



Review

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A holistic view of marine regime shifts

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Understanding marine regime shifts is important not only for ecology but also for developing marine management that assures the provision of ecosystem services to humanity. While regime shift theory is well developed, there is still no common understanding on drivers, mechanisms and characteristic of abrupt changes in real marine ecosystems. Based on contributions to the present theme issue, we highlight some general issues that need to be overcome for developing a more comprehensive understanding of marine ecosystem regime shifts. We find a great divide between benthic reef and pelagic ocean systems in how regime shift theory is linked to observed abrupt changes. Furthermore, we suggest that the long-lasting discussion on the prevalence of top-down trophic or bottom-up physical drivers in inducing regime shifts may be overcome by taking into consideration the synergistic interactions of multiple stressors, and the special characteristics of different ecosystem types. We present a framework for the holistic investigation of marine regime shifts that considers multiple exogenous drivers that interact with endogenous mechanisms to cause abrupt, catastrophic change. This framework takes into account the time-delayed synergies of these stressors, which erode the resilience of the ecosystem and eventually enable the crossing of ecological thresholds. Finally, considering that increased pressures in the marine environment are predicted by the current climate change assessments, in order to avoid major losses of ecosystem services, we suggest that marine management approaches should incorporate knowledge on environmental thresholds and develop tools that consider regime shift dynamics and characteristics. This grand challenge can only be achieved through a holistic view of marine ecosystem dynamics as evidenced by this theme issue.

1. Introduction

Ecosystems are exposed to both gradual and sudden changes in climate, nutrient loading, habitat fragmentation or biotic exploitation. The ecosystem

Box 1. Definitions

Ecological regime shift—Dramatic, abrupt changes in the community structure, encompassing multiple variables, and including key structural species (*definition from this Theme Issue*) (figure 1). Note that the term *regime shift* is synonymous with *phase shift*, the former being used prevalently in open ocean systems, the latter in spatially fixed systems such as reefs. Also termed *state shifts* or *ecosystem reorganizations*. Regime shifts that involve the crossing of a tipping point and pertain to systems with alternative states are also called *critical transitions*.

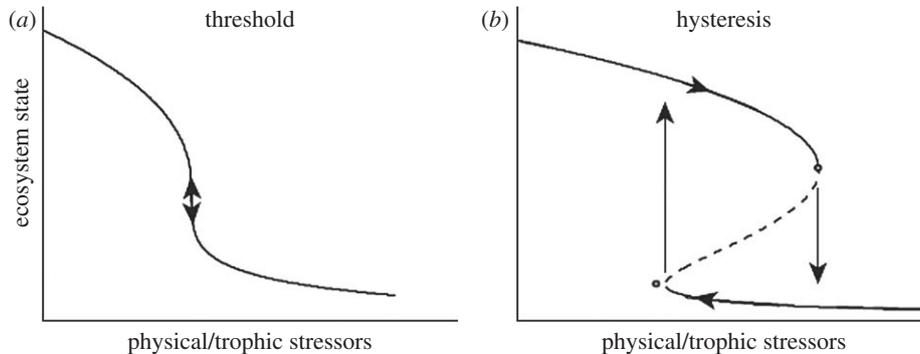


Figure 1. Examples of regime shift. Two different responses are shown, one without (a), and the other with hysteresis (b), both of which are encompassed by our working definition of regime shifts (adapted from [5]).

Attractor—The dynamic regime to which a system converges under constant environmental condition.

Alternative stable states—The different attractors to which a system may converge. Also known as *alternative dynamic regimes* or *alternative attractors*. The size of the basin of attraction in ecosystems with alternative stable states is often referred to as ‘ecological resilience’ [6].

Critical threshold—The point at which the qualitative behaviour of a system changes. It is usually associated with the shift between two alternative dynamic regimes. Also known as *tipping point* or *bifurcation* [7].

Regime shifts characteristics—*Smooth* regime shifts are represented by a quasi-linear relationship between the response and control variables. *Abrupt* regime shifts exhibit a strong but continuous nonlinear relationship between the response and control variables. *Discontinuous* regime shifts are characterized by different trajectories of the response variable when the forcing variable increases versus when it decreases (i.e. occurrence of hysteresis) [8].

Hysteresis—In a discontinuous regime shift, the phenomenon for which the return path from altered to original state can be drastically different from that leading to the altered state (figure 1b). The critical threshold that triggers the shift from regime A to B differs from the threshold at which the system shifts from regime B to A [7].

Feedbacks—feedbacks can stabilise or destabilise ecosystem states. *Negative* (‘dampening’ or ‘stabilizing’) feedbacks mechanisms contribute to maintain ecosystem state (until perturbations are large enough). *Positive* (‘amplifying’ or ‘destabilizing’) feedbacks are necessary to move the ecosystem to an alternate state [1,8,9].

Resilience—The capacity of a system to absorb disturbance and reorganize while undergoing change, so as to still retain essentially the same functions, structure, identity and feedbacks [10].

response to these changes is usually assumed to be smooth and predictable. However, studies in terrestrial ecosystems, lakes, coral reefs and the oceans have shown sudden and unexpected shifts to contrasting and lasting states [1]. This form of variability has been given various terms such as ‘ecological regime shifts’, ‘phase shifts’, ‘state shifts’, ‘ecosystem reorganizations’ or ‘catastrophic transitions’.

As a single definition is still not entirely agreed upon by the scientific community [2], as we have already seen in the Introduction [3] and in the papers of this theme issue, we propose a broad working definition of regime shift that is based on empirical evidence rather than on the theory of catastrophic transitions. We define *ECOLOGICAL REGIME SHIFTS* as dramatic, abrupt changes in the community structure that are persistent in time, encompass multiple variables, and include key structural species—independently of the mechanisms causing them, and whether or not they can

be associated with basins of attraction. We suggest this observation-based definition as it is practical for marine management purposes and can be used for both benthic and pelagic regime shifts, even where the link with the mathematical theory is not yet fully established.

The mathematical theory behind regime shifts (or catastrophic transitions) postulates the existence of alternative stable states, or alternative attractors, and the presence of critical thresholds (or catastrophic bifurcations) that mark the sudden passage from one stable state to another [4]. Regime shifts involve substantial changes in the structure and dynamics of a marine ecosystem and can be smooth or abrupt, and even discontinuous when hysteresis is involved [4]. Some of the characteristics and definitions related to regime shifts are summarized in box 1.

During the last few decades, regime shifts have been identified around the world, in most basins where

multi-decadal time series exist (e.g. [11–19]). Regime shifts have drawn much attention from both empirical and theoretical ecologists, as a complete understanding of the nonlinear dynamics behind these dramatic changes may reveal yet unknown ecological laws on single-species dynamics or inter-species relationships within an ecosystem. More importantly, ecological regime shifts can have dramatic consequences on economies and societies [1,20–23], as in many cases they correspond to the collapse of an ecosystem and the loss of the services that the ecosystem provides. Knowledge on the drivers and mechanisms behind regime shifts is hence of fundamental importance for managers as well as policy makers.

However, despite prominent publications, special issues and reviews that have tried to clarify the theory on abrupt transitions [1,2,4,7,24–28], there is still considerable scientific debate and the marine community is largely divided into ‘believers’ and ‘sceptics’ [24] of the regime shift concept. There is especially no consensus on the dominance of top-down trophic versus bottom-up physical controls in inducing regime shifts as shown by the overfishing versus climate change debate (see review by Pershing *et al.* [29]). Further debate also commonly arises about the existence of alternative stable states or whether abrupt shifts in marine population are simply stochastic noise [30,31]. Overall, a general holistic view on marine regime shifts is clearly lacking.

In this new era of the Anthropocene [32], where human actions shape the biosphere not only locally but also globally [33], global social and ecological interconnections can propagate and cascade across countries and regions [34–36], shaping marine ecosystems and their resilience worldwide. The imprints on marine ecosystem dynamics of this global human enterprise are reflected in climate effects (e.g. temperature change, ocean acidification and altered ocean circulation), marine pollution (e.g. chemicals and nutrients) and worldwide fishing (coastal, offshore and deep sea), all influencing productivity, species, functional groups, food web interactions, habitats and resilience. Humans shape marine ecosystem dynamics through actions that may cause changes in ecosystem states or alter resilience, making ecosystems susceptible to regime shifts triggered by environmental forcing and disturbance events.

Because of the importance that regime shift science holds for both ecology and economy, the theme issue *Marine regime shifts around the globe: theory, drivers and impacts* in the *Philosophical Transactions of the Royal Society* has addressed theoretical ecology and management of marine regime shifts. The scope of this paper is to highlight the lessons learnt from the contributions to this theme issue and to synthesize them into a more holistic view on marine ecosystem regime shifts.

2. Lessons learnt from the theme issue

(a) Linking observed regime shifts to theory: a benthic–pelagic divide

Linking abrupt shifts in real ecosystems to critical transition theory is complex. Exploring regime shift characteristics such as nonlinear interactions of drivers, alternative stable states, feedbacks and hysteresis can be achieved most convincingly through experimentation or modelling [24,37]. This is facilitated on reefs where local species move slowly relatively to the investigators’ sampling frequency, which allows

reliable fixed-grid sampling of the same populations, as well as manipulation. Furthermore, on reefs different regimes may exist next to each other over small spatial scales, facilitating the exploration of regime characteristics. Hence most of the progress in mapping observed marine shifts to theory has been recently made in benthic temperate and tropical reef systems. Examples are provided by the benthic contributions to this issue: basins of attraction are often clearly defined and readily observable; for example, see the coral–algal attractors in tropical coral reefs [38,39] and the macroalgal–sea urchin barren attractors in temperate kelp beds [40]. Another example of progress in making the field–theory connection is given by Ling *et al.* [40], who provide compelling empirical evidence for hysteresis via a circumglobal (13 systems in six continents) comparison of critical transitions in temperate rocky reef ecosystems.

Open ocean pelagic ecosystems create greater challenges for testing regime shift theory. Most of these ecosystems are not amenable to experimentation, mainly due to logistical and financial constraints. Contrary to benthic systems, no fixed or enclosed habitats exist that serve as natural borders or spatial delineations of these systems, and the concept of space confluences with water mass. Shifts in ecosystem structure are difficult to observe in moving water masses as the typical Eulerian (fixed transect/area) sampling protocol fails to repeatedly sample the same populations. Furthermore, this sampling protocol often fails to identify distributional changes in the open ocean, as the geographical sampling resolution can be much smaller than the biogeographical distribution of the populations. Typically, regime shifts in the pelagic realm are empirically inferred through abrupt changes in single species or matrices of abiotic and biotic time series [11,13,41–45]. Yet, such shifts, rather than corresponding to actual abrupt changes in the population densities, may instead correspond to biogeographical range shifts, where the populations sampled at a certain location and time have subsequently moved elsewhere. Typical examples are the northward shifts in multiple planktonic species in the North Sea and in the eastern North Atlantic, attributed to temperature increase [45,46], or the pelagic shifts in the western North Atlantic, attributed to climate-modified transport [44,47]. Thus, the potential for confounding variations in space with variations in time is higher in oceanic pelagic systems than benthic ones, and hence renders an analysis in relation to regime shift theory difficult.

Because experimentation is impossible, identifying basins of attraction in open pelagic ecosystems relies primarily on the analysis of (generally Eulerian) time series. Some indications have been drawn from observed temporal patterns: a prominent example is the collapse of cod (*Gadus morhua*) populations and the hysteresis in their recovery, potentially caused by predation feedbacks on the survival of cod early-life stages [48–51]. An advancement of the field is provided by Gårdmark *et al.* [52] in this issue. By applying new approaches for the identification of alternative stable states, based on a theory of size-structured community dynamics, they show evidence for alternative stable states in pelagic food webs when the shifts are caused by trophic drivers. Furthermore, they identify some of the underlying predator–prey interactions that act as feedback mechanisms in preventing a return to the previous state.

Nevertheless, whether a regime shift is associated with true alternative states remains a challenge for pelagic marine systems. Indeed, regime shifts can occur without

alternative stable states. For example, in this issue, Beaugrand [53] shows that planktonic systems can be explained just by the interaction of temperature with the ecological niche of the ecosystem's key species, and a small change can trigger a shift if these are near their thermal range limit. Furthermore, other studies negate the necessity of a forcing agent and explain planktonic shifts simply as stochastic noise resulting from the biological integration of the external physical variability [30,31].

A way to improve the mapping of observations to theory in real ecosystems that are unamenable to experimentation is to conduct multi-ecosystem comparisons [54]. This issue provides several examples on how this approach can be used to extract general principles of regime shifts. For example, the comparison of several systems has facilitated identifying a coherent and global pattern of hysteresis between algal and barren attractors in temperate reefs [40], multiple attractors in coral reefs [39], multiple drivers that vary spatially within open marine basins [55], co-occurrence of drivers in most marine regime shifts [56] and a quasi-synchronous period of regime shifts in the late 1980s in the Northern Hemisphere related to temperature and the Arctic circulation [57].

(b) Overcoming the top-down versus bottom-up debate: the importance of ecosystem type

A major debate in ecological research is whether marine regime shifts are due to top-down (predator) or bottom-up (prey and environment) control [29]. We consider that this bottom-up/top-down distinction, although widely used, may not be entirely correct for the marine environment. In fact, bottom-up processes impacting primary production typically include climate-related variables, such as temperature and other physical factors, which, in this environment, are likely to affect simultaneously several trophic levels in the food chain [58]. Hence, these drivers are not operating in a strictly 'bottom-up' manner (note that most marine organisms have at least a planktonic stage, and thus are equally vulnerable to, for example, temperature or ocean circulation changes). Hence, a better distinction with regards to identifying regime shift drivers would be between 'trophic/biological' and 'physical/environmental' stressors or drivers. Physical/environmental stressors include temperature changes (e.g. due to the ongoing global warming), which affect marine biogeography and species ecological niches, from offshore pelagic species to inshore benthic species [59–63], as well as atmospheric oscillations, and resulting ocean circulation alterations, which impact the hydrographic properties of the water masses, water transport, and the distribution of associated holoplanktonic and meroplanktonic species [18,44,64–70]. *Trophic/biological stressors*, on the other hand, correspond to the effects of predator–prey or species-specific competitive interactions on some level of the food web. They can be related to direct anthropogenic impact on a system, e.g. overfishing and associated top predator species removal/reduction, introduction of alien, invasive species, species responses to nutrient enrichment and related eutrophication, or acidification and associated reduced biological calcification [11,43,51,71–73].

While the dominance of physical or trophic control is still hotly debated in the pelagic domain [29], this discussion may be antiquated, as a multitude of studies from a diversity of habitats now show that both controls usually exist in

parallel, and their dominance is strongly context dependent [66,74–78]. Furthermore, there may as well be fundamental differences in the susceptibility of marine ecosystem types to external drivers, as suggested in the *driver versus spatial-constraint* hypothesis by Pershing *et al.* [29] in this issue, here renamed as *stressor versus ecosystem-type* hypothesis. Spatially (or mobility) restricted ecosystems (e.g. reefs), as well as semi-enclosed basins (e.g. the Baltic and Black Seas), are often more susceptible to top-down trophic cascades, while open shelf or open ocean ecosystems are more susceptible to physical drivers, such as temperature. In spatially restricted (or low mobility) ecosystems, individuals in fact cannot escape or relocate to neighbouring areas, hence trophic predator–prey interactions with associated cascading effects can have a prevailing role [29,38,40,43,79–81]. By contrast, in more open, pelagic ecosystems, where species can unrestrictedly move or can be transported by altered ocean circulation far from the regular sampling area, predator–prey interactions are likely to be weaker due to limited predator–prey overlaps, and physical stressors such as temperature or climate-induced circulation changes are likely to be the main drivers of observed ecosystem changes [29,53,57,65,82,83].

(c) Multiple drivers and their interaction

Traditionally, many studies try to associate observed marine regime shifts to a single driver, which is in part due to the difficulty of finding data on all potential stressors. However, increasingly, studies on regime shifts are embracing the concept of multiple drivers likely (but not exclusively) contributing to abrupt change [84–88], and several papers in this issue attest to this [29,38–40,55–57]. In addition, an important concept to consider is 'time-delayed' synergies, i.e. some stressors may operate by reducing the resilience [10] of a system, well before a regime shift actually occurs, hence they may 'pre-condition' the ecosystems towards a shift, while others more directly push it to cross a threshold (e.g. [1,24]). Using examples from this issue, in some temperate reefs modified ocean circulation has allowed supply and development of urchin larvae to kelp beds where, in the absence of effective predators (because of overfishing), urchin populations have subsequently exceeded critical thresholds of overgrazing, leading to an alternative and unproductive barren state [40,66,89]. Similarly, Caribbean coral reefs have switched from coral to macroalgal attractors after epizootics decimated key coral species and a dominant herbivore and made the reefs then susceptible to other stressors such as temperature or hurricanes [38,90]. Also in the pelagic realm, multiple stressors are able to reduce the resilience of a system way before a regime shift occurs. For example, the climate-modified circulation in the Baltic Sea has paved the way to an overfishing-induced regime shift [49], and overfishing in the Black Sea, in combination with climate-modified circulation, has allowed a ctenophore-invasion induced regime shift [43,91].

Hence, measuring resilience in real ecosystems, or how stressors modulate it [2], has become a priority topic for research. For instance, the same stressor may trigger a regime shift in a system with low resilience, and apparently not affect a system with higher resilience [19,40], or may have multiple impacts on the same system: for example Bozec and Mumby's model [38] shows that temperature can have an acute episodic impact in moving a coral reef closer to an unstable equilibrium, while also having a synergistic chronic impact by moving the location

of the unstable equilibrium to increase the size of the undesirable macroalgal basin of attraction.

Ways towards measuring resilience have been developed according to dynamical system theory [92]. Thereby indirect (e.g. indicators of critical slowing down) and direct estimates of ecosystem resilience (measured recovery times after a disturbance) can be used [92]. While direct estimates of return times can be obtained from temporal observation data of interacting species [93], these are only applicable to small-scale systems with few species. The benefit of direct estimates is that covariates determining recovery rates (i.e. drivers of ecosystem resilience) can be identified. Moreover, such analyses of abundance data of interacting species can also show shifts in trophic control, which is a proximate mechanism affecting resilience that has been shown to be associated with ecosystem restructuring in several marine ecosystems in the Northern Hemisphere (see Fisher *et al.* [55] for a review; but see Pershing *et al.* [29]).

(d) Challenges for marine management

The contributions on the challenge of managing regime shifts in this issue clearly illustrate that ecosystem dynamics and regime shifts are not just biophysical phenomena but that humans are strongly involved. As human pressures on the marine environment are expected to increase [94], it is likely that regime shifts will become more frequent. Regime shifts potentially carry important losses of ecosystem services: hence they should be integrated into management.

While the scientific community has made great strides in understanding the causes and mechanisms of regime shifts, there is still a scarcity of strategies and practical tools for managers to anticipate and respond to ecosystem shifts. A strategy for sectorial fisheries management would not focus on directly integrating regime shifts into traditional fish stock assessments or in estimating biological reference points, but would rather use them as supporting information to management advice, and Management Strategy Evaluation approaches would be needed for testing tactical models based on knowledge of regime shifts and states [95]. In a cross-sectorial scheme, the recently developed concept of Integrated Ecosystem Assessments (IEA [96–98]) has great potential to incorporate regime shifts into an ecosystem-based management approach.

In terms of tools, indicators of resilience [92] are useful for achieving specific management goals [98]. Quantifying resilience can help guide management focused on the recovery of desired ecosystem states from degraded ones and can help avoiding regime shifts in the first place. In Europe, the European Community Marine Strategy Framework (http://ec.europa.eu/environment/marine/eu-coast-and-marine-policy/marine-strategy-framework-directive/index_en.htm), which focuses on identifying Good Environmental Status indicators, may provide a good arena and testing ground for the development of this new field.

Eventually, information and knowledge on environmental thresholds is a further critical component to management success [99]. Management consideration of environmental thresholds appears to be scale-dependent and is more effective at smaller scales. Hence, a spatially nested approach, i.e. a common large-scale framework with nested spatial authorities, may provide an optimal balance between the large scale of marine ecosystems and the small scale of effective governance [99]. The worldwide scale of global fishing activities, with its potential role in driving

marine regime shifts [100], presents a relevant case study for such a spatially nested management approach.

3. Conclusion

The papers of the present theme issue highlight some general issues that need to be overcome when developing a holistic view on marine ecosystem regime shifts. First, there is a great divide in how regime shift theory is linked to abrupt changes in real ecosystems. Benthic reef systems are generally better understood in terms of theory than pelagic ocean systems, which is mainly due to the open nature and sampling limitations of the latter. Second, the prevalence of top-down trophic versus bottom-up physical drivers in inducing regime shifts may be considered a false dichotomy, and progress can be made on this long-lasting discussion by embracing a holistic view in which time-delayed synergies, multiple stressors and the special characteristics of different ecosystem types are incorporated (figure 2). Generally, there exists a gradient between stationary reef systems over semi-enclosed basins to open pelagic systems in how they respond to different stressors. The low mobility of species in reefs or in geographically constrained systems allows the predominance of biological stressors, while geographically unconstrained (high mobility) pelagic open systems are less prone to it (figure 2a). Both overcoming the benthic–pelagic divide and getting a better understanding of the relative importance of different stressors call for multi-ecosystem comparison studies.

Furthermore, a holistic view on marine regime shifts calls for a framework for their investigation based on the theory of critical transitions (figure 2b). Here, multiple exogenous (external) drivers interact with endogenous (internal) mechanisms to cause abrupt, catastrophic change [4]. In this framework, *endogenous* (internal) food web dynamics correspond to the direct or indirect effects of predator–prey interactions between trophic levels, or competitive interactions within a trophic level, and *exogenous* (external) stressors correspond to the environmental stressors impacting on the food web. The overall dynamics of the food web, and its susceptibility to abrupt shifts, then depends on endogenous trophic interactions impacted by multiple interacting exogenous stressors. These interactions are often time-delayed, with some stressors eroding the resilience of the ecosystem long before a regime shift is manifest. Following such a holistic framework will be in many cases hampered by data availability, but we assume that in the future more integrated data networks will facilitate also more integrated studies. We strongly believe that the joint analysis of multiple exogenous stressors on the internal dynamics and resilience of marine systems will provide ways for a more complete interpretation on how regime shifts function.

Marine regime shifts present major challenges for ecosystem management: managers confront a world of increasingly prevalent human pressures [94], one in which it is likely that the frequency of regime shifts may increase, with potentially large socio-economical impacts. It is therefore crucial that managers and planners incorporate knowledge on regime shifts into their activities. Eventually, marine management approaches and tools need to be developed accounting for regime shift dynamics and characteristics in order to avoid major losses in ecosystem services. This grand challenge can only be achieved by a holistic view on marine ecosystem dynamics as evidenced by this theme issue.

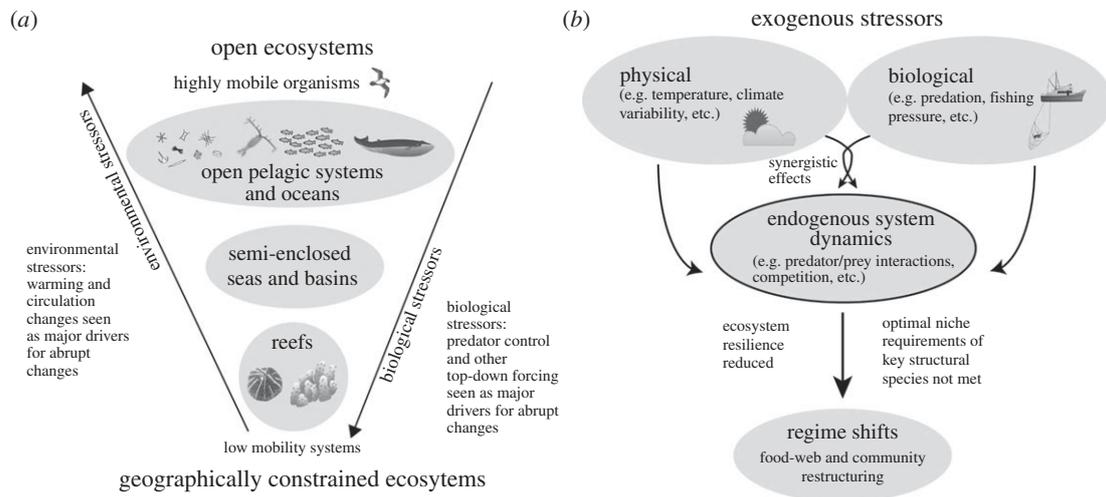


Figure 2. A holistic view of marine regime shifts. (a) Difference in the susceptibility of marine ecosystem types to external stressors (*stressor versus ecosystem-type hypothesis*): trophic top-down control diminishes from low mobility, spatially constrained benthic reef systems, over semi-enclosed pelagic systems, to pelagic open shelf and ocean systems dominated by wide ranging planktonic and fish species. Physical/environmental control is important for all habitats, however its relative importance increases along the same gradient, because trophic control becomes less strong. (b) A generalizable framework for investigating regime shifts: multiple exogenous (external) stressors impact the endogenous (internal) mechanisms of the food web. The exogenous stressors can be physical/environmental, affecting the habitat of the species, or biological/trophic, affecting specific trophic levels, which can result in trophic cascading. The synergies among stressors can happen over time, with some stressor(s) modifying species habitat and reducing the ecosystem resilience (paving the way) long before other stressor(s) trigger a regime shift.

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