

Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts

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Large-scale transitions between alternative states in ecosystems are known as regime shifts. Once described as healthy and dominated by various marine predators, the Black Sea ecosystem by the late 20th century had experienced anthropogenic impacts such as heavy fishing, cultural eutrophication, and invasions by alien species. We studied changes related to these “natural experiments” to reveal the mechanisms of regime shifts. Two major shifts were detected, the first related to a depletion of marine predators and the second to an outburst of the alien comb jelly *Mnemiopsis leidyi*; both shifts were triggered by intense fishing resulting in system-wide trophic cascades. The complex nature of ecosystem responses to human activities calls for more elaborate approaches than currently provided by traditional environmental and fisheries management. This implies challenging existing practices and implementing explanatory models of ecosystem interactions that can better reconcile conservation and ecosystem management ideals.

Black Sea | disturbance | foodweb control | invasive species | top predators

Complex marine ecosystems are believed to exist in internally consistent dynamic states, which have been variously dubbed stable states, basins of attraction, or dynamic regimes (1, 2). Switches between alternative regimes are called regime shifts and can be driven by both external forcing (climate change, alien invasions, cultural eutrophication, overfishing) and internal perturbations (1–4). Some shifts are triggered by disproportionately small forces until a critical threshold is passed, and then the system would require substantially stronger driving forces to recover to its initial state, a process referred to as hysteresis (1). Although there are theoretical guidelines on how to detect regime shifts (1, 5), exploring them in real ecosystems is not a trivial task and requires a broad and flexible approach (3, 6).

Trophic cascades have been described as indirect top-down effects on two or more trophic levels (7, 8) that have the potential to drive regime shifts in aquatic systems (3, 9). In the marine environment, trophic cascades are found mostly in coastal and benthic system (10, 11) but are believed to be uncommon in the open ocean (12, 13). Only recently, system-wide trophic cascades have been reported in two large marine ecosystems (14, 15). Predation and fishing are potentially important in changing marine ecosystem structure and functioning (16, 17).

Once described by Aristotle (4th century B.C.) (18) as healthy and dominated by various marine predators, the Black Sea ecosystem had experienced, by the late 20th century, anthropogenic impacts such as heavy fishing, cultural eutrophication, and invasions by alien species. Initially most changes were attributed solely to eutrophication (19, 20). More recently other factors, such as the hydroclimate (21, 22), predation effects, and fishing (14) have been recognized as contributing to the changes.

Here, we analyze long-term changes over several trophic levels in the Black Sea, a large marine ecosystem. We examine regime shift and trophic cascade phenomena and provide an explanation from the perspective of foodweb theory. We provide evidence that excessive fishing can trigger ecosystem-scale re-

gime shifts that result in fisheries collapses and blooms of microalgae and gelatinous plankton.

Results

We studied time series of five groups of pelagic populations across four trophic levels: phytoplankton, zooplankton, gelatinous and fish planktivores, and piscivores (Fig. 1). Data collected in different areas of the Black Sea showed consistent trends [supporting information (SI) Fig. 4].

We applied the automatic sequential method (23) to detect regime shifts in time series indicative of overall changes in the ecosystem. Major shifts were detected by using a cut-off period of 15 years in the early 1970s and early 1990s (Fig. 1 and SI Table 1). They cascade in inverse directions in adjacent trophic levels, implying that trophic cascades are a possible causal mechanism behind the shifts (Fig. 1). A decrease in consumer (top-down) control implies an increase in variance as a response to environmental fluctuations (bottom-up forcing). Therefore, a decrease or an increase in variance is related to strengthening or relinquishing of consumer control, respectively, and may foreshadow regime shifts. Changes in variance were consistent with the regimes detected, but they do not necessarily match exactly the timing of the shifts in the mean (SI Table 1). Minor shifts, possibly attributable to a reverse trophic cascade (recovery), were detected in the mid-1980s and early 2000s by decreasing the cut-off period to 7 years (Fig. 1 and SI Table 1). Correlations between adjacent trophic levels were inverse and significant, whereas correlations between nonadjacent trophic levels (e.g., trophic level 3, jellyfish; and trophic level 1, phytoplankton) were positive (SI Table 2), accounting for direct and indirect consumer effects, respectively, characteristic of trophic cascades (9).

To explore the causality behind the shifts, we plotted consumer (as drivers) against resource (response) into the phase space (Fig. 2). Fig. 3 summarizes the conceptual model explaining the mechanism of the shifts. The plots allow us to observe the coevolution of consumer/resource populations over subsequent regimes. The plots show that changes in consumers are followed by changes in resource, so that they form a quasirectangular nonlinear pattern, which suggests different forward and return paths characterizing hysteretic systems. The angles indicate quasi-table regimes, and sides parallel to the axes indicate regime shifts (Fig. 3B). A decrease or an increase in consumers provoked a reciprocal response in the resources, indicating switches in trophic control at consecutive trophic levels (Fig. 2). Low-resource/high-consumer regimes indicating dominant top-down

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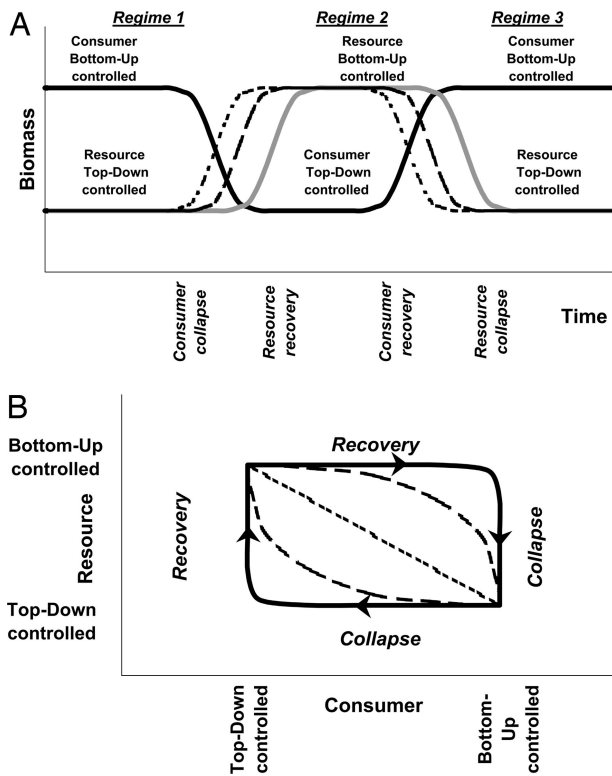


Fig. 3. Sketch of alternating regimes in consumer and resource populations. (A) State space representation: both consumer (solid black line) and resource (gray, broken, and dotted lines depending on the reaction time) can hold alternatively either bottom-up or top-down controlled stable regimes and switch between them; shifts are referred to as collapse and recovery. (B) Phase space representation: the sides of the rectangle represent regime shifts (collapse or recovery). Consumer/resource relationship may follow quasirectangular (solid black line), crescent (broken line), or linear (dotted line) trajectories depending on the delay of the response in resource to the shifts in consumers (simultaneous and slightly delayed response are shown with dotted and broken lines, respectively, in A; see *Conceptual Model* and *Results* for explanation).

2). Later, they were depleted by heavy fishing, releasing the predation pressure on planktivorous fish, which rapidly increased during the periods 1964–70 and 1974–77 (Figs. 1B and 2A). As a response to increased planktivory of the fish consumers, zooplankton crashed after 1973 (Figs. 1D and 2B). Phytoplankton responded to the decline in zooplankton by increasing in biomass sharply after 1973 (Figs. 1E and 2C). There is no pronounced curvature on Fig. 2C around 1973, but clearly the fastest rate of change in both zoo- and phytoplankton was between 1973 and 1975 (Fig. 1D and E). Oxygen concentration at the surface first increased during the period 1962–1970, which corresponds to low phytoplankton and then dropped after 1974 in response to increased oxygen demand attributable to respiration and decomposition of the surplus algal biomass and detritus in the water (Figs. 1F and 2D).

Fig. 2E–H are more complicated because they show both the second major shift of the early 1990s and the less significant reverse shifts of the 1980s and after 2000. The effect of fishing was strongest between 1977 and 1988 and strongly reduced abundance of planktivorous fish (Figs. 1B and 2E). After 1990, fishing effort dropped because of the shortage of fish, and stocks started to recover. The first increase in gelatinous plankton (1977–1980) is linked to the burgeoning abundance of *Aurelia aurita*, which later decreased between 1980 and 1985 (Figs. 1C and 2F). Consumer control was tight and zooplankton biomass

less variable between 1976 and 1989 (Fig. 2F). The second outburst in gelatinous plankton (1989–1994) was caused mainly by the introduction and spread of *M. leidy* (Figs. 1C and 2F). During that period, zooplankton abundance declined even more. After 1996, the gelatinous plankton decreased, and zooplankton recovered after 1998 (Figs. 1D and 2F). After the decrease in zooplankton, phytoplankton again increased over the period 1994–1997 and was followed by a reverse cascade, a recovery in zooplankton and a decrease in algal biomass, between 1998 and 2000 (Figs. 1E and 2G). Oxygen concentration dropped again during the period 1991–1997 but then recovered in response to a fall in algal biomass in 1999 and 2000 (Figs. 1E and 2H). The minor shifts detected by using a cut-off length of 7 years in the mid-1980s and early 2000s can be seen as smaller loops on the phase plots (Fig. 2E–H).

Conceptual Model

According to the hypothesis of Hairston and coworkers (24, 25), foodweb populations are controlled alternatively by consumption (top-down control) or by production and availability of resources (bottom-up control). When applying this theory to Black Sea data, we can define alternative regimes of, respectively, consumer and resource populations (Fig. 3). Populations are top-down controlled when their productivity is low and/or they are heavily exploited by consumers, so the consumption/production ratio [also referred to as ecotrophic efficiency (26)] is high and tends toward 1. As a result, top-down-controlled populations sustain relatively low biomass (resource in regime 1 on Fig. 3A). Populations are bottom-up controlled when they are only lightly exploited and/or productivity is high, in which cases the ecotrophic efficiency is low, and the standing stock biomass is relatively high (consumer in regime 1 on Fig. 3A) (25). In such systems, a switch to an alternative regime is driven by overexploitation of the consumer population (regime 2 on Fig. 3). In most cases, overexploitation (including overfishing) is attributable to a combination of low productivity (poor recruitment and slow somatic growth) and sustained heavy fishing or predation, resulting in a rise in exploitation mortality (approximate ecotrophic efficiency) and ultimately biomass collapse. The return to initial states (regime 3 on Fig. 3) follows a different path (hysteresis, Fig. 3B) and leads to recovery of consumer biomass, which subsequently suppresses the resource biomass at a lower level. The response of the resource population is delayed by some reaction time (that may be related to the resource population generation time). The trajectory in the phase space (Figs. 2 and 3B) is pronouncedly nonlinear (rectangular) when the change in the resource (response variable) follows the change in the consumer (driver variable). Alternatively, the resource population may respond simultaneously or with minor delay, which would result in a linear or crescent pattern of the phase space trajectory, respectively (Fig. 3).

Discussion

The major shifts in the Black Sea during the 1970s and 1990s were associated with important perturbations of the upper levels of the pelagic foodweb. The first event was related to depletion of top predators, which provoked a system-wide trophic cascade involving four trophic levels, nutrients, and oxygen in the surface water (Fig. 1). The second event was associated with a great reduction of planktivorous fish and an outburst of the alien *M. leidy*, which resulted in a second system-wide trophic cascade, with similar alternating effects on zoo- and phytoplankton, and water chemistry. We therefore interpret the patterns we observed as a “replicated natural experiment,” provided that the second event did indeed verify the initial trophic cascade hypothesis. Minor reverse shifts (recovery) during the mid-1980s and after 2000 also confirm the suggested mechanism.

The system-wide regime shifts in the Black Sea can be explained by foodweb theory. In a foodweb, top-down (consumer) and bottom-up (resource) controls compete for dominance at each trophic link. Top predators experience only resource limitation, but they regulate the abundance of their prey and, at each successively lower trophic level, populations are alternately either regulated in a dominantly bottom-up (underexploited) or top-down (overexploited) way (14, 24, 25). Therefore, the impact of top predators cascades down the trophic pyramid, generating an alternating trophic control (ATC) pattern and ultimately regulating primary production (8, 24).

When the top predators were eliminated, the Black Sea system switched from a configuration with four trophic levels to one with three levels, namely high zooplanktivore (top level), low zooplankton, and high phytoplankton. The shift in the 1990s was not a switch in control dominance, but rather the dominant top-down control on zooplankton being switched from fish-dominated (selective feeding) to ctenophore-dominated (unselective feeding; *M. leidyi*), leading to an even stronger trophic cascade. The removal of the top level in an ATC-structured web may result in several possible indirect effects. The first and most obvious is a straight trophic cascade that produces inverse changes in abundance down the trophic pyramid. The new dominant groups proliferate because of weakened consumer control and compensatory growth (27). They are also impacted by the increase in basal productivity through bottom-up control, e.g., through eutrophication. Bottom-up forcing, however, seems to act only within the framework of an established ATC structure, whereas structural transformations should rather be attributed to top-down effects (14). In a modeling experiment (14) with both predation and eutrophication, eutrophication forcing has increased the amplitude of the trends without changing their direction, which has been controlled by predation. Similar interpretation arises from patterns in data (Fig. 1): in 1980, when riverine nutrient enrichment was at a maximum (21), biomass peaked mainly in bottom-up-controlled groups (phytoplankton, planktivorous fish, and jellyfish), whereas top-down-controlled groups [zooplankton, oxygen, and surface phosphate (14)] were generally suppressed (note, however, an isolated increase in zooplankton in 1980–1981, Fig. 1 and SI Fig. 4). Further increase in phytoplankton in 1990s was probably top-down driven (by the drop in zooplankton resulting from proliferation of *M. leidyi*), because nutrient input decreased over that period (21). The strong correlation between nonadjacent bottom-up controlled trophic levels, e.g., phytoplankton and gelatinous plankton ($r = 0.7$ SI Table 2, Fig. 1), exemplifies possible synchrony of trophodynamic effects. Rearrangement of the ATC structure may have another effect related to a decrease in the efficiency of trophic transfer. In a three-level system, the base level (phytoplankton) is only weakly controlled by grazing and can still force the system from below through burgeoning algal and detrital production (a consequence of underexploitation by grazers). Therefore, a reduction from a four- to a three-level system may create conditions for autocatalyst bottom-up forcing, which will not contribute to increased productivity of zooplankton and fish, but will rather be channeled into the microbial/jellyfish loop. Such a development suggests changes in the ecosystem functions, such as productivity, consumption, production of detritus, and nutrient regeneration, leading to plankton blooms, turbidity, and marine snow, hypoxia, and circulation changes (19, 20, 28). Shifts in oxygen content (Fig. 1F) are only a small part of the functional changes. They are directly related to the extent of bottom hypoxia and hydrogen sulfide production (21).

Two of the criteria defining a regime shift are the formation of distinct stable states and hysteresis or a return to the previous state through a different path (1, 3, 5). In this study the existence of sustained alternative states and the timing of switches between them are identified by an objective statistical analysis (23) (Fig.

1, SI Table 1). The cause of establishing and sustaining persistent new regimes is recognized to be the shift in trophic control (ATC) and a trophic cascade after disturbance of the upper trophic levels. Tendencies of a return to a previous state are found by examination of reverse cascades that occurred in the mid-1980s and 2000s. The first reversal was detected as a decrease of gelatinous plankton (*A. aurita*) and phytoplankton, and an increase in oxygen (Fig. 1). It also corresponded to a drop in fish biomass, an increase in fishing mortality (Fig. 1B), and changes in variance (although not significant) of top predators (SI Table 1). Hysteresis loops are most clear at the basal levels, where the oxygen increased between 1983 and 1987 as a response to the decrease in phytoplankton in the years 1980–1983 (Figs. 1F and 2H), and in the phase plot of zooplankton against phytoplankton (Fig. 2G). The recovery did not continue long, and in the 1990s, the gelatinous biomass dominated by *M. leidyi* burgeoned, leading to a further decrease in zooplankton and planktivorous fish. The second recovery was related to an increase in planktivorous fish and a decrease in *M. leidyi* by the late 1990s, leading to a subsequent increase/decrease/increase in zooplankton/phytoplankton/oxygen (Figs. 1 and 2 and SI Table 1) and showed evidence of hysteresis at all levels from fish to oxygen (Fig. 2E–H). This corresponded to a general (although limited) improvement of the environmental quality (29).

Regime shifts are often explained by structural/functional transformations, including positive and negative feedbacks, and interactions between fast and slow processes (1, 2, 5). Overfishing and collapses happen when declining stocks (a fast process) are confronted with conservative (overcapacity, a slow process) or growing fishing effort (e.g., through greater efficiency/technology) because of the inability of fishery management to forecast and to adapt quickly to changes in fish stocks (30). When overfishing only is implicated, regime shifts can be explained by increased catchability or depensation in stock productivity at low stock levels, leading to greater mortality and further biomass reduction [positive feedback (30, 31)]. Similar effects may arise between predators and prey (9, 32).

The triggering factor in both shifts in the Black Sea ecosystem appears to be overfishing and stock collapse of pelagic predators before 1970 and of planktivorous fish in 1990. Consequently, fisheries for pelagic predatory fish vanished in most of the Black Sea, and one species, mackerel *Scomber scomber*, disappeared from the Black Sea (14). In the 1990s, anchovy, sprat, and horse mackerel catches dropped by a factor of six (33), causing estimated losses of \$16.8 million from the anchovy fisheries alone (34). The first event resulted in a classical trophic cascade, ultimately affecting primary production and water chemistry, whereas the second took place at the same time as the invasive *M. leidyi* was entering the system. *M. leidyi* has been recorded in the Black Sea since 1982 (35), but its population expanded in 1990 when decreased zooplanktivory by overfished stocks created a favorable trophic condition of surplus zooplankton productivity to be used by the burgeoning *M. leidyi* population (36). The ctenophores are particularly efficient consumers when food density is high (37). Therefore, the *M. leidyi* bloom seems to have been triggered by a fish stock collapse, and, indeed, such a scenario is confirmed by the timing of the shifts in fish and *M. leidyi* (Fig. 1, SI Table 1). The fast development of *M. leidyi* in subsequent years led to a massive decline in zooplankton biomass, strong competition for food, and a further decrease in fish stocks (36). The newly introduced predatory ctenophore *Beroe ovata* was hypothesized to contribute to the regulation of *M. leidyi* and to lead to a recovery of fish stocks (29). However, sprat and anchovy stocks started to recover after the decrease in fishing pressure, when *M. leidyi* were still abundant (Fig. 1). Another type of interaction is suggested as an explanation of the quasisynchronous increase in planktivorous fish and jellyfish *A. aurita* in the 1980s (14). The growing fish population selectively

reduced large zooplankton, leading to a compensatory increase of small zooplankton and creating favorable trophic conditions for *A. aurita* (14). Consequently, both large and small zooplankton decreased under the combined predation of fish and jellyfish, creating conditions for competition between planktivores [negative feedback, e.g., reverse cycles of sprat and *A. aurita* (SI Fig. 4)] (21). Our analyses indicate that, although the major effects on zooplankton could be related to predation by gelatinous plankton, changes in zooplanktivory in both cases were initiated by changes in abundance of zooplanktivorous fish. Other interactions could be linked to the cascade's increase in phytoplankton and its fate as detritus, which, together with the detritus from dead gelatinous plankton, feeds back to both zooplankton and jellyfish. The increased algal blooms and organic matter could have reduced visibility and negatively impacted the ability of visual predators to find food (38). Indeed, since the 1980s, the migration routes of bonito have changed, and they seem to avoid the turbid northwestern shelf waters of the Black Sea (33).

The quasidecadal temporal pattern of regime shifts in the Black Sea suggests that hydroclimate may have also been involved in their generation (21, 22), but the complexity of subsystems, linkages, and possible mechanisms implies that its influence would, rather, be modulated by the existing system of trophic controls and interactions.

An important question remaining is whether regime shifts are reversible and whether it is possible for the system to recover to its previous state. Although top predators have not recovered, the 1980s fisheries partially "replaced" them by exploiting planktivorous fish, finally driving the stocks to virtual collapse (Fig. 1 *A* and *B*) (36). Instead of recovery to the previous state of high zooplankton and low phytoplankton, this led to an outburst of *M. leidy*, which further strengthened the cascade through zoo- and phytoplankton. In the new conditions, a return to the previous state (i.e., the 1960s) was not an optimal configuration. In the 2000s, the *M. leidy* population stabilized, planktivorous fish partially recovered, and *Beroe ovata* (a predator of *M. leidy*) entered the pelagic foodweb. Our conclusion is, therefore, that when the structure changes, complex systems are unlikely to recover to their exact previous state but will, rather, adapt to the immediate local conditions. The recent recovery and the minor reverse cascade of the mid 1980s (Fig. 1 and SI Table 1), however, suggest some potential for recovery, perhaps if a four-level trophic structure is restored. Further elucidation of this problem needs better understanding of population dynamics and the foodweb effects of top predators.

The recent improvement appears to be due to a combination of warming hydroclimate, decrease of nutrient load, recovery of planktivorous fish, and predation of *M. leidy* by *B. ovata*. The system has been stressed, however, simultaneously by various factors: heavy fishing on several species, nutrient discharge, and invasive species. Any attempt to recover the system to a more desirable and resilient state would necessarily need a deliberate consideration of the main anthropogenic impacts, but, even in such a case, recovery through new system configurations will require management to adapt consistently.

Recognizing that fishing and other anthropogenic activities affect not only some ecosystem components (e.g., fish stocks) but can be responsible for large-scale ecosystem perturbation is essential for modern ecological understanding, and it could have profound implications for management. Fisheries and pollution are subject to management control that must target a recovery of damaged ecosystems into healthy and resilient states. Partial recovery of only some components (e.g., the fishery-targeted fish stocks) is not a stable objective, and further change in another component (e.g., unfavorable climate or alien species) may drive the system into the next catastrophic loop. Recovery of a resilient ecosystem should mean restoring all important components into the new desirable state (39): reducing the anthropogenic impact, increasing biodiversity, normalizing species interactions (e.g., optimizing trophic efficiency), buffering trophic cascades, and improving environmental quality. Large marine ecosystems such as the Black Sea are strongly interconnected, and fisheries management should account for this multitude of linkages and mechanisms (33) behind system dynamics if it wishes to conserve ecosystem integrity, function, and diversity and to assure sustainable use of the nature resources. Conventional fisheries science is often insufficient to predict complex issues such as ecosystem regime shifts and recovery. The future science and management should extend the scope of possible hypotheses by challenging the existing paradigms and adding new knowledge of the phenomena being observed.

Materials and Methods

Time series of fish stocks and plankton, representative for the whole Black Sea, were compiled based on data from long-term monitoring (SI Text).

The automatic sequential algorithm (23) was used to detect regime shifts. The method detects regime shifts by accounting for statistically significant differences between the means and variances in subsequent segments in time series. Parameters that need to be defined by the users are target significance level and cut-off length of the segments to be tested (similar to the cut-off window in filtering). Standard statistical *t* and *F* tests are applied to test means and variances, respectively. Cut-off lengths of 15 and 7 years were used to detect shifts of different time scales based on previous evidence of long-term periodicity in Black Sea time series (21). The algorithm is equipped with various techniques that can account for serial correlation and the influence of outliers. More details of the methods are provided in SI Text and online at www.beringclimate.noaa.gov.

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