (diatoms model) or diatoms (small copepods model) for that year is above (red) or below (black) the corresponding threshold values. A comparable number of red and black points with a good spread over the time series is desired. Right column: GCV score for a range of r values to include in the non-additive relationships: a low GCV score with a v-shaped valley is desired. The threshold value (θ and blue lines) defining the high (red) and low (black) regimes is indicated.
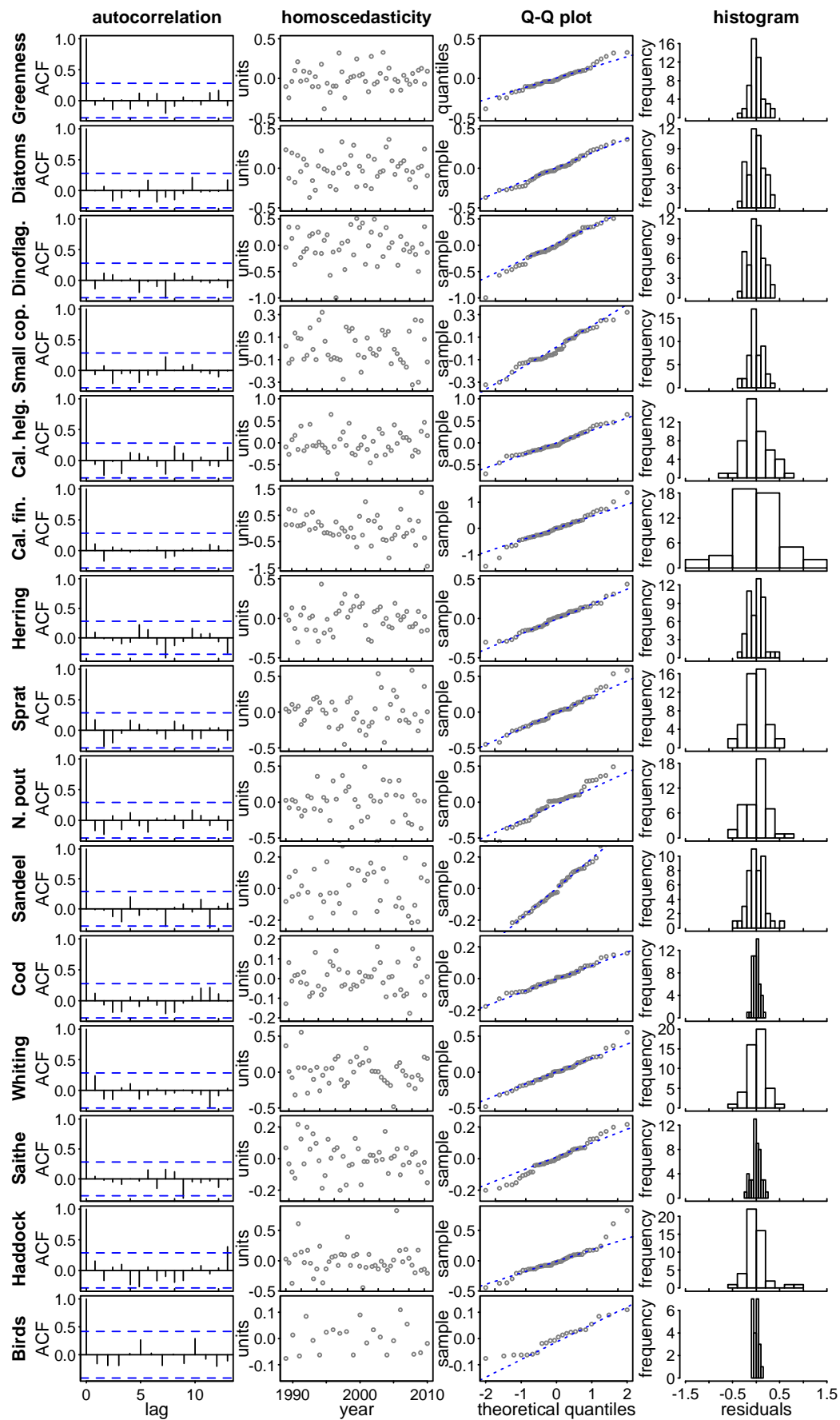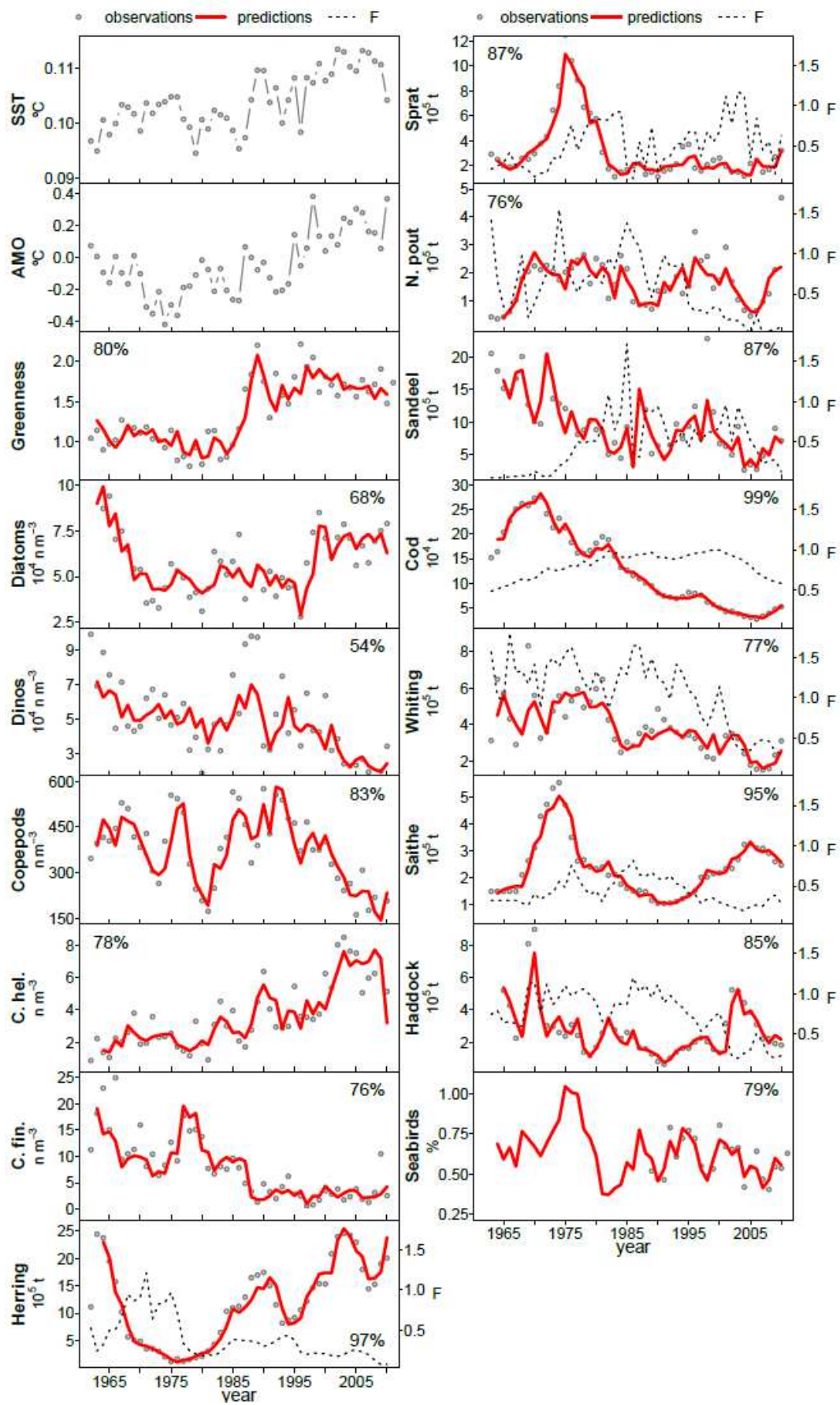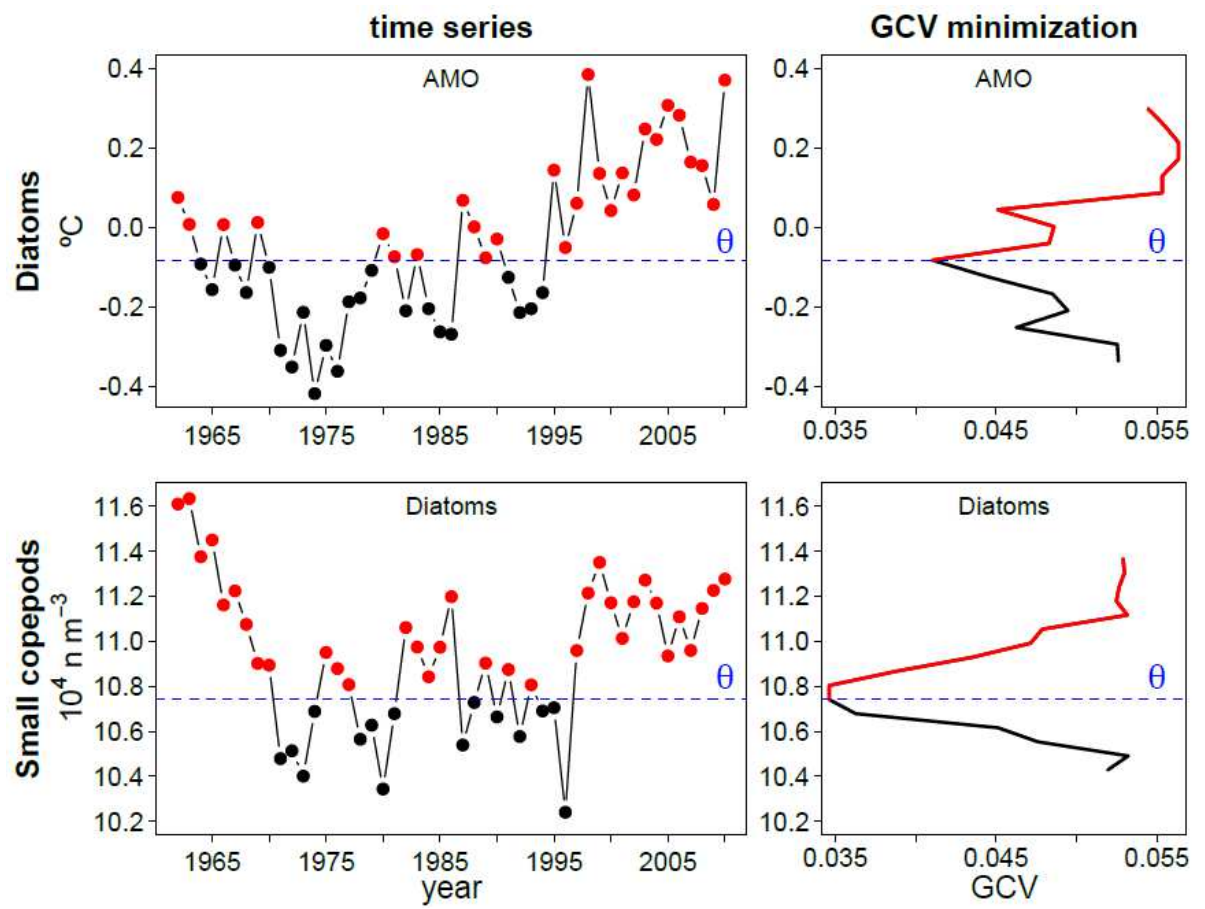
Figure S6

Figure S7

18

Figure S8

Part IV – marine bird data

The following species were included in the seabird breeding success index:

Arctic skua, Arctic tern, Atlantic puffin, Black guillemot, Black-headed gull, Common guillemot, Common gull, Common tern, fulmar, Great skua, Herring gull, kittiwake, lesser black-backed gull, Little tern, Northern gannet, razorbill, Roseate tern, Sandwich tern shag. Four species were excluded due to limited records: Comic tern, Great black-backed gull, Great cormorant and Mediterranean gull. Of the 19 species selected, 16 were recorded every year from 1989, while the remaining species (Black guillemot, Black-headed gull, and Roseate tern) were retained since they were each recorded in all but one year and had records before that missing year. The combined index is, therefore, coarse and weighted towards the more abundant species in the colonies observed, but it serves as a useful and simple indicator of the general productivity of seabirds that forage, at least partly, in the North Sea. This component of the community shall be investigated further in future studies.

Colonies selected (300 from 751) as representative of 'North Sea' seabirds:

Abberton Reservoir
Aberlady
Ackergillshore
Aikerness
Alton Water
Auskerry
Backaskaill
Barry Buddon
Barry Burn
Bay of Creekland
Bempton Cliffs RSPB
Benacre
Berney Marshes
Big Waters
Billingham Pond
Binga Fea
Birsay Moors RSPB
Black Park RSPB
Blacktoft Sands RSPB
Blakeney Point
Boar's Head Rock
Boddam to Collieston
Boultham Mere
Boyton Marsh
Brading Marshes
Bradwell Cockle Spit
Brancaster
Breck of Linkquoy
Breil Newk
Breydon Water
Brindister Loch
Brinefields 5
Brings
Bure Marshes
Burntwick
Burray Haas
Caister
Cantick Head
Cara
Castle Coote
Cata Sand West
Ceann Leathad nam Bo
Chelmer Pitts
Clett Head
Cliffe Pits
Cloddach Quarry
Coatham
Cobmarsh Island
Colne Point

Compass Head

Copinsay

Copperas Bay

Coquet Island

Costa Head

Covehithe

Covesea

Cowpen Marsh

Craig Loch

Crimdon Dene

Culbin Bar (East) & Culbin Coast

Deadmans Island

Dingle / Corporation Marshes

Donna Nook

Dunbar Coast and Harbour

Dunnet Beach

Dunnet Head RSPB

Easington Lagoon NR

Easton

Eccles

Eday

Eden Estuary

Elliot Mouth

Eshaness

Eyebroughty

Eynhallow

Fair Isle

Fara

Faray

Farne Islands

Fast Castle Head

Felixstowe Docks

Fetlar

Fetlar RSPB

Fidra

Fishtown of Usan

Fitful Head

Flanders Mare

Flanders Mare Swale Estuary - Elmley RSPB Reserve

Flotta & Calf of Flotta

Fort George

Forth Rail Bridge

Foula

Foulness Point/ Maplin Bank

Fowlsheugh RSPB

Frampton Marsh

Gallo Hill

Garmouth Viaduct

Gibraltar Point NNR

Glimps Holm
Gosworth Park Lake
Granton Harbour
Grass Holm
Greatham Creek Brine Fields
Greatham Creek Brine Fields
Greenabella Marsh
Greenborough
Grutfea
Gultak
Ha Wick
Hamford Water
Hardley Flood
Havergate Island
Haverton Hill Ponds
Hermaness
Hickling Broad
Hildasay
Hobbister RSPB
Holkham NNR
Holm Of Papa Westray
Holm Of Rendall
Holm, Deerness and Tankerness
Holme Dunes NNR
Holy Islands Sands
Horsey SSSI
Housay
Hoxa Head
Hoy RSPB Reserve
Hunda
Hunstanton Cliffs SSSI
Hunstanton Town
ICI Wilton
Inchmickery
Invershore
Ires Geo
Isle of May
Jaywick (Martello)
John Muir Country Park
Kessingland Beach
Kettlaness
Kingsfleet
Kinloss Aerodrome
Kinnaber
Kirkhill Industrial Estate
Lagenhoe Point
Lamb Hoga
Lamb Holm
Landguard

Leith Docks

Lerwick Marina

Littlequoy

Loch of Banks RSPB

Loch of Kinnordy

Loch of Skene

Loch of Strathbeg

Loch Spynie

Lodge Road

Long Craig

Long Nanny

Lossiemouth East Beach

Lower River Spey Islands

Lowestoft

Lowries Water

Lumbister RSPB

Lund

Lushan

Lyness

Lyrawa Bay

Lyrawa Hill

Manse Loch

Marwick Head

McDermott's

Methil Docks

Mill Dam

Minsmere Scrape & Beach

Mio Ness

Montrose Tern Raft

Mor Stein

Mossy Hill

Mousa RSPB

Muckle Skerry

Mull Head - cliff-nesters

Newcastle to Seaton Sluice

Newtonhill - May Craig

Noness

Nor Marsh RSPB

North Denes

North Mainland - Whalwick Taing to Point of Quida Stac

North Ronaldsay Whole Coast

North Warren

Noss Hill, Spiggie

Noss Sound

Noss Whole Island

Old Hall Marshes

Old Man of Hoy to Rora Head

Onziebust RSPB

Ord of Caithness 2

Ore Terminal
Orford Beach
Out Skerries
Packingshed Island
Papa Stour
Papa Westray - North Hill RSPB
Papa Westray
Pewet Island
Point of Buckquoy to Skipi Geo
Port Edgar
Pye's Hall
RAF Leuchars
Ranworth Broad
Read's Island
Reculver Oyster Farm
River Dee
River Swale NNR
Rosyth Dockyard
Rothiesholm Head
Rousay - Faraclett Head
Row Head
Saltburn Cliffs (Huntcliff)
Saltfleet
Saltfleetby - Theddlethorpe Dunes
Saltholme Farm
Saltholme Pool
Saltholme RSPB
Saltness
Sanday
Sands Of Forvie
Sandy Loch
Scalloway Islands
Scolt Head Island NNR
Scroby Sands
SE Yell (inc. Burravoe)
Seaton Snook
Shapinsay
Sheepheight
Shell Ness
Shingle Street
Shotley
Site X
Skipi Geo, Birsay
Skirza Head
Snettisham Wash
South Essex Marshes
South Gare
Southwold Beach
Spurn Head

St Abb's Head NNR
St Cyrus
St Fergus Gas Terminal
St Johns Point
St. Ninian's Isle
Staxigoe
Stiffkey
Stines Moss
Stoke Ooze
Stourdale
Strandburgh Ness
Stronsay
Strumpshaw Fen
Sule Skerry Whole Island
Sullom Voe Terminal
Sumburgh Head
Sunderland Docks
Swona
Tantallon
Tentsmuir
Tern Island
Tetney Marsh
The Brough
The Bu of Burray
The Houb
The Loons RSPB
The Naze
The Ouse
Titchwell
Tollesbury Wick