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Evaluating trophic cascades as drivers of regime shifts in different ocean ecosystems

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In ecosystems that are strongly structured by predation, reducing top predator abundance can alter several lower trophic levels—a process known as a trophic cascade. A persistent trophic cascade also fits the definition of a regime shift. Such 'trophic cascade regime shifts' have been reported in a few pelagic marine systems—notably the Black Sea, Baltic Sea and eastern Scotian Shelf—raising the question of how common this phenomenon is in the marine environment. We provide a general methodology for distinguishing top-down and bottom-up effects and apply this methodology to time series from these three ecosystems. We found evidence for top-down forcing in the Black Sea due primarily to gelatinous zooplankton. Changes in the Baltic Sea are primarily bottom-up, strongly structured by salinity, but top-down forcing related to changes in cod abundance also shapes the ecosystem. Changes in the eastern Scotian Shelf that were originally attributed to declines in groundfish are better explained by changes in stratification. Our review suggests that trophic cascade regime shifts are rare in open ocean ecosystems and that their likelihood increases as the residence time of water in the system increases. Our work challenges the assumption that negative correlation between consecutive trophic levels implies top-down forcing.

1. Introduction

Regime shifts are characterized as persistent, high-amplitude changes that affect many components of large ecosystems [1–5]. Regime shifts must span not only multiple species but also multiple trophic levels, such that energy flow through the system is altered [1,2]. Most regime shifts in pelagic marine ecosystems have been linked to changes in conditions that alter bottom-up forcing [6–10]. The majority of these shifts have been related to large-scale changes in the physical environment, often associated with climate modes such as the Pacific decadal oscillation [7,11,12], North Atlantic oscillation (NAO) [13–15] or Arctic oscillation [16,10].

Although climate variability can clearly drive large-scale changes in marine ecosystems, the standard regime shift definitions (i.e. [1]) do not specify that the forcing must come from the physical system. Human activities, particularly fishing, also exert strong forces on pelagic ecosystems (defined as plankton, invertebrates, fish and mammals that feed in the water column) [17]. Fishing reduces the abundance and alters the population structure of harvested species, creating opportunities for the exploited species' prey and competitors to flourish. There are many examples of reductions in marine predators leading to changes in prey abundance (reviewed by Baum & Worm [18]). However, most of the reported examples only involve a predator and its immediate prey, and thus would not meet the multi-trophic level and multi-species criteria required by the regime shift definition. If top-down forcing is especially strong,

a decline in upper-level predators can affect several lower trophic levels, a situation known as a trophic cascade [19]. A trophic cascade that induces persistent changes would meet the definition of a regime shift—one driven by top-down, rather than bottom-up, processes.

(a) Trophic cascade regime shifts

Paine [20] introduced the term ‘trophic cascade’, but the idea of predatory influence extending through many trophic levels has its origins with the ‘green-world’ hypothesis of Hairston *et al.* [21]. Pace *et al.* [22] defined a trophic cascade as ‘reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population, community or trophic level across more than one link in a food web’ (p. 483). Building from this definition, we introduce a new term ‘trophic cascade regime shift’, for cases that satisfy three requirements beyond those of a regime shift. The first requirement is an apparent change in the abundance, biomass or productivity of a key species or multiple species at a high trophic level. Second, in addition to impacting the next trophic level down, top-down changes in the system must extend through additional lower trophic levels. Thus, there should be identifiable direct effects between adjacent trophic levels and indirect effects between non-adjacent trophic levels. The third requirement is a timing constraint; the change in adjacent trophic levels must occur in an ecologically logical manner, including appropriate lags between changes at different trophic levels.

Either direct consumptive or non-consumptive effects [23] could contribute to the top-down forcing that may result in trophic cascades. Ideally, experimental exclusion or addition of predators would be used to establish whether a change in the predator population is actually responsible for the shift. Such experiments are not often possible in pelagic ecosystems outside of lakes. In marine ecosystems, negative correlations between adjacent trophic levels are interpreted as evidence of top-down forcing [24].

Strong [19] famously posed the question ‘are trophic cascades all wet?’ and speculated that most cascades have algae at their base. This hypothesis grouped many of the well-documented cascades from rivers and lakes [25] with those from intertidal and subtidal communities [20]. Since then, many examples of trophic cascades in marine benthic environments have been reported. Estes *et al.* [26] documented a trophic cascade caused by the removal of sea otters that led to the loss of kelp forests. More recently, Myers *et al.* [27] described how overfishing on large sharks resulted in an explosion in skates and rays and a reduction in scallops.

Despite widespread changes in fish populations [28–30] and their dependence on primary production from algae, there are few examples of trophic cascades in pelagic marine ecosystems. The leading exceptions, identified by Essington [31], are from the Black Sea [32,33], Baltic Sea [34–36] and eastern Scotian Shelf [37,38]. While fishing has a profound effect on marine trophic structure [17], it is not the only external driver in these systems. Changes in physical conditions, external supply of nutrients and invasive species have also been documented [16,39–41], and the relative importance of top-down versus bottom-up forcing is a source of debate [42,43]. This raises the question of how to identify the direction of forcing (top-down and bottom-up) in pelagic ocean regime shifts. We review three case studies and analyse their respective time

series using a common methodology designed to distinguish top-down and bottom-up forcing. Our goal is to understand the necessary conditions for trophic cascade regime shifts in the pelagic ocean.

2. Material and methods

Consistent with most trophic cascade and regime shift studies, we examined correlations between multiple trophic levels over many years. To address causation, we tested the effect of removing the top-down or bottom-up forcing signal on the pattern of correlations. Our approach provides a common methodology for evaluating the strength of different drivers producing the ecosystem patterns observed across all three cases.

We selected time series from one representative paper for each of the three cases: Black Sea [33], Baltic Sea [36] and eastern Scotian Shelf [37]. Time series were extracted by digitizing the figures, mapping the plotted data onto calibrated axes and manually selecting each data point. This method can be applied to any data presented in graphical format, regardless of whether the original data are still available, and it allowed us to apply a standard methodology across the three case studies. We analysed variables within each case study in a pairwise manner, where a ‘variable’ was a trophic level metric, such as abundance or biomass.

In a trophic cascade regime shift, changes in individual trophic levels may lag behind one another, depending upon the biology of its representative organisms and their relationships to the rest of the food web. We therefore examined the autocorrelation for each variable and cross-correlations between each pair of variables for lags from 0 to 10 years. High levels of autocorrelation were noted in many of the variables, leading to cross-correlation patterns that persisted over many years in the lagged relationships. Because the cross-correlation patterns remained relatively stable over time, we simplified our subsequent analyses by proceeding with unlagged data.

We first examined Pearson product moment correlations among the time series for each case. Based on these correlations, we identified variables that showed strong correlations with many other variables within each ecosystem. These variables were further investigated as potential bottom-up and top-down drivers of the trophic cascade reported in each case. In the Black Sea, we used phytoplankton biomass and predatory fish (biomass of catch) as our respective bottom-up and top-down drivers. In the Baltic Sea, we selected salinity and cod biomass, and for the eastern Scotian Shelf, we selected water column stratification and groundfish biomass. In the Black Sea case, we also considered the influence of invasive gelatinous zooplankton, an intermediate trophic level that is not controlled by fish predators but that exerts top-down control on lower trophic levels of the ecosystem. Consistent with Daskalov *et al.* [33], we treat the gelatinous species as a single guild.

To evaluate the relative importance of potential bottom-up versus top-down factors as drivers of the regime shift, we removed the influence of each candidate driver one at a time and examined changes in the cross-correlation patterns. For each candidate driver, we fit a linear regression model expressing each variable as a function of the driver. We subsequently created new time series of the residuals off of these relationships, thereby separately removing bottom-up and top-down effects from the original time series. The strength of forcing was evaluated by comparing the correlation matrix formed using the residual time series to the original correlation matrix. Factors that affected more pairwise correlations were interpreted as acting as the dominant driver of trophic structure in the ecosystem. In all analyses, we applied penalties for autocorrelation when computing the significance of the correlation values [44].

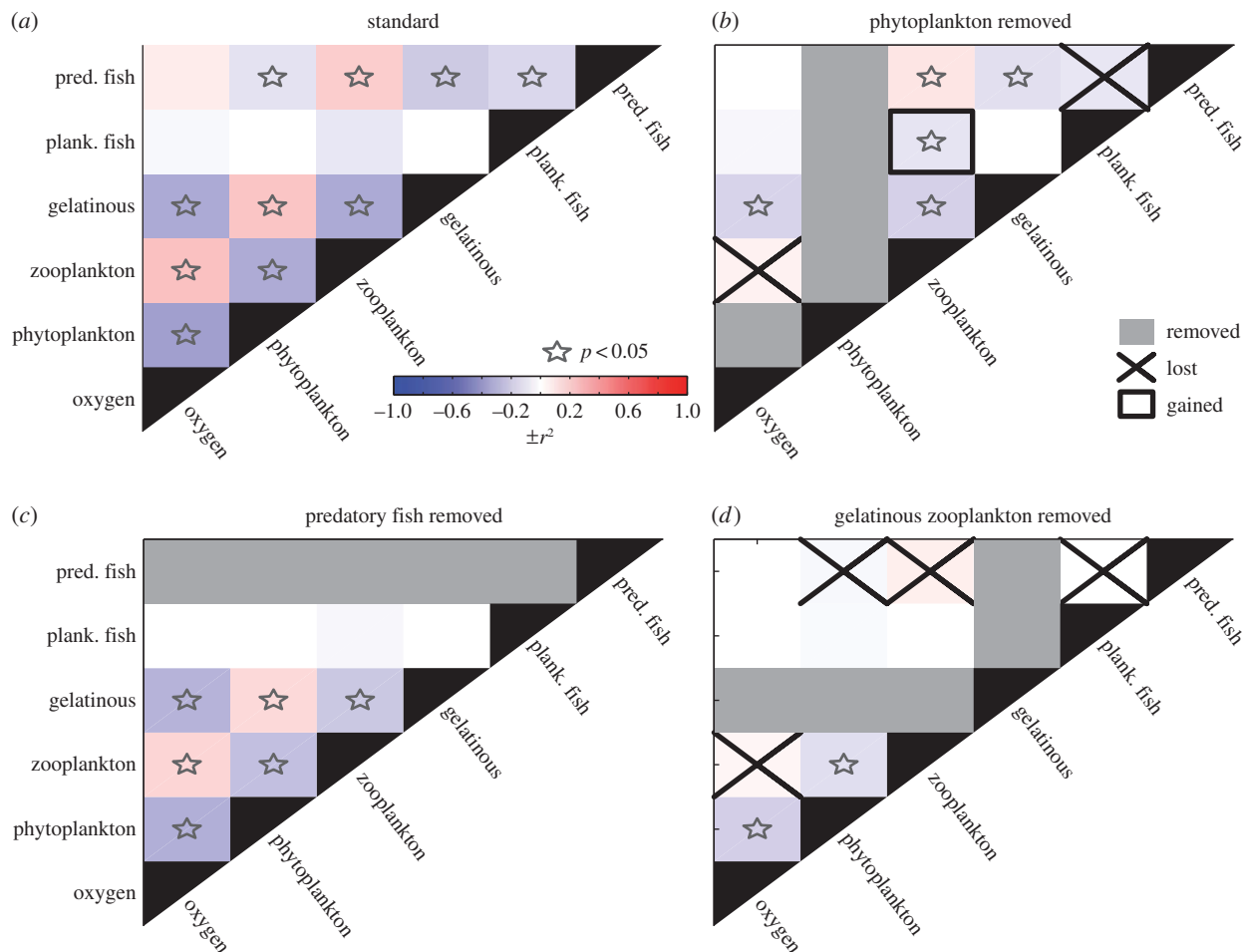


Figure 1. Correlation matrices for the Black Sea using data from [33]. (a) Correlation using the original time series. Colours indicate the strength (expressed as r^2) and sign of the correlation (see colourbar) and stars indicate correlations that are significant at the 95% level after correcting for autocorrelation. (b) Correlations of the residual time series after removing the bottom-up signal from chlorophyll. (c) Correlations after removing the top-down signal from piscivorous fish. (d) Correlations after removing the gelatinous zooplankton signal. In (b–d), an 'X' indicates a correlation that was significant in (a), but is now non-significant, while a black box indicates a new significant correlation (see key in (b)).

3. Results

Our analysis revealed a gradient of scenarios, including one regime shift originally interpreted as a trophic cascade that, according to our analysis, is driven primarily by bottom-up forcing. We present our results from each system, including a brief description from the original studies for context.

(a) Black Sea

Over five decades, there have been significant changes across five pelagic population groups representing four trophic levels in the Black Sea: phytoplankton, non-gelatinous zooplankton, gelatinous zooplankton, planktivorous fish and piscivorous fish [33]. Daskalov *et al.* [33], our reference study and data source, also included oxygen concentration as a proxy for eutrophication. As originally described (in [33]), the trophic cascade was initiated by declines in predatory fish, which led to increases in planktivorous fish, declines in zooplankton and increases in phytoplankton; phytoplankton biomass was also inversely correlated with oxygen concentration. In addition, invasive gelatinous zooplankton, particularly *Aurelia aurita* and *Mnemiopsis leidyi*, contributed to regime shifts in the Black Sea as they became important predators of zooplankton and restructured trophic relationships in the ecosystem.

The trophic cascade reported by Daskalov *et al.* [33] can be tracked through the correlations of the time-series data. These correlations display a distinct 'checker-board' pattern, with negative correlations between adjacent trophic levels and positive correlations between trophic levels separated by two links, indicating an apparent trophic cascade (figure 1a). In tracing this cascade through the correlation matrix, it is important to note that while declines in piscivorous fish are associated with increases in planktivorous fish, the planktivorous fish are not significantly correlated with lower trophic levels. There is, however, a pattern of correlations of alternating signs among the gelatinous zooplankton, zooplankton, phytoplankton and oxygen.

In the Black Sea, we examined potential bottom-up influences by removing the effect of phytoplankton on all other ecosystem variables. After removing this signal, correlation patterns indicating top-down structuring at higher trophic levels were weakened but not eliminated (figure 1b). Removing the effect of phytoplankton caused the negative correlation between predatory fish and planktivorous fish to disappear along with the positive correlation between oxygen and zooplankton. The negative correlations between predators and gelatinous zooplankton and between gelatinous zooplankton and non-gelatinous zooplankton remained (figure 1b). In addition, the negative correlation between planktivores and non-gelatinous zooplankton was strengthened and became significant (figure 1b).

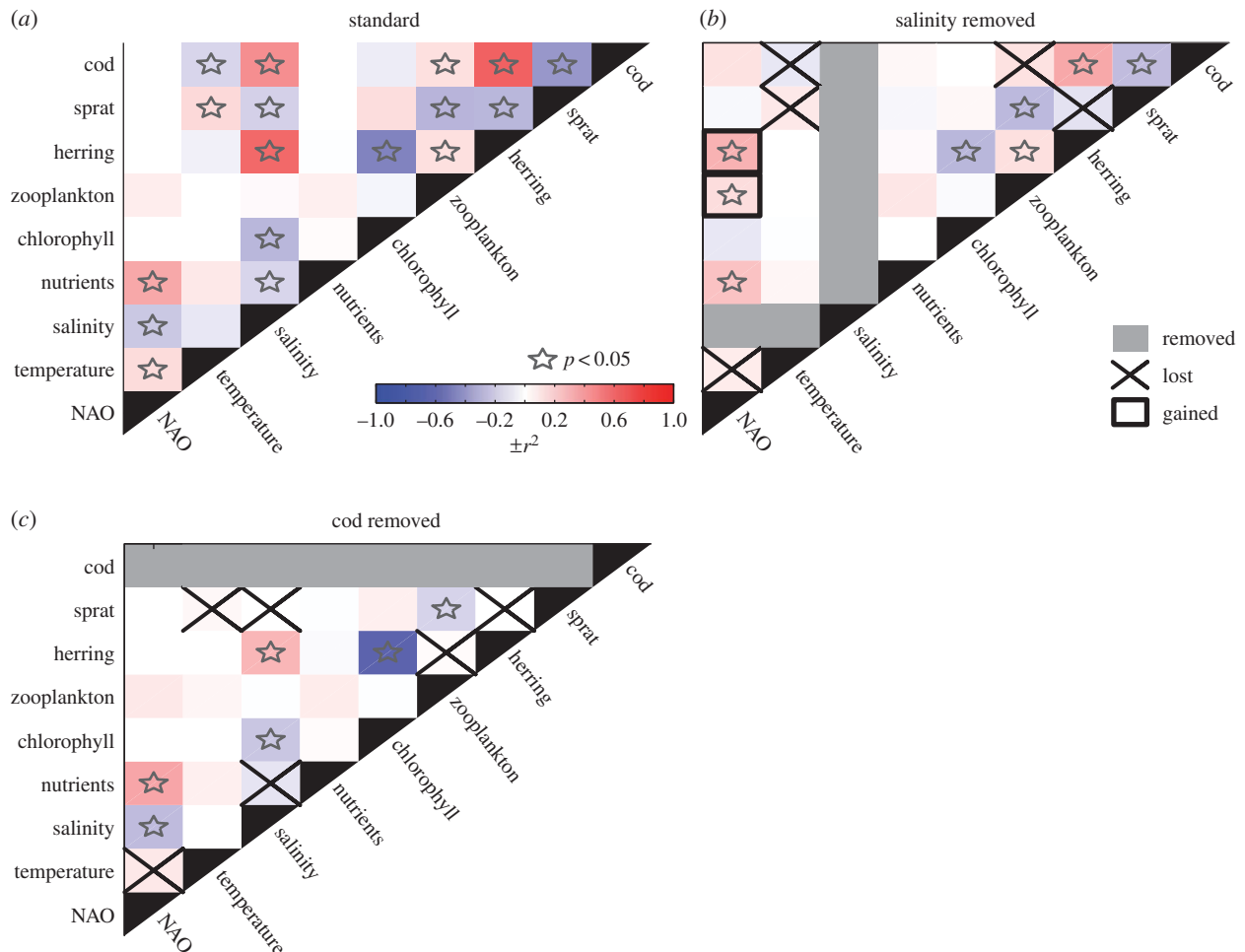


Figure 2. Correlation matrices for the Baltic Sea using data from [36]. (a) Correlation using the original time series. Colours indicate the strength (expressed as r^2) and sign of the correlation (see colourbar) and stars indicate correlations that are significant at the 95% level after correcting for autocorrelation. (b) Correlations of the residual time series after removing the bottom-up signal from salinity. (c) Correlations after removing the top-down signal from cod. In (b,c), an 'X' indicates a correlation that was significant in (a), but is now non-significant, while a black box indicates a new significant correlation (see key in (b)).

Daskalov *et al.* [33] indicate that the first shift in the Black Sea ecosystem occurred following the depletion of predatory fish due to overfishing. When we removed the top-down influence of predators on the suite of Black Sea variables, the pattern of negative correlations between trophic levels remained intact from the gelatinous zooplankton through to oxygen (figure 1c). However, the strength of these correlations was reduced.

When *M. leidyi* invaded the Black Sea, the dominant top-down control on zooplankton switched from planktivorous fish to ctenophores [33]. Removing the influence of gelatinous zooplankton restricts significant correlations to the lowest trophic levels of the ecosystem (figure 1d), with negative correlations between zooplankton and phytoplankton, and between phytoplankton and oxygen. These correlations indicate that gelatinous zooplankton have exerted the strongest forcing on the interannual variability of the Black Sea ecosystem over the full time period analysed.

(b) Baltic Sea

The trophic organization and biological composition of the Baltic Sea have transformed over the last three decades. Casini *et al.* [36] attributed a portion of the changes to a trophic cascade involving cod, sprat, zooplankton and phytoplankton. Cod are considered the top predators in the system, and declines in cod were associated with increased sprat,

decreased zooplankton and increased chlorophyll levels. Changes in salinity and the NAO were interpreted as having secondary impacts that reinforced the trophic changes in the ecosystem [36].

The Baltic Sea trophic cascade as reported by Casini *et al.* [36] is most apparent in the correlations between cod biomass and the other variables (figure 2a). Sprat, one trophic level below cod, are negatively correlated with cod, while zooplankton, two trophic levels below, are positively correlated with cod. The correlation between cod and chlorophyll is negative as expected in a trophic cascade scenario, but not significant. Herring is positively correlated with both cod and zooplankton, and thus is not part of the trophic cascade, potentially due to different feeding patterns between sprat and herring [36].

Casini *et al.*'s original study [36] considers three potential bottom-up drivers: the NAO, temperature and salinity. Among these, we found that salinity is most strongly correlated with the other physical and biological variables, including nutrients (negative), chlorophyll (negative), herring (positive), sprat (negative) and cod (positive) (figure 2a). Overall, there are strong correlations among the physical and lower trophic level variables, and among the fish and zooplankton variables (figure 2a).

We examined the influence of salinity as a bottom-up forcing variable in the ecosystem by removing its influence on all other ecosystem variables. After removing this signal,

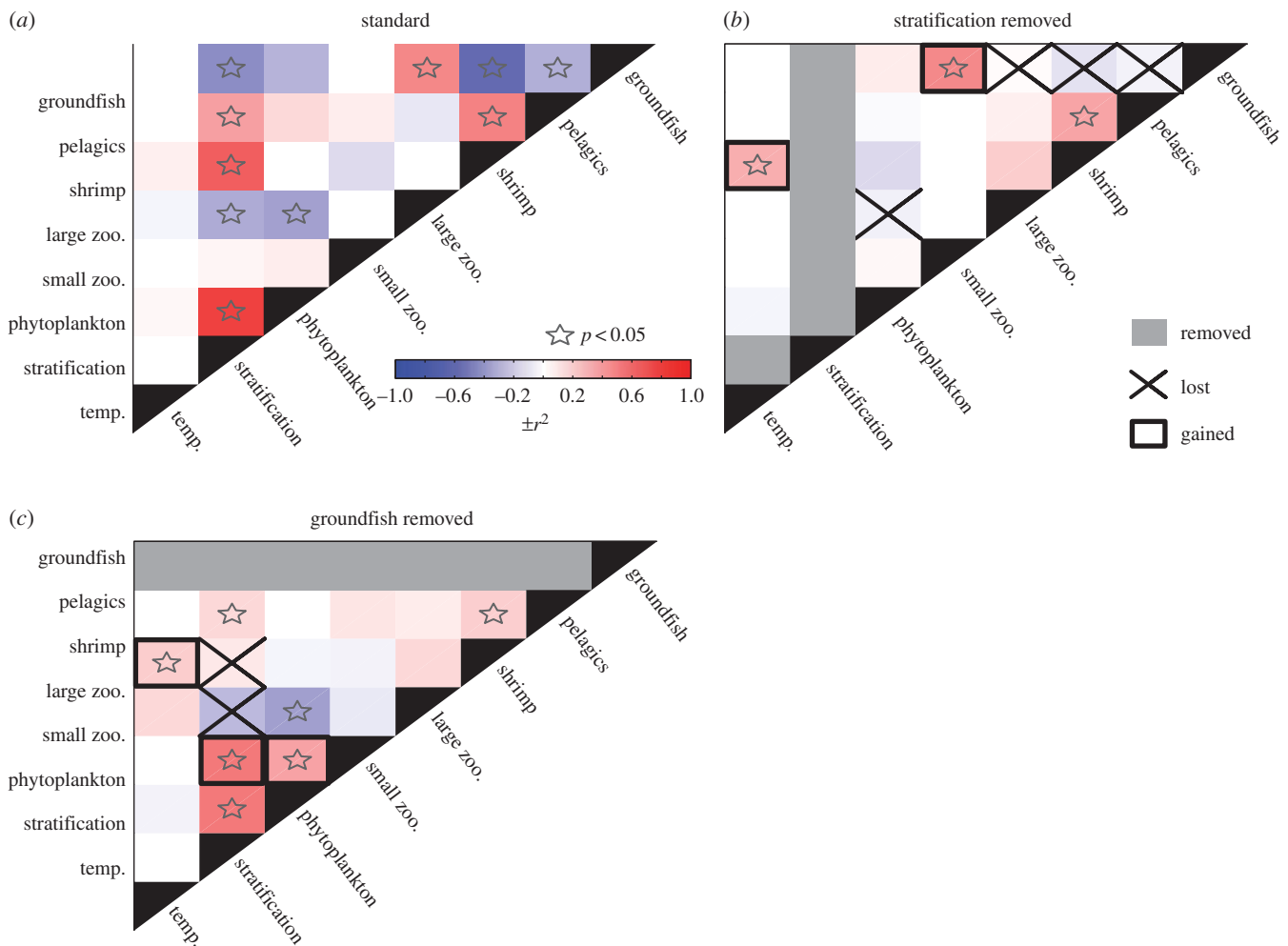


Figure 3. Correlation matrices for the eastern Scotian Shelf using data from [37]. (a) Correlation using the original time series. Colours indicate the strength (expressed as r^2) and sign of the correlation (see colourbar) and stars indicate correlations that are significant at the 95% level after correcting for autocorrelation. (b) Correlations of the residual time series after removing the bottom-up signal from stratification. (c) Correlations after removing the top-down signal from groundfish. In (b,c), an 'X' indicates a correlation that was significant in (a), but is now non-significant, while a black box indicates a new significant correlation (see key in (b)).

many of the correlations between physical and lower trophic level variables weaken (figure 2b). However, several new correlations involving the NAO emerge, including correlations with nutrients, herring and zooplankton. With the exception of sprat–herring and cod–zooplankton, all other correlations among upper trophic levels remained significant.

Removing the cod signal eliminated most of the significant correlations that made up Casini *et al.*'s [36] trophic cascade, with the exception of the negative correlation between sprat and zooplankton (figure 2c). The sprat–salinity and sprat–temperature correlations also disappeared when the influence of cod was removed (figure 2c). In addition, the salinity–nutrient and NAO–temperature relationships weakened (figure 2c).

(c) Eastern Scotian shelf

Over approximately four decades, there have been changes in nutrients, phytoplankton, small and large zooplankton, pelagic fish and shrimp, and groundfish on the eastern Scotian Shelf, which have been attributed to a trophic cascade driven by a decline in groundfish [37]. Frank *et al.*'s [37] reporting of these changes also includes an index of water column stratification that increases as the groundfish populations decline. The trophic cascade described in [37] appears as a sequence of alternating negative and positive correlations along the top row of

the standard correlation matrix (figure 3a). However, the statistical significance of this cascade disappears below the large zooplankton. The ecosystem components comprising the cascade are also significantly correlated with the stratification time series (figure 3a), suggesting that the changes on the eastern Scotian Shelf may be related to physical conditions.

Removing the stratification signal has a strong impact on the correlation pattern (figure 3b). Notably, all of the groundfish correlations that are part of the trophic cascade disappear, as does the correlation between small and large zooplankton. However, positive correlations between groundfish and small zooplankton and between temperature and shrimp emerge (figure 3b).

When the groundfish signal is removed, many of the other correlations persist and, in some cases, strengthen (figure 3c). A block of strong positive correlations appears among stratification, phytoplankton and small zooplankton, and the negative correlation between large zooplankton and phytoplankton remains. The pattern of phytoplankton being positively correlated with small zooplankton but negatively correlated with large zooplankton is characteristic of the plankton community across the entire northwest Atlantic Shelf [45]. The positive correlation between shrimp and pelagic fish persists, and a positive correlation between temperature and shrimp emerges. The strong influence of removing

stratification and limited impact of removing groundfish suggest that bottom-up forcing played the primary role in the eastern Scotian Shelf regime shift.

4. Discussion

Using our simple procedure for isolating the influence of potential top-down and bottom-up drivers, we found strong support for a trophic cascade regime shift in the Black Sea driven by the appearance of gelatinous predators. The results were more complex in the Baltic Sea and on the eastern Scotian Shelf. In the Baltic Sea, we found evidence for top-down forcing but also significant bottom-up forcing through salinity and the NAO. In the eastern Scotian Shelf, our analysis suggests that changes in stratification played a stronger role in structuring the ecosystem than did changes in groundfish abundance.

In our analyses, the Black Sea displays strong top-down structuring, but trophic forcing in the ecosystem is complex with top-down and bottom-up drivers being important during different time periods [33]. Over the full time period, the introduction of gelatinous zooplankton drove a regime shift that strongly influenced the trophic structure of the ecosystem (figure 1*d*). Our analysis indicates a stronger impact of gelatinous zooplankton invasions than of piscivorous fish declines.

The impact of removing the cod signal in the Baltic Sea supports the strong top-down forcing hypothesized by Casini *et al.* [35,36]. However, we also found evidence for bottom-up forcing, particularly on lower trophic levels of the ecosystem. The physical forcing on the Baltic system involves local processes such as heating and run off and larger scale processes represented by the NAO. Salinity is a particularly important physical variable in the Baltic Sea, where reductions in the inflow of Atlantic water and input from the many rivers in the region can change the system from oceanic to brackish [35,40]. The NAO has also been implicated in some of the changes in this system. Notably, a transition period during the late 1980s and early 1990s, during which the trophic organization in the Baltic shifted from cod-dominated to clupeid-dominated, coincided with a shift in the NAO index [35,40]. The emergence of several NAO correlations when the salinity signal is removed suggests that a more careful treatment of the physical and chemical drivers of this system, beyond our simple correlational approach, is needed.

The most striking result from our analysis is the lack of support for a trophic cascade on the eastern Scotian Shelf. Although this region has clearly experienced a large reduction in predatory fish, the reduction coincided with substantial changes in the physical system represented by the stratification index. If the stratification signal is removed, the correlations that were consistent with a trophic cascade disappear (figure 3*b*). If the groundfish signal is removed, many of the original correlations remain (figure 3*c*). These results suggest that the ecosystem shifts on the eastern Scotian Shelf are more consistent with bottom-up forcing than with a groundfish-driven trophic cascade. Although most studies of the eastern Scotian Shelf ecosystem shifts have focused on overfishing as a likely driver, Choi *et al.* [39] identified stratification as an important factor. A recent update to the eastern Scotian Shelf analysis found that many of the changes in the 1990s began reversing in the early 2000s [38]. The timing of the reversal coincides with a reduction in stratification [15,16,46], consistent with the bottom-up mechanism implied by our analysis.

Negative correlations between adjacent trophic levels can appear, on the surface, to provide evidence for a trophic cascade. While these negative correlations could indicate top-down forcing between species in an ecosystem, they are not sufficient by themselves for diagnosing a trophic cascade. Negative correlations can also arise from bottom-up processes. For example, a similar shift in the plankton community in the Gulf of Maine associated with hydrographic changes has been interpreted as evidence of bottom-up forcing [47]. In that hypothesis, a shift towards more stratified conditions leads to a longer phytoplankton growing season and favours smaller phytoplankton (i.e. dinoflagellates over diatoms). The smaller phytoplankton community in turn favours smaller zooplankton, leading to a negative correlation between phytoplankton abundance and large copepods, identical to the correlation pattern on the eastern Scotian Shelf and in the broader northwest Atlantic [45]. Macroecological studies that rely solely on negative correlations to identify top-down forcing are particularly susceptible to seeing such forcing where none occurs. Our work underscores the importance of considering alternative explanations when interpreting correlations.

(a) Why are trophic cascades rare in the ocean?

Reported cases of trophic cascades are rare in large marine ecosystems and our analyses suggest that even some of the commonly cited examples may be strongly influenced by bottom-up forcing. If top-down structuring were the rule in pelagic marine ecosystems, then we would expect to see many more examples of trophic cascade regime shifts corresponding with major collapses of commercial fish populations. For example, the North Sea is one of the most heavily impacted ecosystems in the world [17]. Cod populations exploded during the 1960s gadoid outburst and then declined due to overfishing [48]. In this ecosystem, changes in the abundance of mid-trophic level species and plankton are consistently explained by shifts in the physical system [13,49,50]. While it is impossible to say that trophic cascades can never occur in open ocean pelagic ecosystems, the weight of evidence suggests that they are unlikely. By contrast, many examples of trophic cascades have been found in the pelagic communities in lakes [25] and in enclosed seas such as the Black and Baltic Seas considered above.

Strong [19] suggests that ‘runaway consumption’, where one trophic level reduces the abundance of its prey to very low levels, is a necessary condition for a trophic cascade. Ecosystems with strong spatial constraints are more prone to trophic cascades [51,52]. In these systems, prey populations can only rebuild through local reproduction. By contrast, in open ecosystems, prey lost to mortality or emigration can be replaced through advection or immigration, and variations in supply can overwhelm local dynamics [53,54]. We hypothesize two factors in pelagic marine systems that reduce the likelihood of runaway consumption: (i) the advective nature of pelagic ecosystems and (ii) the increase in diversity at lower trophic levels. These properties reduce the likelihood that top-down forcing can drive regime shifts in the ocean; conversely, when these properties are altered, trophic cascades are more likely.

The gradient of top-down forcing in our examples, from strong in the Black and Baltic Seas to weak on the eastern Scotian Shelf, is consistent with spatial constraints in these ecosystems. The residence time, defined as the volume of

the ecosystem divided by the flux of water through the system, provides a rough indication of spatial constraints. The residence times of the near-surface waters of the Black and Baltic Seas are on the order of tens of years [55,56]. The residence time in the eastern Scotian Shelf is much shorter than either of the enclosed seas. Assuming an average depth of 50 m, a surface area of $7.3 \times 10^{10} \text{ m}^2$, and a flux of $6 \times 10^7 \text{ m}^3 \text{ s}^{-1}$ [57], the residence time on the Scotian Shelf is approximately 60 days. The Scotian Shelf residence time is comparable to the generation time of the copepods in this ecosystem, magnifying variation in supply [54,58] and emphasizing processes such as changes in stratification or temperature that are likely to covary over large scales.

The residence time argument described above may explain the prevalence of strong top-down effects in benthic and demersal ecosystems. In these systems, predators can readily reduce the abundance of prey in an area and lost prey can only be replaced by active migration or, for sessile species, recruitment. For example, Myers *et al.* [27] report a trophic cascade where overfishing on large predatory sharks released smaller elasmobranchs (rays, skates and small sharks) from predation. In turn, the cownose ray decimated the bay scallop population. This trophic cascade depends on the ability of rays to substantially reduce the abundance of bay scallops in an area and the slow recruitment of new scallops into a cleared area. There are examples of rocky intertidal zones worldwide that have faced reported regime shifts related to urchin over-grazing of kelp [59], some of which are trophic cascade regime shifts [26]. The effects which lead to trophic cascade regime shifts in these spatially constrained systems are in contrast to the difficulty with which a pelagic predator might clear a water volume, and the relatively high likelihood of a pelagic organism being quickly replaced through migration or advection.

The structure of pelagic food webs may also provide an inherent barrier to trophic cascades. Several authors have hypothesized that high species or functional diversity dilutes the impact of a change in top predator abundance [18,24]. In marine foodwebs, diversity generally decreases as trophic level increases. The change in diversity is especially large between zooplankton and their predators; Micheli [60] suggests that zooplankton may serve as a barrier to cascades in aquatic systems. Gelatinous predators such as ctenophores may be the exception to this pattern, due to their high consumption rates and fast reproduction. The introduction of the ctenophore *M. leidyi* was the main driver of the trophic cascade regime shift in the Black Sea. In the nearby Caspian Sea, outbreaks of *M. leidyi* resulted in a decrease in mesozooplankton diversity as well as abundance [61].

5. Conclusion

Regime shifts are a well-established feature of large marine ecosystems. When we applied a uniform methodology to three examples of regime shifts attributed to trophic cascades, we found evidence for top-down forcing in the Black Sea,

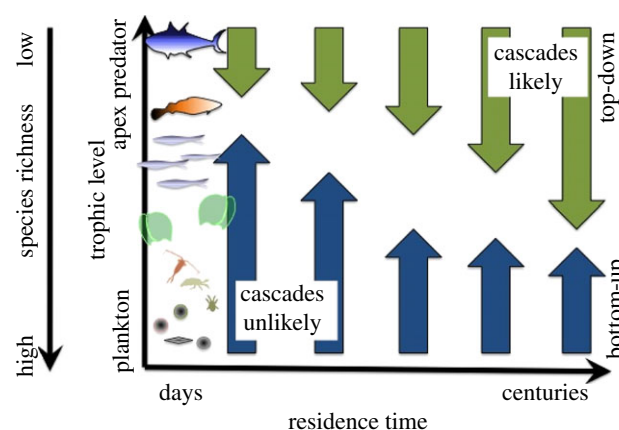


Figure 4. Diagram depicting the hypothesized strength of top-down and bottom-up forcing as a function of the residence time of the ecosystem. (Online version in colour.)

bottom-up forcing in the eastern Scotian Shelf and a mix of both top-down and bottom-up in the Baltic Sea. Based on this analysis, we propose a conceptual model where top-down forcing competes with bottom-up forcing (figure 4). Ecosystems that are spatially constrained or that have reduced diversity at the lower trophic levels should have stronger top-down forcing, explaining why cascades are common in lakes and the benthos. This model also explains why we found strong top-down signals in the Black and Baltic Seas and a strong bottom-up signal in the more open eastern Scotian Shelf ecosystem. In the ocean, high diversity at low trophic levels coupled with the open nature of the system mitigates the effect of top-down forcing, thereby reducing the likelihood of a trophic cascade that penetrates and controls multiple levels of the ecosystem.

Our review suggests that top-down processes are unlikely to be a major driver of regime shifts in open ocean pelagic ecosystems, despite the widespread impact of fishing. Even in ecosystems such as the Baltic Sea, where top-down control is strong, bottom-up forcing through climate and physical conditions shapes the structure and dynamics of the ecosystem [30,38]. We propose that bottom-up forcing should be the leading hypothesis when diagnosing the mechanisms behind any regime shift in pelagic ecosystems [10]. Any study of the potential impact of changes in predator populations should evaluate the evidence of top-down forcing against potential bottom-up drivers.

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References

1. de Young B, Harris RP, Alheit J, Beaugrand G, Mantua N, Shannon L. 2004 Detecting regime shifts in the ocean: data considerations. *Prog. Oceanogr.* **60**, 143–164. (doi:10.1016/j.pocean.2004.02.017)
2. Cury P, Shannon L. 2004 Regime shifts in upwelling ecosystems: observed changes and possible

- mechanisms in the northern and southern Benguela. *Prog. Oceanogr.* **60**, 223–243. (doi:10.1016/j.pocean.2004.02.007)
3. Collie JS, Richardson K, Steele JH. 2004 Regime shifts: can ecological theory illuminate the mechanisms? *Prog. Oceanogr.* **60**, 281–302. (doi:10.1016/j.pocean.2004.02.013)
 4. Lees K, Pitois S, Scott C, Frid C, Mackinson S. 2006 Characterizing regime shifts in the marine environment. *Fish Fish.* **7**, 104–127. (doi:10.1111/j.1467-2979.2006.00215.x)
 5. Wooster WS, Zhang CI. 2004 Regime shifts of the North Pacific: early indications of the 1976–1977 event. *Prog. Oceanogr.* **60**, 183–200. (doi:10.1016/j.pocean.2004.02.005)
 6. Anderson PJ, Piatt JF. 1999 Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar. Ecol. Prog. Ser.* **189**, 117–123. (doi:10.3354/meps189117)
 7. Mantua NJ, Hare SR. 2002 The Pacific decadal oscillation. *J. Oceanogr.* **58**, 35–44. (doi:10.1023/A:1015820616384)
 8. Polovina JJ. 2005 Climate variation, regime shifts, and implications for sustainable fisheries. *Bull. Mar. Sci.* **76**, 233–244.
 9. Aschan M, Fosheim M, Greenacre M, Primicerio R. 2013 Change in fish community structure in the Barents Sea. *PLoS ONE* **8**, e62748. (doi:10.1371/journal.pone.0062748)
 10. Beaugrand G *et al.* 2015 Synchronous marine pelagic regime shifts in the Northern Hemisphere. *Phil. Trans. R. Soc. B* **370**, 20130272. (doi:10.1098/rstb.2013.0272)
 11. Hare S, Mantua N. 2000 Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* **47**, 103–145. (doi:10.1016/S0079-6611(00)00033-1)
 12. Chavez FP, Ryan J, Lluch-Cota SE, Niquen M. 2003 From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**, 217–221. (doi:10.1126/science.1075880)
 13. Beaugrand G. 2004 The North Sea regime shift: evidence, causes, mechanisms and consequences. *Prog. Oceanogr.* **60**, 245–262. (doi:10.1016/j.pocean.2004.02.018)
 14. Pitois SG, Lynam CP, Jansen T, Halliday N, Edwards M. 2012 Bottom-up effects of climate on fish populations: data from the continuous plankton recorder. *Mar. Ecol. Prog. Ser.* **456**, 169–186. (doi:10.3354/meps09710)
 15. Greene CH *et al.* 2013 Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. *Limnol. Oceanogr.* **58**, 803–816. (doi:10.4319/lo.2013.58.3.0803)
 16. MERCINA. 2012 Recent Arctic climate change and its remote forcing of Northwest Atlantic Shelf ecosystems. *Oceanography* **25**, 208–213. (doi:10.5670/oceanog.2012.64)
 17. Halpern BS *et al.* 2008 A global map of human impact on marine ecosystems. *Science* **319**, 948–952. (doi:10.1126/science.1149345)
 18. Baum JK, Worm B. 2009 Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.* **78**, 699–714. (doi:10.1111/j.1365-2656.2009.01531.x)
 19. Strong DR. 1992 Are trophic cascades all wet—differentiation and donor-control in speciose ecosystems. *Ecology* **73**, 747–754. (doi:10.2307/1940154)
 20. Paine RT. 1980 Food webs—linkage, interaction strength and community infrastructure—the 3rd Tansley Lecture. *J. Anim. Ecol.* **49**, 667–685. (doi:10.2307/4220)
 21. Hairston NG, Smith FE, Slobodkin LB. 1960 Community structure, population control, and competition. *Am. Nat.* **94**, 421–425. (doi:10.1086/282146)
 22. Pace ML, Cole JJ, Carpenter SR, Kitchell JF. 1999 Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* **14**, 483–488. (doi:10.1016/S0169-5347(99)01723-1)
 23. Preisser EL, Bolnick DI, Grabowski JH. 2009 Resource dynamics influence the strength of non-consumptive predator effects on prey. *Ecol. Lett.* **12**, 315–323. (doi:10.1111/j.1461-0248.2009.01290.x)
 24. Frank KT, Petrie B, Shackell NL. 2007 The ups and downs of trophic control in continental shelf ecosystems. *Trends Ecol. Evol.* **22**, 236–242. (doi:10.1016/j.tree.2007.03.002)
 25. Carpenter SR, Kitchell JF, Hodgson JR. 1985 Cascading trophic interactions and lake productivity. *BioScience* **35**, 634–639. (doi:10.2307/1309989)
 26. Estes JA, Danner EM, Doak DF, Konar B, Springer AM, Steinberg PD, Tinker MT, Williams TM. 2004 Complex trophic interactions in kelp forest ecosystems. *Bull. Mar. Sci.* **74**, 621–638.
 27. Myers RA, Baum JK, Shepherd TD, Powers SP, Peterson CH. 2007 Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**, 1846–1850. (doi:10.1126/science.1138657)
 28. Pauly D, Christensen V, Dalsgaard J, Froese R, Torres Jr F. 1998 Fishing down marine food webs. *Science* **279**, 860–863. (doi:10.1126/science.279.5352.860)
 29. Jackson JBC *et al.* 2001 Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637. (doi:10.1126/science.1059199)
 30. Myers RA, Worm B. 2003 Rapid worldwide depletion of predatory fish communities. *Nature* **423**, 280–283. (doi:10.1038/nature01610)
 31. Essington TE. 2010 Trophic cascades in the open ocean. In *Trophic cascades: predators, prey, and the changing dynamics of nature* (eds J Terborgh, JA Estes), pp. 91–105. Washington, DC: Island Press.
 32. Daskalov GM. 2002 Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.* **225**, 53–63. (doi:10.3354/meps225053)
 33. Daskalov GM, Grishin AN, Rodionov S, Mihneva V. 2007 Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc. Natl Acad. Sci. USA* **104**, 10 518–10 523. (doi:10.1073/pnas.0701100104)
 34. Mollmann C, Muller-Karulis B, Kornilovs G, St John MA. 2008 Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES J. Mar. Sci.* **65**, 302–310. (doi:10.1093/icesjms/fsm197)
 35. Casini M, Hjelm J, Molinero JC, Lovgren J, Cardinale M, Bartolino V, Belgrano A, Kornilovs G. 2009 Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. *Proc. Natl Acad. Sci. USA* **106**, 197–202. (doi:10.1073/pnas.0806649105)
 36. Casini M, Lovgren J, Hjelm J, Cardinale M, Molinero JC, Kornilovs G. 2008 Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proc. R. Soc. B* **275**, 1793–1801. (doi:10.1098/rspb.2007.1752)
 37. Frank KT, Petrie B, Choi JS, Leggett WC. 2005 Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**, 1621–1623. (doi:10.1126/science.1113075)
 38. Frank KT, Petrie B, Fisher JAD, Leggett WC. 2011 Transient dynamics of an altered large marine ecosystem. *Nature* **477**, U86–U98. (doi:10.1038/nature10285)
 39. Choi JS, Frank KT, Leggett WC, Drinkwater K. 2004 Transition to an alternate state in a continental shelf ecosystem. *Can. J. Fish. Aquat. Sci.* **61**, 505–510. (doi:10.1139/f04-079)
 40. Mollmann C, Diekmann R, Muller-Karulis B, Kornilovs G, Plikshs M, Axe P. 2009 Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a discontinuous regime shift in the Central Baltic Sea. *Glob. Change Biol.* **15**, 1377–1393. (doi:10.1111/j.1365-2486.2008.01814.x)
 41. Oguz T, Gilbert D. 2007 Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960–2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. *Deep Sea Res. I Oceanogr. Res. Pap.* **54**, 220–242. (doi:10.1016/j.dsr.2006.09.010)
 42. Greene CH. 2013 Towards a more balanced view of marine ecosystems. *Fish Ocean* **22**, 140–142. (doi:10.1111/fog.12006)
 43. Frank KT, Petrie B, Fisher JAD, Leggett WC. 2013 Setting the record straight on drivers of changing ecosystem states. *Fish Ocean* **22**, 143–146. (doi:10.1111/fog.12007)
 44. Pyper BJ, Peterman RM. 1998 Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**, 2127–2140. (doi:10.1139/f98-104)
 45. Pershing AJ, Head EHJ, Greene CH, Jossi JW. 2010 Pattern and scale of variability among Northwest Atlantic Shelf plankton communities. *J. Plankton Res.* **32**, 1675–1684. (doi:10.1093/plankt/fbq058)
 46. Herbert D, Pettipas R, Petrie B. 2011 Meteorological, sea ice and physical oceanographic conditions on the Scotian Shelf and in the Gulf of Maine during 2009 and 2010. DFO Canadian Science Advisory Secretariat. Research Document.
 47. Greene CH, Pershing AJ. 2007 Climate drives sea change. *Science* **315**, 1084–1085. (doi:10.1126/science.1136495)
 48. Kenny AJ, Skjoldal HR, Engelhard GH, Kershaw PJ, Reid JB. 2009 An integrated approach for assessing the relative significance of human pressures and

- environmental forcing on the status of large marine ecosystems. *Prog. Oceanogr.* **81**, 132–148. (doi:10.1016/j.pocean.2009.04.007)
49. Reid PC, Borges MD, Svendsen E. 2001 A regime shift in the North Sea circa 1988 linked to changes in the North Sea fishery. *Fish Res.* **50**, 163–171. (doi:10.1016/S0165-7836(00)00249-6)
 50. Weijerman M, Lindeboom H, Zuur AF. 2005 Regime shifts in marine ecosystems of the North Sea and Wadden Sea. *Mar. Ecol. Prog. Ser.* **298**, 21–39. (doi:10.3354/meps298021)
 51. Heck KL, Valentine JF. 2007 The primacy of top-down effects in shallow benthic ecosystems. *Estuaries Coasts* **30**, 371–381. (doi:10.1007/BF02819384)
 52. Steneck RS, Sala EA. 2005 Large marine carnivores: trophic cascades and top-down controls in coastal ecosystems past and present. In *Large carnivores and the conservation of biodiversity* (eds J Ray, K Redford, R Steneck, J Berger), pp. 110–137. Washington, DC: Island Press.
 53. Gaines S, Roughgarden J. 1985 Larval settlement rate—a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl Acad. Sci. USA* **82**, 3707–3711. (doi:10.1073/pnas.82.11.3707)
 54. MERCINA. 2004 Supply-side ecology and the response of zooplankton to climate-driven changes in North Atlantic Ocean circulation. *Oceanography* **17**, 60–71. (doi:10.5670/oceanog.2004.31)
 55. Lee BS, Bullister JL, Murray JW, Sonnerup RE. 2002 Anthropogenic chlorofluorocarbons in the Black Sea and the Sea of Marmara. *Deep Sea Res. I Oceanogr. Res. Pap.* **49**, 895–913. (doi:10.1016/S0967-0637(02)00005-5)
 56. Matthaus W, Schinke H. 1999 The influence of river runoff on deep water conditions of the Baltic Sea. *Hydrobiologia* **393**, 1–10. (doi:10.1023/a:1003573328473)
 57. Loder JW, Petrie B, Gawarkiewicz G. 1998 The coastal ocean off northeastern North America: a large-scale view. In *The Sea* (eds AR Robinson, KH Brink), pp. 105–133. Hoboken, NJ: John Wiley and Sons.
 58. Aksnes DL, Blindheim J. 1996 Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. *Ophelia* **44**, 7–28. (doi:10.1080/00785326.1995.10429836)
 59. Ling SD *et al.* 2015 Global regime shift dynamics of catastrophic sea urchin overgrazing. *Phil. Trans. R. Soc. B* **370**, 20130269. (doi:10.1098/rstb.2013.0269)
 60. Micheli F. 1999 Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* **285**, 1396–1398. (doi:10.1126/science.285.5432.1396)
 61. Roohi A, Zulfigar Y, Kideys AE, Hwai ATS, Khanari AG, Eker-Develi E. 2008 Impact of a new invasive ctenophore (*Mnemiopsis leidyi*) on the zooplankton community of the Southern Caspian Sea. *Mar. Ecol.* **29**, 421–434. (doi:10.1111/j.1439-0485.2008.00254.x)