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# Resilience of the trophic cascades in the Black Sea and Baltic Sea regime shifts

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## Summary
The Black Sea and the Baltic Sea are two European lake-like marine systems where regime shifts have occurred. Both ecosystems show similar features and hold comparable long-term records for the main food web components and external pressures. Here, we analyse Black Sea and Baltic Sea multi-trophic time series applying the same statistical tool, which allowed us to characterize tipping points and quantify the main dynamics ruling each regime phase. In both systems a trophic cascade, consequence of overfishing, drove a shift between regimes. This work focuses on the robustness of this ecological mechanism. By simulating environmental scenarios we tested whether enhanced bottom-up effects could counteract the development of the trophic cascades once these have been triggered. We found that under certain environmental settings the trophic cascade signals blur at different levels suggesting that the observed changes resulted from a combination of heavy fishing and unfavourable conditions.

## Introduction
The recent history of the Black and the Baltic is a combination of abrupt ecological events, which provide us with the closest thing to what would be a large-scale manipulation experiment. The Black Sea and the Baltic Sea have drawn lately much attention as natural laboratories on which to investigate the mechanisms of regime shifts from a marine perspective. These regimes shifts are among the best investigated in the literature (Oguz & Gilbert 2007; Daskalov et al. 2007; Möllmann et al. 2008, 2009; Casini et al. 2009; Lindegren et al. 2012). Trophic cascades are increasingly revealed as a mechanism driver of regimes shifts also in marine systems. Here, we focus on this particular mechanism which has been documented both in the Black Sea (Daskalov et al. 2007; Oguz 2007) and the Baltic Sea (Österblom et al. 2007; Möllmann et al. 2009; Casini et al. 2009) as the transition period between alternate states.

## Materials and Methods
The dataset covers roughly the last 30-40 years of the previous century, from 1964 to 2001 in the Black Sea and from 1974 to 2007 in the Baltic Sea. The Black Sea database presented here was first compiled and its trophic cascade described by Daskalov et al. (2007). The Baltic Sea database is a joint compilation effort of countries adjoining the Baltic Sea held by the ICES/HELCOM Working Group on Integrated Assessment of the Baltic Sea (WGIAB).

For the statistical analysis we used a modified Generalized Additive Model (GAM) formulation, the threshold GAM (tGAM), which apart from accounting for non linear relationships it is able to detect and incorporate regime dependent effects (Ciannelli et al. 2004). This feature allows for non additive effects of the explanatory variables below and above a certain value of a threshold variable, i.e., the regression structure is allowed to switch between two GAMs.

## Results and Discussion
In the Black Sea, a slight increase of nutrients, given certain climate conditions, could have erased the trophic cascade signal at its lowest level, between autotrophs (phytoplankton) and herbivores (zooplankton). Translating this into the particular Black Sea history means that an earlier onset of the eutrophication event there occurred, exactly at the time of the trophic cascade, would have erased its signal at the level of plankton due to the enhancement of bottom-up effects. This bottom-up effect would not have been able to propagate upwards in the food web. The mechanism that we inferred from the models was that these enhanced nutrient levels crossed an ecosystem threshold opening a window for climate to operate (Llope et al. 2011). The combination of favourable climate and nutrient conditions enhanced autotrophs, releasing them from herbivore control, and consequently decoupling

them from the upper levels.

In the Baltic Sea, a similar experiment suggested that it was also possible to disrupt the trophic cascade signal between secondary (cod) and primary carnivores (sprat) by enhancing bottom-up effects. Here, favourable conditions (high salinity) for herbivores (*Pseudocalanus*) had a direct and positive influence on secondary carnivores (cod) via recruitment. According to our results, low consumption by primary carnivores (sprat and herring) on this copepod given unfavourable conditions for them (low temperatures and high fishing on herring) could suffice for cod eggs and larvae to break out of their larval predator pit. This result agrees with Möllmann and collaborators' (2008) view that climate rather than overfishing was the first cause of the regime shift and indicates that the predator-prey reversal could have been stopped, at least at the time of the trophic cascade progression.

Consideration of regime shifts and resilience in management is timely as we move toward developing ecosystem-based approaches to managing marine systems. Resilience management aims at understanding the underlying mechanisms that must be maintained or enhanced in order to preserve the desired functions of a system. In comparison, the Baltic Sea appears as more likely to positively respond to regime shift management than the Black Sea for a number of reasons: (i) the possibility to act at the level of the *Pseudocalanus*-cod feedback loop, (ii) a simpler food web structure with all trophic levels responding to hydroclimate in contrasting ways and (iii) the absence of a well-established level of gelatinous carnivores.

The potential for management depends on the characteristics of the drivers. In the Baltic Sea inflows of Atlantic water from the North Sea bring higher salinities, while temperature would be more influenced by climate. The state of these two drivers should be considered when adjusting the fishing quotas on herring, sprat and cod. An appropriate management response could be to adopt regime-specific harvest rates, reducing the fishing pressure on cod if conditions are less favourable (as for the current regime) and target clupeids instead in order to enhance the *Pseudocalanus*-cod feedback loop.

In the Black Sea the situation looks more complicated. Climate effects seem to be restricted to the lowest trophic levels, reducing the options of taking advantage of optimal environmental windows as discussed for the Baltic Sea. Additionally, the new level of gelatinous plankton, which now competes with the small pelagics, makes things more difficult. In theory, the reconstruction of the trophic architecture could help build resilience but on the other hand it could have an undesired effect as predation on small pelagics could favour their gelatinous competitors.

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