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

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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

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, 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.

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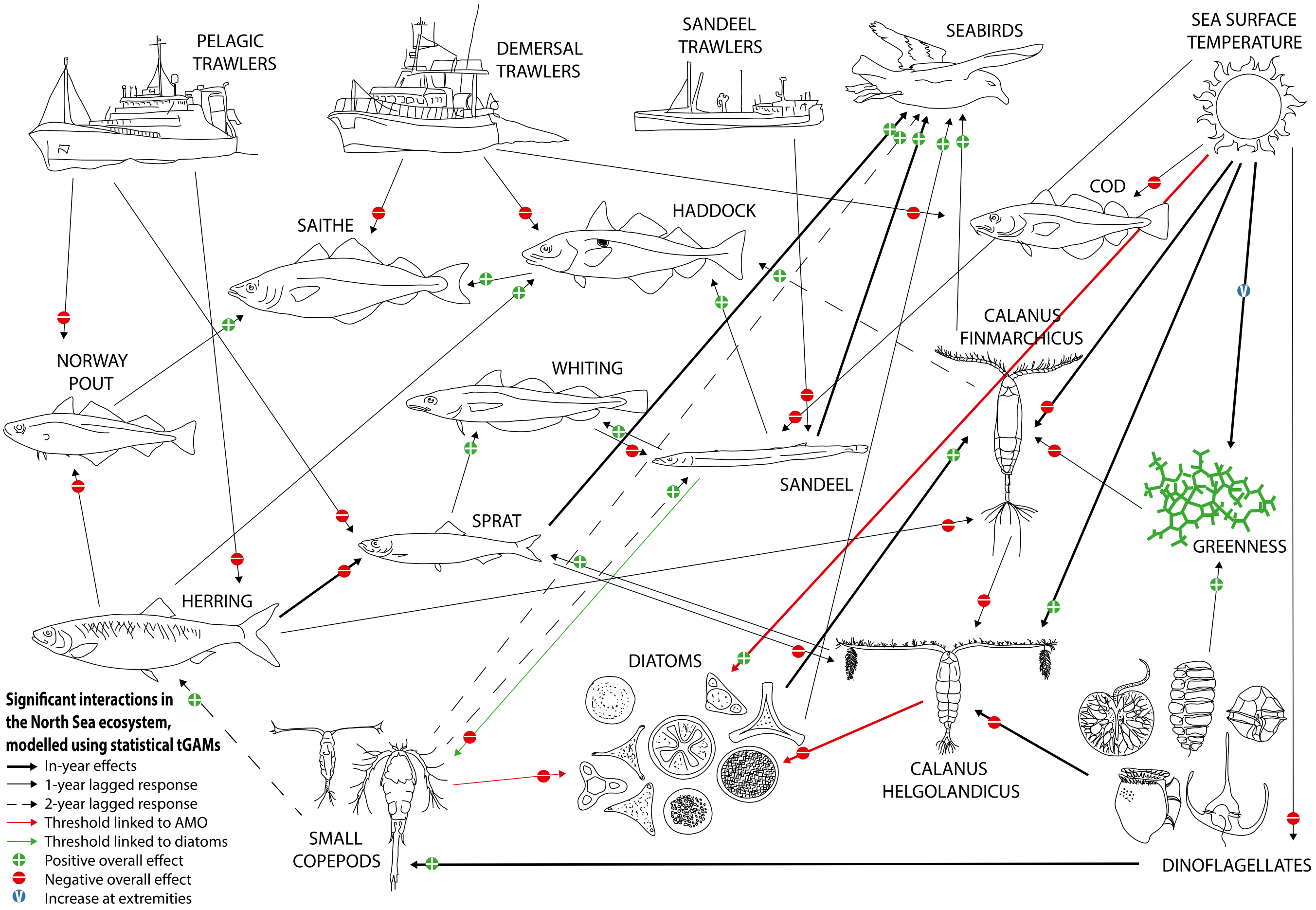

Fig. 1. Diagrammatic representation of the significant interactions modeled between functional groups and drivers. Thresholds in the relationships are indicated by colored lines dependent on whether the threshold variable is the AMO (red) or diatom abundance (green). Lines point from predictor to response 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 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.

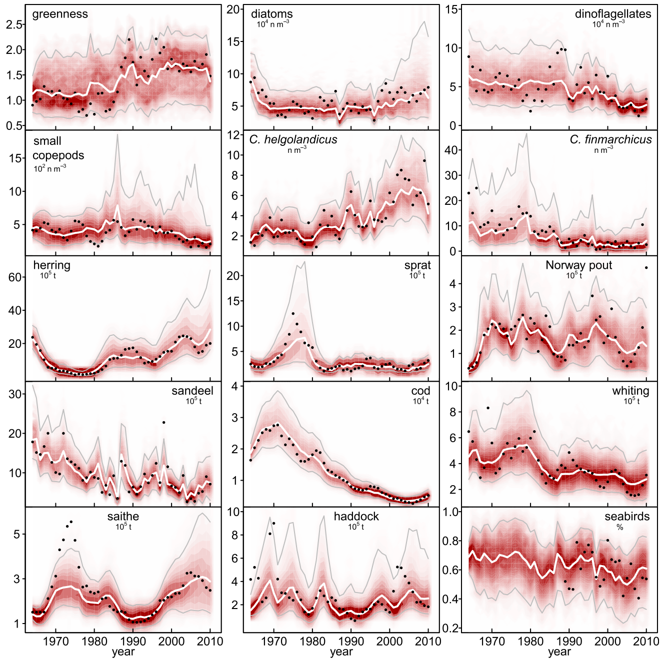

Fig. 2. Simulations to 2010 based solely on predictions from initial conditions in 1964 and the time series of SST and fishing mortality to 2010 (*SI Appendix*, Fig. S3). The best estimates (median values) of the simulations are shown by the white lines and the 95% confidence bands by the gray lines: red shading indicates the annual probability density of simulated values (dark red, high likelihood). Data used for calibration are shown by points.

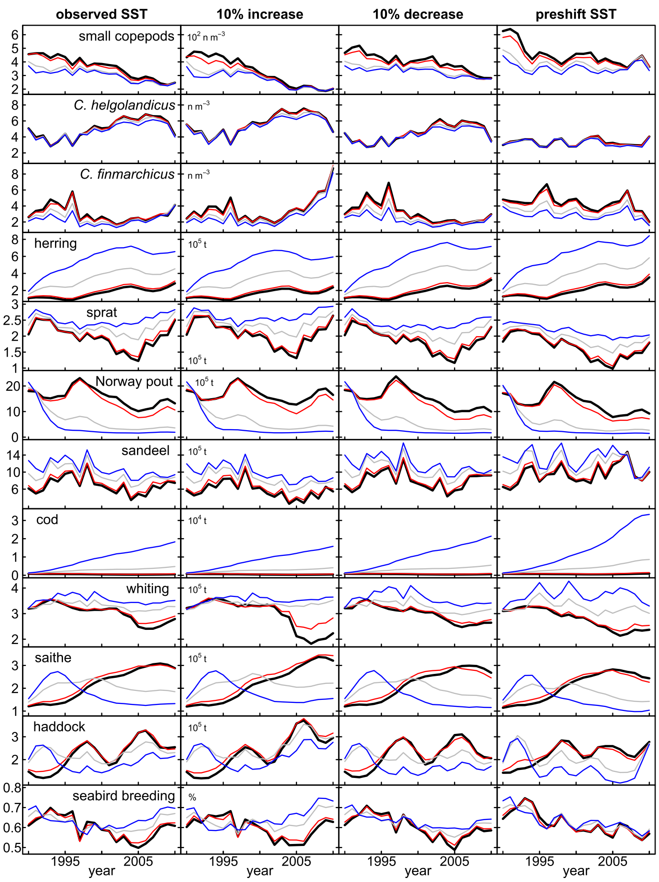

Fig. 3. Sensitivity of the interaction web to fishing levels under four climate scenarios (see *SI Appendix*, Fig. S3). The lines result from the median of 999 simulations and show change in zooplankton abundance, fish biomass, and seabird breeding success (*y* axis) over time (*x* axis) as a function 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.

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).

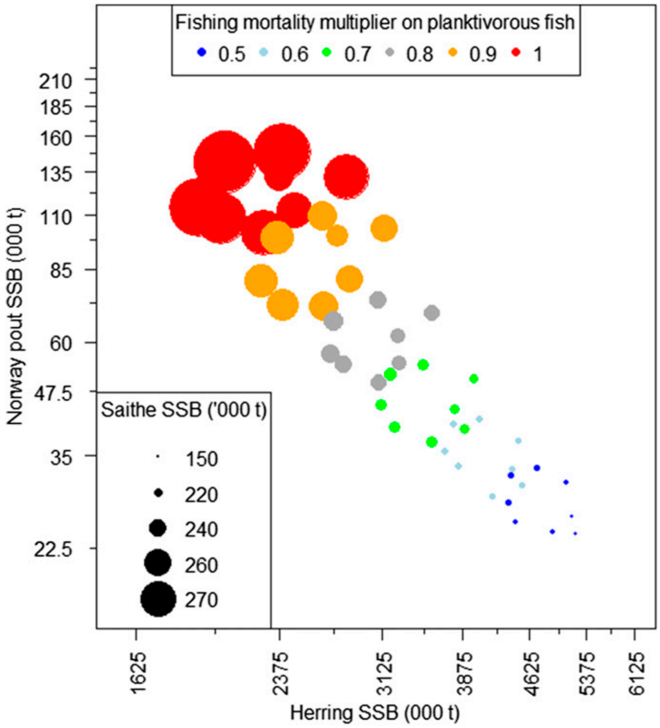

Fig. 4. Indirect effects on piscivorous saithe through fishing on prey species. The recovery of herring biomass (along the *x* axis) follows a decrease in fishing mortality (see color scale) on all planktivorous fish (herring, sprat, sandeel, and Norway pout). Despite the decreases in fishing mortality, 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 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 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).

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