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Opinion

Emergent Properties Delineate Marine Ecosystem Perturbation and Recovery

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Whether there are common and emergent patterns from marine ecosystems remains an important question because marine ecosystems provide billions of dollars of ecosystem services to the global community, but face many perturbations with significant consequences. Here, we develop cumulative trophic patterns for marine ecosystems, featuring sigmoidal cumulative biomass (cumB)–trophic level (TL) and 'hockey-stick' production (cumP)–cumB curves. The patterns have a trophodynamic theoretical basis and capitalize on emergent, fundamental, and invariant features of marine ecosystems. These patterns have strong global support, being observed in over 120 marine ecosystems. Parameters from these curves elucidate the direction and magnitude of marine ecosystem perturbation or recovery; if biomass and productivity can be monitored effectively over time, such relations may prove to be broadly useful. Curve parameters are proposed as possible ecosystem thresholds, perhaps to better manage the marine ecosystems of the world.

Trends

Despite ongoing debate, we assert that there are consistent, fundamental features of marine ecosystems.

Key fundamental features are emergent properties of marine ecosystems that include sigmoidal cumulative biomass–trophic-level and 'hockey-stick' cumulative production–biomass curves.

These consistent, theoretically supported patterns occur in over 120 marine ecosystems.

A developing cumulative trophic theory builds upon past advances, widespread empirical support, and confirmation of simple predictions with observed responses.

Cumulative curve parameters can help delineate when marine ecosystems are perturbed or recovered, integrating across a range of stressors and response mechanisms.

Are there Fundamental Patterns of Marine Ecosystems?

The question remains whether there are common patterns from ecosystems that arise from underlying, fundamental ecosystem processes [1]. Several have been proposed [2] and often such proposed patterns are emergent properties of ecosystems [3,4]. Yet, whether such emergent patterns are germane for marine ecosystems remains unclear due to the distinctiveness of the marine environment [5,6] (Box 1). Detecting any such common emergent patterns in marine ecosystems is useful to understand the effects of perturbations and delineate practical management applications.

Marine ecosystems provide a range of highly visible, desirable, and valuable goods and services, from nutrient cycling to food production to recreation, even cultural inspiration and identity [7,8]. Yet, marine ecosystems face significant pressures. Eutrophication, habitat modification, toxic deposition, oil spills, overfishing, hypoxia, dredging, dumping, invasive species, and now acidification and climate change have all perturbed marine ecosystems [9–15]. A full range of pressures can alter the structure, functioning, and resilience of marine ecosystems, and often act in concert to produce cumulative effects [9,12]. Cognizant of this globally pervasive situation, a robust approach is needed to delineate when marine ecosystems have been notably perturbed, and to also assess when they have recovered.

Indicators and Patterns

Indicators are needed to assess the degree of perturbation or recovery of marine ecosystems [11,16]. Addressing elements of marine ecosystem response to perturbations has typically

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Box 1. Cumulative Trophic Theory

A central theme key to understanding marine ecosystem structure, function, and resilience has been the measure of energy flow among organisms (i.e., trophodynamics) [43]. Building upon extant trophodynamic theory, a cumulative trophic theory emerges that capitalizes on the observed, fundamental emergent features of marine ecosystems. First, ultimately reflective of the first law of thermodynamics, we know that primary production is highest at the base of the food web, and then declines with increasing TL (Figure IA) [40–43]. This then results in size spectra dynamics [27,47] and is seen as an Eltonian pyramid (Figure IB) [41]. Marine ecosystems are distinct from their terrestrial counterparts [5,6], with one key distinction being that, although the production pyramid is common in all food webs, a rhomboid shape of biomass occurs in marine food webs, with the greatest accumulation of biomass usually occurring at TL 2 or 3 (Figure IB). A mild reversion to pyramidal structure occurs for systems receiving copious allochthonous inputs, such as reefs or estuaries. Then, transposing these axes results in a slight unimodal biomass curve across TLs (Figure 1C) with the curvilinear response between the first and second TL. Trophic spectra work notes that, although individual biomass can be distributed across a range of taxa across a range of TLs, biomass is ultimately constrained within an overall system (Figure 1D) [23,48,49], set by energetic limits of primary production (i.e., carrying capacity). These underlying features of marine ecosystems, and their associated theoretical bases, form the foundation for a cumulative trophic theory of marine ecosystems.

From this and properties of the cumulative distribution function of normally distributed (here, biomass) data, a sigmoidal pattern then results when plotting cumB against TL (Figure 1A, main text). The underlying theory expressed as these cumulative curves captures the variation in biomass across TL, which is then collectively predicted to result in this consistent shape of systemic biomass accumulation. This reflects the largest accumulation of biomass at a given TL (Figure IB). From this and the known decline of production across TL (Figure IA), contrasting cumP with cumB, an asymptotic curve is expected (Figure 1B, main text). Where the largest decline in marine ecosystem production occurs results in cumP–cum B curves resembling 'hockey-stick' plots, with the 'blade' denoting this major shift in production (Figure 1B, main text).

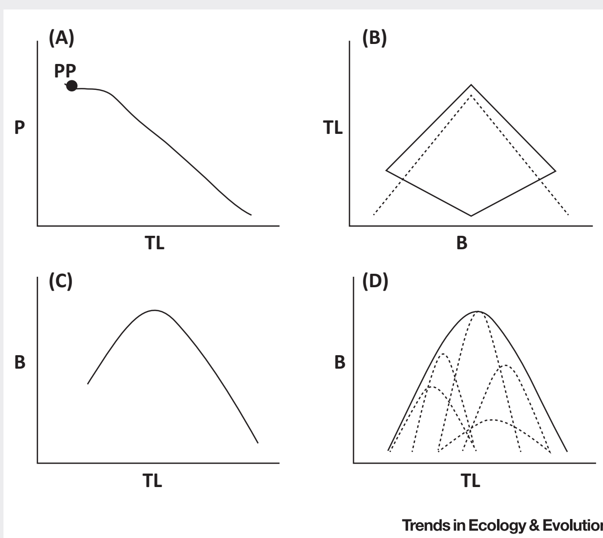

Figure I. Schematic of General Patterns of Ecosystem Dynamics Resulting in the Cumulative Trophic Theory (A–D). (A) The decline of productivity (P) across increasing trophic levels (TLs), starting at the point where primary production (PP) is estimated. (B) The trophic pyramid (broken; aka Eltonian pyramid) and rhomboid (unbroken) of biomass (B) with increasing TL. Note the rhomboid as being distinct for marine ecosystems compared with terrestrial examples. (C) The unimodal distribution of biomass over TLs. (D) The trophic spectra of biomasses of individual populations within a total, systemic biomass constraint. (A–C) represent known theory and observations, (D) represent constraints, the patterns in Figure IA,B (main text) represent the resultant theory, and in Figure 1C,D (main text) represent predictions from the theory.

emphasized a population or habitat level that disregards community- or systemic-level compensation and dynamics. However, aggregative or system-level patterns tend to be more robust and integrative [17,18]. Further, if changes in aggregative or system-level patterns are persistent, they represent bigger concerns than can be observed in fluctuating populations or habitats that are a subset of the marine ecosystem. Ultimately, cumulative effects need to be better understood, which requires response indicators that encompass the integration of entire ecosystem processes.

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