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

Christopher Philip Lynama, Marcos Llopec, Christian Möllmand, Pierre Helouett, Georgia Anne Bayliss-Brownf, and Nils C. Stensethg,h,1

aCentre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Lowestoft, Suffolk NR33 0HT, United Kingdom; bInstituto Español de Oceanografía, Centro Oceanográfico de Cádiz, E-11006 Cádiz, Andalusia, Spain; cCentre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, NO-0316 Oslo, Norway; dInstitute of Hydrobiology and Fisheries Sciences, University of Hamburg, 22767 Hamburg, Germany; eSir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, United Kingdom; fAquaTT, Dublin 8, Ireland; gFledsvikens Marine Research Station, Institute of Marine Research, NO-4817 His, Norway; and hCentre for Coastal Research, University of Agder, 4604 Kristiansand, Norway

Contributed by Nils Chr. Stenseth, December 28, 2016 (sent for review December 7, 2016; reviewed by Lorenzo Ciannelli, Mark Dickey-Collas, and Eva de Oceanografía, Centro Oceanográfico de Cádiz, E-11006 Cádiz, Andalusia, Spain; cCentre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, NO-0316 Oslo, Norway; and hCentre 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.

The 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 of how interactions in their complex food webs mediate the influence of both top-down (e.g., predation) 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.


Reviewers: L.C., Oregon State University; M.D.-C., International Council for the Exploration of the Sea; and E.E.P., CSIRO Oceans and Atmosphere. The authors declare no conflict of interest.

Freely available online through the PNAS open access option.

1To whom correspondence should be addressed. Email: n.c.stenseth@ibv.uio.no.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1621037114/-/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.1621037114

PNAS Early Edition | 1 of 6
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 regime 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 fishing mortality...
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 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 scenario, sandeel and saithe moved completely from the simulations, then the modeled biomass of whiting simulated under 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).
Interestingly, long indirect pathways occur that exemplify the complexity of the interaction web. For instance, sandeel, 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 (sandal and saithe), but also to the abundance of zooplankton. The 2-yr 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 reliable 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 population 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/ieohandle/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).

**ACKNOWLEDGMENTS.** The research was initiated by the European Network of Excellence EUR-OCEANS “EcoScenarios” Project and further supported by UK Department for Environment, Food and Rural Affairs Project MF1228, “From Fisheries to Fisheries;” EU FP7 (Grant Agreement 308392) DEVOTES (Development of Innovative Tools for Understanding Marine Biodiversity and Assessing Good Environmental Status), www.devotes-project.eu; and GreenMAR (Green Growth Based on Marine Resources: Ecological and Socio-Economic Constraints), www.greenmar.uio.no.

17. Anderson HB, Evans PGH, Potts JM, Harris MP, Wanless S (2014) The diet of Common Guillemots (Ammodytes�is) simulating scenarios of change to 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/ieohandle/10508/10771.
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](http://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/](http://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,
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 \( \geq 0.05 \) 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.
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
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**

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
Figure S1b
Figure S3

[Graph showing AMO and SST scenarios with temperature changes over years, and catches of different fish species like herring, cod, sprat, saithe, Norway pout, and haddock with observed and projected values.]
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.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>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)</th>
<th>GCV</th>
<th>% deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRE</td>
<td>s(GRE_1, edf=3.21) + s(SST, edf=2.70) + DIN</td>
<td>0.0284</td>
<td>80</td>
</tr>
<tr>
<td>DIA</td>
<td>s(DIA_1, 2.18) + If (AMO &gt;= r) s(SST, 1.33) + s(COP_1, 1.33) + s(HEL_1, 1.33)</td>
<td>0.0402</td>
<td>68</td>
</tr>
<tr>
<td>DIN</td>
<td>DIN_1 + s(SST_1, 1.91)</td>
<td>0.1175</td>
<td>54</td>
</tr>
<tr>
<td>COP</td>
<td>DIN + s(DIN_1, 1.94) + s(COP_1, 1.86) + If (DIA &lt;= r) s(SAN, 3.80)</td>
<td>0.0346</td>
<td>83</td>
</tr>
<tr>
<td>HEL</td>
<td>s(SST, 2.72) + s(FIN_1, 2.47) + DIN + s(SPR_1, 1.31)</td>
<td>0.0997</td>
<td>79</td>
</tr>
<tr>
<td>FIN</td>
<td>SST + HER + s(DIA_1, GRE_1, 2)</td>
<td>0.3069</td>
<td>70</td>
</tr>
<tr>
<td>HER</td>
<td>s(F_1, 1.96) + s(HER_1, 1.87) + COP_2</td>
<td>0.0328</td>
<td>97</td>
</tr>
<tr>
<td>SPR</td>
<td>F_1 + SPR_1 + HEL_1 + s(HER, 2.07)</td>
<td>0.0611</td>
<td>87</td>
</tr>
<tr>
<td>NPO</td>
<td>F_1 + s(HER_1, 2.76) + s(NOP_1, 2.81) + NOP_2</td>
<td>0.0992</td>
<td>76</td>
</tr>
<tr>
<td>SAN</td>
<td>s(F_1, 1.41) + s(SAN_2, 2.78) + SST_2 + s(COP_2, 3.58) + WHI_1</td>
<td>0.0549</td>
<td>87</td>
</tr>
<tr>
<td>HAD</td>
<td>s(F_1, 1.63) + HAD_1 + HAD_2 + FIN_2 + s(SAN_1, HER_1, 3.52)</td>
<td>0.0757</td>
<td>83</td>
</tr>
<tr>
<td>SAI</td>
<td>F_1 + s(SAI_1, 1.91) + s(NOP_1, 1.89) + HAD_1</td>
<td>0.0129</td>
<td>95</td>
</tr>
<tr>
<td>WHI</td>
<td>s(WHI_1, 1.90) + SPR_1 + s(SAN_1, 3.28)</td>
<td>0.0490</td>
<td>77</td>
</tr>
<tr>
<td>COD</td>
<td>F_1 + COD_1 + SST_1</td>
<td>0.0063</td>
<td>99</td>
</tr>
<tr>
<td>BIR</td>
<td>DIA_1 + COP_2 + s(FIN_1, edf=2.31) + s(SAN, SPR, 2.17)</td>
<td>0.0066</td>
<td>79</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>model</th>
<th>GAM</th>
<th>tGAM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diatoms</td>
<td>0.2344</td>
<td>0.2367</td>
</tr>
<tr>
<td>Small copepods</td>
<td>0.2525</td>
<td>0.2214</td>
</tr>
</tbody>
</table>

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 S7
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
Fowlisheugh 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
Kett lainess
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
Onzibust 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