Cumulative Biomass-Trophic Level Curves

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SEDAR 103: US Caribbean Application of Alternate Assessment Methods

Summary

Cumulative Biomass-Trophic Level (TL) curves synthesize a suite of information into a readily compact depiction of an ecosystem's status, and the curve properties can ascertain the health of an ecosystem (whether it is recovering, depleting or otherwise perturbed). These curves have been, remarkably, found in every situation where they have been examined, and tend to behave in predictable and consistent ways. This approach requires either food web model outputs. or biomass or landings data and TL for all or most of the species represented. It is initially counter-intuitive, but once explained can provide a straightforward means of assessing an ecosystem. There are also known thresholds to the curve properties that can be used to delineate management actions for when an ecosystem is degraded.

I. Introduction

Cumulative trophic theory posits that the cumulative biomass across trophic level, and the cumulative production across cumulative biomass, behaves in a repeatable, consistent, fundamental manner that is readily predicted (Link et al. 2015, 2022). Cumulative biomass-trophic level (cumB-TL) curves result in an "S"-shaped or sigmoidal curve while cumulative production-cumulative biomass (cumB-cumP) curves produce a "hockey stick" shape (Fig. 1, E-F). The theory predicts a shrinking and stretching out of the curves with perturbation, moving closer to the origin whereas a relaxation of perturbation would result in an opposite pattern (Fig. 2). Inflection points and tangents of these curves can also be used to capture dynamics of the system. This concept works regardless of the mechanism of perturbation– mortality, growth, productivity, etc. These curves emerge regardless of the specific input data as long as they are organized via trophic level.

The curves are based on solid trophodynamic theory (Fig. 1) and can be understood to emerge from the concept of trophic concentration from basal trophic levels. Empirical case studies (Pranovi et al. 2012, 2014), thresholds from all kinds of input data

(Libralato et al. 2019, Pranovi et al. 2020), changes over time (Link et al. 2015, Libralato et al. 2019, Pranovi et al. 2020), evaluations of robustness of the method in terms of simulation studies and sensitivity analyses (Pranovi et al. 2020, Link et al. 2022) and robustness of trophic level assignment (Pranovi et al. 2020) have all shown that the method is remarkably consistent and robust. It has been tested and examined in over 200 marine ecosystems of various types, including tropical coral reef ecosystems (Link et al. 2024). It has been recently tested in the Gulf to explore recovery of the ecosystem after the deepwater horizon (Lewis et al. 2024).

II. Method Description

Adapted from Link et al. (2022) and Link et al. (2015):

A Primer on Cumulative Trophic Theory, with an emphasis on emergent properties of cumulative curves

Cumulative trophic curves are the emergent ecosystem properties of examining cumulative biomass (cumB) and cumulative production (cumP) across trophic levels (TLs; Link et al., 2015). Notably, such emergent properties are based on a clear theoretical background of biomass accumulation that is (log-) normally distributed across trophic level (Figure 1c), which when examined cumulatively results in a sigmoidal cumulative biomass-trophic level curve (cumB-TL, discussed further below; Figure 1e). Subsequent transfers of production and biomass are efficiency-limited across trophic level and up through a food chain (Figure 1b), as in the simple trophic transfer equation (EQ 1):

EQ. 1. $$cumP_{max} = \sum_{1=1}^{TL} \quad PP \cdot TE_i^{TL-1}$$

where $cumP_{max}$ is the cumulative production of the system, PP is net primary production (often expressed as net primary production, PP), TL is trophic level, and TE is the average TL transfer efficiency (Libralato et al., 2008). Thus, production at different trophic levels always results in pyramids because the transfer efficiency is always much lower than 1 and usually close to 0.1 (May, 1976; Pauly and Christensen, 1995), and hence cumulative curves of production are monotonically asymptotic tending to plateau (near the sum of all system productivity; i.e., $cumP_{max}$). Fundamental trophodynamic features are represented by overall system limits based on primary production (Figure 1a), turnover of populations, average growth or transfer efficiency and growth in size are the overall system limits that influence the production curve (cf., Link et al., 2015). Additionally, classical biomasses across trophic levels are not necessarily pyramidal in marine systems (see Fath and Killian, 2007; Pranovi and Link, 2009) but are more often rhomboidal due to high standing biomass at TL 2 (i.e., benthos and plankton that can derive energy from dead organic matter and/or from primary producers; i.e., herbivores and detritivores; Figure 1b). The cumulative biomass curve across trophic levels (cumB-TL) is thus a sigmoidal curve, i.e., a curve (Figure 1e) with an inflection point reflective of this rhomboidal nature (Figure 1b) and unimodal, approximately normal (log-) distribution of biomass across TL (Figure 1c). The cumB-TL curves exhibit a typical "S" -shaped pattern that seems to hold regardless of type of ecosystem or type of data used to construct them (Pranovi and Link, 2009; Pranovi et al., 2014). The cumB-cumP curves also tend to consistently exhibit a "hockey stick" -shaped curve (Figure 1f). Broader examination has confirmed the existence and commonality of these curves from over 200 different marine ecosystems around the planet and demonstrated repeatable, consistent and predictable changes in curve shapes due to perturbations that can modify trophodynamic features of large marine ecosystems (LMEs) (Pranovi et al. 2012; 2014; 2020; Link et al. 2015; Libralato et al. 2019).

In this context, we note that perturbations do not modify the fundamental shape of cumulative curves, but rather their key features (Figure 1g, 1h). In a stylized example of the cumB-TL curve (Figure 1g; Link et al., 2015), perturbations result in changes in the "S" -shaped curve over time that become less steep and move toward low TLs. For example, fishing causes depletion of biomass of upper trophic levels and prevalence of lower trophic levels, as highlighted by the fishing down food web phenomenon (Pauly et al., 1998). In the cumulative theory this would be hypothesized to result in the flattening and shrinking of the "S" -shaped cumB-TL curve (Figure 1g). Eutrophication similarly increases the proportion of lower TL biomasses (Micheli, 1999) and species invasions also produce overgrowth of selected lower TL species (Libralato et al., 2015), both hypothesized to result in similar responses in the cumB-TL curve (Figure 1g). Conversely, ecosystem recovery results in increased steepness and movement toward upper TLs of these curves (Figure 1g, 1h). These situations imply measurable changes on the major curve parameters, primarily determinants of the "S" curve such as the biomass inflection point, TL inflection point, and steepness (or slope), which can be tracked over time to determine major shifts in condition of an ecosystem (see Pranovi et al., 2012; 2014, 2020; Libralato et al. 2020). They thus correspond to and detect changes from many instances of known marine ecosystem perturbation. For example, the Gulf of Mexico large marine ecosystem has experienced notable perturbations due to the 2010 Deepwater Horizon oil spill, which has resulted in numerous changes to trophic structure and ecosystem function (Ainsworth, 2021; Woodstock et al. 2021). Those changes have also been detected in cumB-TL curves for the Gulf of Mexico (Libralato et al., 2019; Pranovi et al., 2020). These three simple curve parameters represent emergent properties of LMEs with a surprising degree of insight into ecosystem structure and functioning. Thus, the cumulative curves hold some promise in delineating regions of ecosystem state that require management action. More so, the behavior of these curves under a varying set of conditions warrants further examination.

There are major mechanisms whereby marine populations, their resulting food webs, and ultimately the resulting trophodynamics of marine ecosystems can be perturbed or recovered. These mechanisms group largely into changes to production or growth on the one hand versus changes to mortality or removals on the other, with perhaps some rewiring of the efficiency of internal transfer dynamics. Here we explore this in further detail for a simulated food chain with seven trophic levels using deconstructed features of the simple trophic transfer equation (EQ. 1).

We have plotted cumB-TL and cumP-cumB curves, normalizing each ecosystem so that all could be shown on the same scale. Although not presented here, the same general patterns hold with the absolute data presented. We have calculated percentiles for over 200 marine ecosystems for each of these plots to determine if the patterns held, and did so across the different types of ecosystems. Based on these curves, we estimated the inflection point for the cumB-TL curves, and once that was determined, calculated the inflection point values of TL, % cumB, and the slope at that point. Similarly, we estimated the slope and junction point of the "hockey stick blade" for the cumP-cumB curves, noting values of % cumP and % cumB where the junction point was located in addition to its slope.

Given this theoretical background, widespread empirical support, and common values of curve parameters, we can delineate when a marine ecosystem is in an abnormal state, indicative of probable perturbation. Conversely, we can delineate when a marine ecosystem has "recovered." As noted, changes in the slope and inflection points of the cumB-TL and cumP-cumB curves can be tracked over time and related to particular pressures (Fig. 1). Similar to population or habitat level reference points that are used for status determination and decision criteria, we assert system-level thresholds can be developed.

Based on the reasoning above, observed patterns and extant trophic theory, we have developed a method to delineate marine ecosystem zones of perturbation as depicted in the shaded areas of Fig. 1c,d. Specifically, as the point for which $\frac{\delta'' cumB}{\delta'' TL} = 0$ decreases, such that the inflection point and slope decrease beyond some policy choice of risk tolerance (or actually, global thresholds), we would delineate such a marine ecosystem as perturbed. Similarly, as $\frac{\delta' cumP}{\delta' cumB} \rightarrow 0$ such that the cumP intercept and the cumB intercept values at the “hockey stick blade” junction is less than some policy choice of risk tolerance, we would delineate such a marine ecosystem as perturbed. These zones capture the predicted and observed results that reflect biomass maxima shifting to lower trophic levels or to lowered biomass values due to perturbation. These zones can also identify regions that are rarely observed, or where there may be “zones of impossibility” – where laws of thermodynamics or the path dependency of system dynamics preclude occupancy of a particular region on the cumulative curve.

No matter how one assesses marine ecosystem perturbation thresholds, major perturbations to significant portions of cumB will impact the structure, function and resilience of marine ecosystems. Thus, we stress that any detectable and thus notable shifts in curve parameters relative to these thresholds, regardless of what thresholds are chosen, should represent a major impact to a large portion of cumB and cumP in a marine ecosystem. The impacts thereof are consequential. Further, the observed asymptote for the cumP-cumB curves is indicative of total removal limits, such that the rate (i.e., slope up to that asymptote) of systemic removals should be at or below that level of production, indicating a total mortality rate not to be exceeded. The thresholds methodology we propose from these curves provides an overall assessment of ecosystem perturbation, and more so the directional response of a marine ecosystem to a myriad of possible pressures. If it is possible to define such thresholds, it is also possible to quickly communicate to managers, stakeholders and other interested parties the status of a system relative to that threshold and to other, comparable systems.

A. Data Inputs

- Food Web model outputs,
- or
- Biomass or Landings data
- and
- TL of all/most species

B. Analyses/Data Outputs

- CumB-TL “S” curve
- CumB-CumP “hockey stick”curve
- with curve properties servings as RPs

C. Implications for Management

Potential Indicator of EOF
Specifically,

- cumB-TL, at inflection point, where slope/steepness approaches 0, have perturbation
- cumP-cumB, at tangent max is positive
- Where tangent approach 0 and cumB constant, perturbation
- Or where tangent constant and cumB declines, perturbation
- Specifically, as the point for which decreases, such that the inflection point and steepness decrease beyond some policy choice of risk tolerance, we would delineate such a marine ecosystem as perturbed. Similarly, as such that the cumP intercept and the cumB intercept at the hockey stick blade junction (i.e. tangent) is less than some policy choice of risk tolerance, we again would delineate such a marine ecosystem as perturbed.
- Every marine ecosystem exhibits these emergent patterns (>200 cases) of cumB-TL, cumB-cumP
- The “S” and hockey stick curves always stretch, shrink and move toward origin under perturbation
- Tracking curve parameters follows dynamics of an ecosystem and indicates degree of recovery/ perturbation
- Globally, empirical and modeled thresholds emerge when tracking perturbation wrt 1st & 2nd derivative (i.e. slope & inflection point) on “S” curve
    - cumBinfl pt ~33%
    - TLinfl ptT~3.38
    - Slope~0.5

D. Caveats

- Inflection levels depend on inclusion of PP or not, but can be adjusted for
- FW model output caveats
- veracity/robustness of landings data
- does not need copious information as might be implied, especially if just using landings data
- TL assignments robust based on sensitivity analyses/simulations
- behavior very predictable

III. Applications of the Method

- Has been used to track recovery in Gulf of Mexico/America from DWH impacts (Lewis et al. 2024).
- Has been used to test and inform policy on good environmental status in the EU under their MSFD auspices (ICES 2014, Tam et al. 2017).
- Has been used to identify and verify gradients/levels of human-induced perturbation in remote Pacific tropical reefs (Link et al. 2024).

- Backstopping and testing for EOF, especially with ecosystem-level Kobe plots, in the US (Link 2021; e.g. Fig. 3).
- Identified EOF for African LMEs and used to inform sustainable development decisions (Link et al. 2020).
- Reported on in various national and regional Ecosystem Status Reports

IV. Discussion

The approach here is a derived, emergent product whose output is sometimes difficult to explain and readily comprehend. However, once grasped, the concepts are remarkably universal. If this approach mertis consideration wrt data veracity and certainty, we recommend that if selected, this method be calculated using extant food web models if they are trusted, but more likely using landings data coupled with known databases of fish trophic level. We would propose that the curve properties of the cumB-TL curve primarily be tracked as a diagnostic. If any curve thresholds surpass global limits (i.e. if 60-65% of known biomass has been removed), then suitable fisheries management action should be enacted. The outputs of this method can serve as an ecosystem reference point or a measure of ecosystem overfishing.

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VI. Tables and Figures

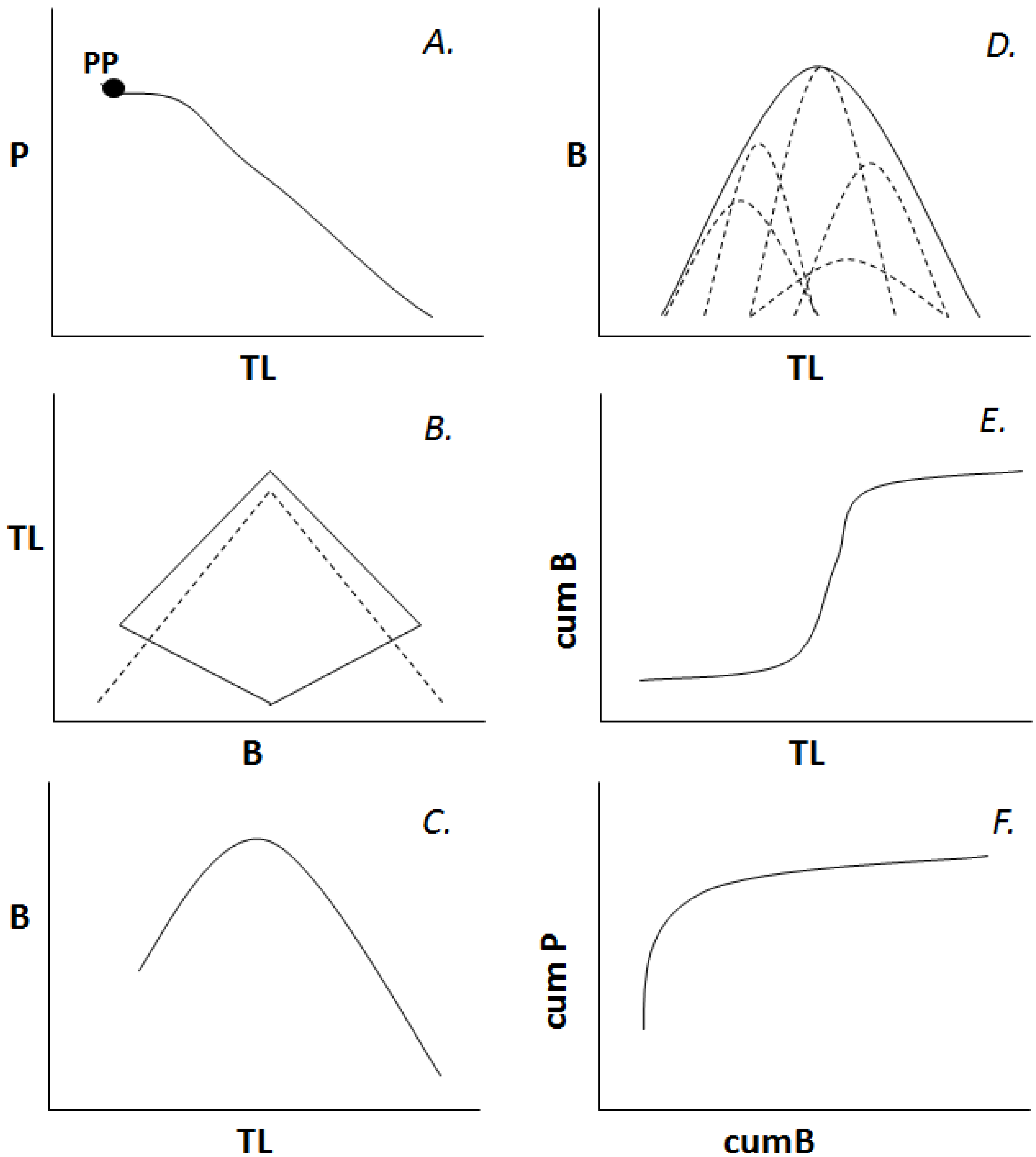

Figure 1. A. Thermodynamic constraints, Lindeman TL concept; B. Eltonian pyramid and ME rhomboid modifier; C. System Biomass distribution; D. Trophic spectra of component spp biomass; E. Resultant sigmoidal curve; F. Resultant hockey stick (Link et al. 2015).

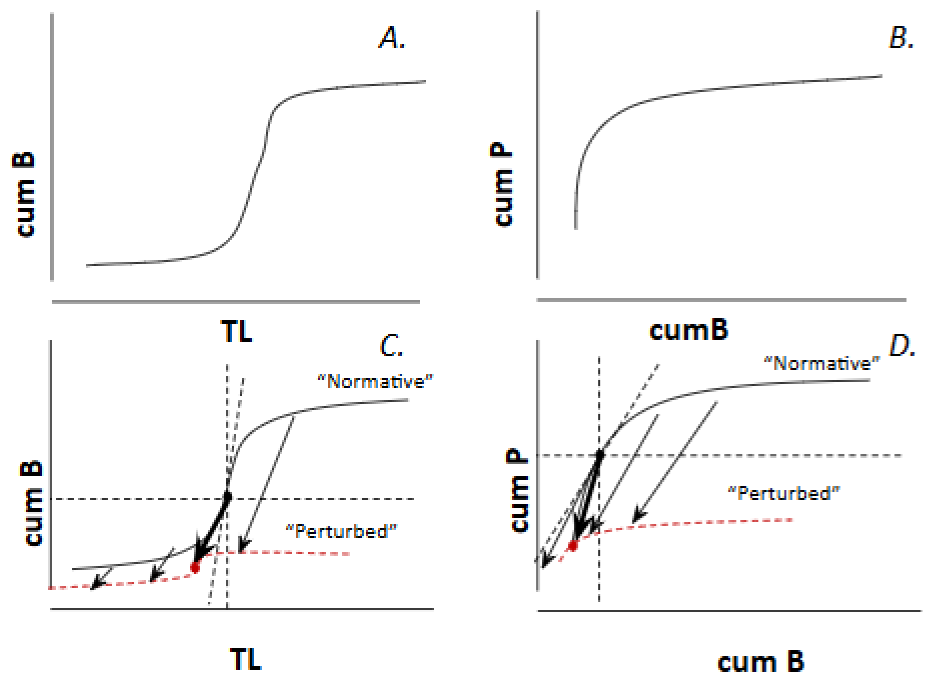

Figure 2. Direction of curve features indicative of ecosystem perturbation (shrinking and moving towards the origin) or recover.

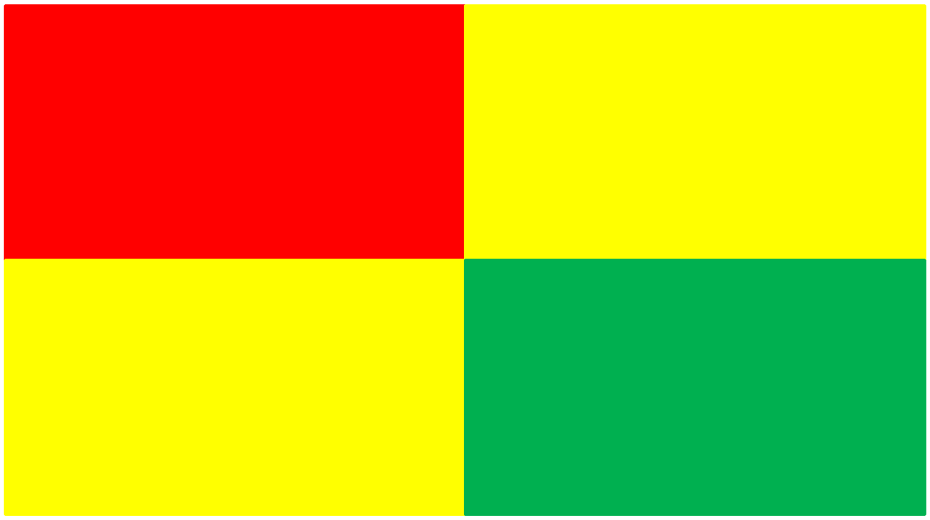

Figure 3. Example of an ecosystem “Kobe” plot of ecosystem overfishing (Ryther index) and perturbation (Biomass level at the inflection point) for the Caribbean.