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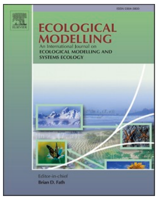

Simulations and interpretations of cumulative trophic theory

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ABSTRACT

Examining marine ecosystems in a distinct way can produce new ecological, theoretical and applied insights. The common "S" and "hockey stick" -shaped curves, which result from examining the cumulative biomass and trophic level and the cumulative production and cumulative biomass curves of marine ecosystems, have strong potential to elucidate the mechanisms of marine food webs. These curves are based on the cumulative trophic theory, which can be summarized as the integration of biomass and production across trophic level that results from the relatively simple trophic transfer equation. Here we test the behavior of this theory via modeled simulations of the transfer equation under a variety of common mechanisms that can influence marine ecosystems. The simulated scenarios we present and evaluate here explore bottom-up driven changes (production, growth), internal dynamics (transfer efficiency) or top-down driven changes (mortality, selectivity), as well as multi-mechanism scenarios (overfishing and eutrophication) that are commonly experienced in marine ecosystems. We explore these scenarios at high, medium or low levels of change for each feature to ascertain how they can result in major changes to the realized trophodynamics of a marine ecosystem. Our results lend credence to the generality of the cumulative trophic theory by predicting the empirically observed "S" and "hockey stick" -shaped curves under a wide range of possible mechanisms. Given that common, repeatable and predictable dynamics is a key hallmark of increasingly robust theories, the application of cumulative trophic theory in managing marine ecosystems enables more repeatable and predictable responses across a wide range of conditions.

1. Introduction

The need for robust ecological theory is needed, for both inherent understanding and use in applied situations (Peters, 1991). The many pressures facing ecosystems necessitate understanding of common, repeatable, and predictable dynamics such that these dynamics indicate degrees of ecosystem perturbation, as well as recovery (Link et al., 2002, 2015; Jennings, 2005; Link, 2005; Shin et al., 2010; Tam et al., 2017). This is especially true for marine ecosystems, whose distinctiveness from terrestrial ecosystems is well documented (i.e., scale, different fluid dynamics, difficulty of observations, scope and speed of species movement, etc.; Steele 1985; Link 2002; Carr et al., 2003) and whose difference from terrestrial and smaller scale aquatic ecosystems often results in a lag of ecological theory being developed for and applied to them (Steele, 1985; Townsend et al., 2018). Here we describe how a relatively simple equation, that arises from an ecological theory based on cumulative evaluations of ecosystem properties, can be useful for understanding marine ecosystem responses to a wide range of changes. The understanding of cumulative patterns such that they can detect and predict major, common pressures could suggest potential interventions (Sainsbury and Sumaila, 2003; Jennings, 2005; Link, 2005, 2010, 2018; Link et al., 2011, 2015; Tam et al., 2017) via common mechanisms. Ecological theory that enables one to address the pervasive perturbations facing marine ecosystems via a general mechanism with a clear and robust pattern potentially has global implications.

One such theory is the cumulative trophic theory with its emergent features (Link et al., 2015). This 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. The studies on this topic to-date have demonstrated that there are consistent, fundamental, emergent properties common to all marine ecosystems, and that these cumulative biomass-trophic level (cumB-TL) and cumulative production-cumulative biomass (cumB-cumP) curve patterns are observed in every ecosystem

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that has been examined, albeit with nuanced curve properties across the range of types of ecosystems (Link et al., 2015; Pranovi et al., 2020). The cumB-TL curve results in a "S" -shaped curve, whereas the cumP-cumB curve results in a "hockey stick" shape. The curve shapes have been observed across multiple ecosystems, types of data, etc. in over 200 different marine ecosystems that span over 70 years of data (Pranovi et al., 2012,2014, 2020; Link et al., 2015; Libralato et al., 2019; Fig. 1). Furthermore, these curves respond to perturbation and recovery in known, repeatable, predicable ways, with associated curve parameters being useful to delineate perturbed or recovered ecosystems (Link et al., 2015; Libralato et al., 2019; Pranovi et al., 2020). These dynamics have led to globally proposed thresholds that may be useful for better management of marine ecosystems (Link et al., 2015; Libralato et al., 2019; Pranovi et al., 2020).

The cumulative trophic theory and associated curve parameters have had a largely empirical emphasis on pattern detection and replication, which is understandable as the first step in development of theoretical explanation. Simulating these cumulative theory curves, as an emergent property of ecosystems, from a simple understanding of trophodynamics (Lindeman, 1942; Libralato et al., 2014; Link et al., 2015) would also be valuable. Here we aim to explore a suite of simulations across a range of scenarios and factors common to many marine ecosystems.

1.1. 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 (Fig. 1c), which when examined cumulatively results in a sigmoidal cumulative biomass-trophic level curve (cumB-TL, discussed further below; Fig. 1e). Subsequent transfers of production and biomass are efficiency-limited across trophic level and up through a food chain (Fig. 1b), as in the simple trophic transfer equation (EQ (1)):

$$cumP_{max} = \sum_{1=1}^{TL} PP \cdot TE_i^{TL-1} \tag{1}$$

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 (Fig. 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; Fig. 1b). The cumulative biomass curve across trophic levels (cumB-TL) is thus a sigmoidal curve, i.e., a curve (Fig. 1e) with an inflection point reflective of this rhomboidal nature (Fig. 1b) and unimodal, approximately normal (log-) distribution of biomass across TL (Fig. 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 (Fig. 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 (Fig. 1g, 1h). In a stylized example of the cumB-TL curve (Fig. 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 the 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 (Fig. 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 (Fig. 1g). Conversely, ecosystem recovery results in increased steepness and movement toward upper TLs of these curves (Fig. 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; Libralto 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 et al., 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)).

2. Methods

2.1. Model

Taking EQ (1), in discretized form for distinct (i.e., integer) trophic levels, one can back-calculate production and biomass for each TL. The production (P) at any given trophic level (TL) is effectively obtained by the transfer efficiency declination of primary production (PP),

$$P_{TL} = PP \cdot TE^{TL-1} \tag{2}$$

(c.f., Lindeman, 1942; as described further in Libralato et al., 2008, 2014). As estimates of biomass are often harder to obtain across all taxa in an ecosystem, one can use common ranges of production to biomass ratios (P/B; Shannon and Jarre-Teichmann, 1999; Heymans and Baird, 2000; Heymans et al., 2004). From the P/B ratio, one can obtain biomass (B) at a given TL as

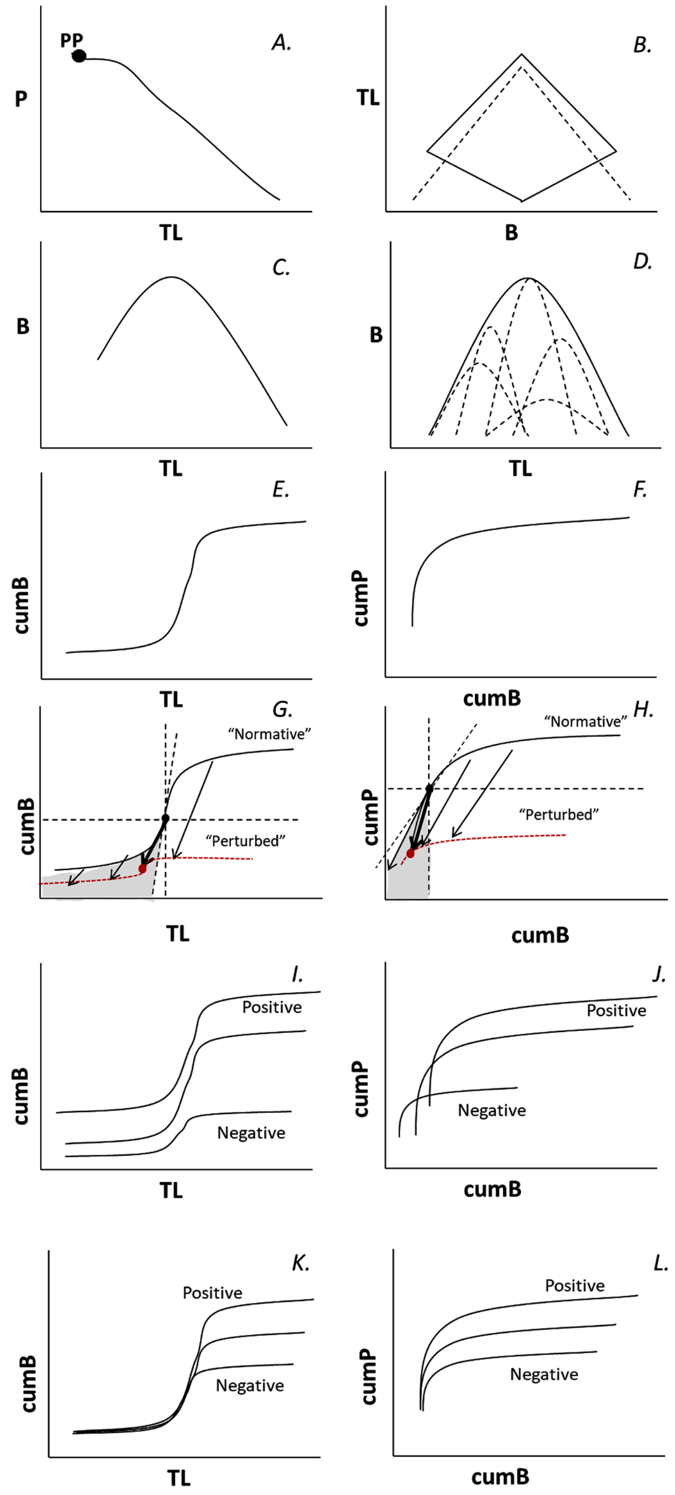

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Fig. 1. Schematic of general patterns of ecosystem dynamics resulting in the cumulative trophic theory (A-H). Panels A-C represent known theory and observations, D constraints, E-F the resultant theory, and G-H predictions from the theory. (A) The decline of productivity across increasing trophic levels, starting at the point where primary production is estimated (Lindeman, 1942; Oksanen, 1991; Strayer, 1991; Teramoto, 1993; Pauly and Christensen, 1995; Friedland et al., 2012; Link et al., 2012). (B) The trophic pyramid (dashed) and rhomboid (solid) of biomass with increasing trophic level (Elton, 1927; Lindeman, 1942). (C) The unimodal distribution of biomass over trophic levels (Lindeman, 1942; Oksanen, 1991; Strayer, 1991; Teramoto, 1993). (D) The trophic spectra of biomasses of individual populations within a total, systemic biomass constraint (Gascuel et al., 2005, 2008; Libralato and Solidoro, 2010). (E) The cumulative biomass sigmoidal pattern ("S" curve) across increasing trophic level. (F) The "hockey stick" of cumulative production across cumulative biomass. (G) Prediction showing the shift in cumulative biomass over trophic level from a "Normative" system as it moves (depicted by arrows) to a perturbed system. Dashed lines intercepting axes represent inflection point values, and angled dashed line represents slope of the curve at the inflection point, the dot represents the inflection point, and shaded areas represents a zone of perturbation below some ecosystem threshold. (H) Similar to (G) but for cumulative production across cumulative biomass. (I) Expected changes to the "S" curve from positive and negative bottom-up effects. (J) Expected changes to the "hockey stick" curve from positive and negative bottom-up effects. (K) Expected changes to the "S" curve from positive and negative top-down effects. (L) I) Expected changes to the "hockey stick" curve from positive and negative top-down effects. *B* = biomass, TL = trophic level, *P* = production, PP = primary production, cumB = cumulative biomass, cumP = cumulative production. Adapted from Link et al., 2015.

$$B_{TL} = P_{TL}/(P/B_{TL}) \tag{3}$$

For some scenarios, we wanted to harvest (i.e., some form of removal) some of the taxa, or at least use a variable form of mortality (M) as a placeholder. This removal (R; e.g., fisheries catch, other mortality, etc.) was estimated as

$$R_{TL} = P_{TL}\left(1 - e^{-M*selectivity}{}_{TL}\right) \tag{4}$$

Where P_{TL} is as before and the selectivity is the amount the production at the trophic level subject to mortality, and which leads to the realized production accounting for any such mortality (PR) as

$$PR = P_{TL} - R_{TL} \tag{5}$$

And then the realized biomass accounting for catch or other sources of mortality that is removed (BR) as

$$BR_{TL} = PR_{TL}/(P/B_{TL}) \tag{6}$$

2.2. Curves and scenarios

The preceding values (i.e., B, P, and PR) were calculated for all steps of the food chain up to TL 7. These were based on the initial PP level and assumptions of realistic values for TE and P/B. Then the values, particularly P and B, were summed across TL to obtain cumulative biomass (cumB) and cumulative production (cumP). The cumB discrete data was plotted against each TL, and cumP was plotted against cumB for each of the scenarios evaluated (see below; c.f. Fig. 1e, f). There are many potential curve features one can estimate from the "S" and "hockey stick" -shaped curves respectively (Pranovi et al., 2014; Link et al., 2015; Libralato et al., 2019), but we do not present all of these here as our primary focus was to examine the shape, size and magnitude of the "S" and "hockey stick" -shaped curves. We present these basic "S" curve and "hockey stick" -shaped plots for each set of scenarios.

We explored these two, distinct curves across a range of simulated conditions. These are loosely grouped into bottom-up driven features that include changes in production (base of the entire ecosystem, as seen modified via PP), in growth (as modified via P/B ratios across various TLs), and top-down driven features such as mortality (as modified by M), and selectivity (a type of TL-based evaluation of mortality, across various TLs). Furthermore, scenarios exploring changes in overarching, internal ecosystem properties, i.e., the efficiency of the food web (as modified by TE) were explored. A special set of scenarios representing two common, major pressures facing marine ecosystems (overfishing and eutrophication, as modified via a combination of parameters) were also examined (Table 1). For eutrophication, the parameters were set to initially mimic increased production, but then as higher levels of eutrophication occurred, less production and increases in (non-fishing) mortality were parameterized to reflect the dynamics of eutrophication. The overfishing scenarios were parameterized to reflect not only (fishing) mortality, but also increases of selectivity for various trophic levels. The full suite of scenarios aimed to answer the following questions: are these pressures resulting in major changes to the realized trophodynamics of a marine ecosystem? How much do different pressures affect the cumulative curves? And does the cumulative curve theory explain observed results?

For each set of scenarios (except the special, mixed scenarios), we held all parameters constant as in the base scenario except the variable under examination (Table 1). The levels of changes in each scenario were intended to cover a range of plausible ecosystem conditions that represent perturbed or recovered states, as realized via the various, common mechanisms that can impact marine ecosystems. We present each set of resulting cumB and cumP curves for the range of scenarios, and also key curve parameters and features relative to the base scenario to demonstrate the magnitude of the scenario response.

Table 1

Curve parameters used in scenarios to estimate and evaluate effects of different classes of perturbation on trophodynamics of marine ecosystems. PP = primary production, TE = transfer efficiency, *F* = fishing removals, *M* = mortality removals, TL = trophic levels, Sel. = selectivity, P/*B* = production to biomass ratio. All base scenario parameters were used unless otherwise indicated for each scenario.

Scenarios		*Parameters*																
		PP	TE	F (or M)	TL1 Sel.	TL2 Sel.	TL 3 Sel.	TL 4 Sel.	TL 5 Sel.	TL 6 Sel.	TL 7 Sel.	TL 1 P/B	TL 2 P/B	TL 3 P/B	TL 4 P/B	TL 5 P/B	TL 6 P/B	TL 7 P/B
Perturbations on	Base	1000	0.1	0.5	0	0.3	0.8	0.9	0.95	0.98	1	150	60	1	0.5	0.2	0.2	0.1
Production																		
	Very, Very High	4000																
	Very High	3000																
	High	2000																
	Moderate-Low	500																
	Low	250																
	Very Low	100																
Growth																		
	High TL 1											300						
	Low TL 1											100						
	High TL 3													7				
	Low TL 3													0.2				
	High TL 5															1		
	Low TL 5															0.05		
	High All TL											300	120	2	1	0.4	0.4	0.2
	Lo All TL											75	30	0.5	0.25	0.1	0.1	0.05
TE																		
	Very, Very High		0.25															
	Very High		0.2															
	Moderate-High		0.16															
	Moderate		0.13															
	Low		0.08															
	Very Low		0.05															
Mortality																		
	Very High			2														
	High			1														
	Moderate			0.5														
	Some			0.2														
	Low			0.1														
	Very Low			0.01														
Selectivity																		
	Very High					0.5	0.9	0.95	0.95	1	1							
	High				0	0.4	0.85	0.95	0.95	1	1							
	Moderate				0	0.3	0.7	0.8	0.9	0.95	1							
	Some				0	0.25	0.65	0.75	0.9	0.95	1							
	Low				0	0.1	0.5	0.7	0.85	0.9	1							
	Very Low				0	0	0.4	0.65	0.8	0.9	0.98							
Mixed																		
	Starting Overfishing UTLs			1														
	Overfishing UTLs			2		0.6	0.95	1	1	1	1							
	Starting Eutrophication	1500		0.5	0	0.3	0.8	0.9	0.95	1	1	250						
	Eutrophication	2000		1.5	0	0.4	0.85	0.95	0.95	1	1	300						
	Strong Eutrophication	1500	0.08	2	0.1	0.5	0.9	0.95	0.95	1	1	300						

3. Results

Overall, we ran 35 different scenarios, in addition to the base case, to explore the many possible ways in which marine food webs can respond to different pressures. Effectively these were in the very high-high-medium-low-very low categories of each of the possible top-down or bottom-up mechanisms that can influence marine ecosystem trophodynamics. When examining the results of these various model runs, it is helpful to compare them to the base case scenario for each particular suite of scenarios (Table 2). It is also helpful to compare them more broadly to Fig. 1g and 1h when ascertaining whether the magnitude and direction a particular scenario result was positive or negative. One can see the stretching and growing of the curves to indicate positive or recovery dynamics, whereas a shrinking and moving towards the origin can indicate negative or perturbation dynamics (Fig. 2-7; Table 2).

For the production scenarios (Fig. 2), the response is as one would expect from cumulative trophic theory. With lower basal production, the "S" -shaped curve flattens out and loses both its steepness and clear inflection point at lower to mid- trophic levels, as well as lowering the amount of total, cumulative biomass observed (Fig. 2a; Table 2). Conversely, as production increases, the "S" -shaped curve becomes more pronounced and heightens the "S" shape, with ultimately a higher cumulative biomass observed (Fig. 2a; Table 2). The cumP-cumB curve shows the classical, very expected pattern of a shrinking "hockey stick" (Fig. 1h), with the curve becoming smaller and closer to the origin as production declines (Fig. 2b; Table 2). Among all the sets of scenarios,

Table 2
Comparison of curve properties relative to the base for the range of scenarios. The cumulative Biomass- Trophic Level (cumB-TL) "S" -shaped curve properties include the trophic level at the inflection point (TL_infl), the biomass at the inflection point (B_infl), the slope at the inflection point, and the maximum biomass (Max B) for the curve at the asymptote. The cumulative Production- cumulative Biomass (cumP-cumB) hockey stick curve properties include the asymptote of production, the biomass at the inflection point (B_infl; i.e., where the "hockey blade" joins the "stick"), the production at the inflection point (P_infl), the biomass at the starting point of the blade (Blade start B), the production at the starting point of the blade (Blade start P), and the blade length. All values are compared relative to the base scenario. Changes >±150% difference from base are indcated by bold text, and changes ±50-150% difference are indciated by italicized text.

Scenarios		*Curve property responses*									
		cumB-TL				cumB-cumP					
		%Diff from Base		%Diff from Base							
		TL infl	B infl	Max B	Slope	Asymptote	B infl	P infl	Blade start B	Blade start P	Blade-base L
	Base	–	–	–	–	–	–	–	–	–	–
Production											
	Very, Very High	−8.0%	**309.1%**	**306.3%**	>Base	**299.8%**	**295.1%**	**299.6%**	**293.9%**	**300.0%**	>Base
	Very High	−4.0%	**209.1%**	**206.3%**	>Base	**200.1%**	**196.3%**	**200.2%**	**203.0%**	**200.0%**	>Base
	High	0.0%	*109.1%*	*100.0%*	>Base	100.4%	*97.5%*	*99.8%*	*97.0%*	*100.0%*	>Base
	Moderate-Low	0.0%	−36.4%	*−50.0%*	<Base	*−50.0%*	*−50.6%*	*−50.0%*	*−54.5%*	*−50.0%*	<Base
	Low	4.0%	*−72.7%*	*−75.0%*	<Base	*−75.0%*	*−75.3%*	*−75.0%*	*−75.8%*	*−75.0%*	<Base
	Very Low	4.0%	*−88.2%*	*−90.0%*	<Base	*−90.0%*	*−90.1%*	*−90.1%*	*−90.9%*	*−90.0%*	<Base
Growth											
	High TL 1	0.0%	−36.4%	−18.8%	=Base	0.0%	−40.7%	0.0%	*−50.0%*	0.0%	=Base
	Low TL 1	0.0%	27.3%	18.8%	=Base	0.0%	35.8%	0.0%	*51.5%*	0.0%	=Base
	High TL 3	−4.0%	−36.4%	−37.5%	<Base	0.0%	0.0%	0.0%	0.0%	0.0%	=Base
	Low TL 3	0.0%	45.5%	43.8%	>Base	0.0%	0.0%	0.0%	0.0%	0.0%	=Base
	High TL 5	0.0%	9.1%	0.0%	=Base	0.0%	0.0%	0.0%	0.0%	0.0%	=Base
	Low TL 5	0.0%	9.1%	6.3%	=Base	0.0%	0.0%	0.0%	0.0%	0.0%	=Base
	High All TL	4.0%	−45.5%	*−50.0%*	<Base	0.0%	*−50.6%*	0.0%	*−50.0%*	0.0%	=Base
	Lo All TL	−4.0%	*109.1%*	*106.3%*	>Base	0.0%	*97.5%*	0.0%	*97.0%*	0.0%	=Base
TE											
	Very, Very High	0.0%	**200.0%**	**450.0%**	>Base	16.2%	23.5%	11.9%	0.0%	0.0%	>Base
	Very High	0.0%	*118.2%*	**225.0%**	>Base	10.2%	17.3%	7.9%	0.0%	0.0%	>Base
	Moderate-High	0.0%	*63.6%*	106.3%	>Base	5.9%	11.1%	4.7%	0.0%	0.0%	>Base
	Moderate	0.0%	36.4%	43.8%	=Base	2.8%	4.9%	2.3%	0.0%	0.0%	>Base
	Low	4.0%	−9.1%	−25.0%	=Base	−1.8%	−3.7%	−1.7%	0.0%	0.0%	<Base
	Very Low	4.0%	−36.4%	−43.8%	<Base	−4.5%	−9.9%	−4.0%	0.0%	0.0%	<Base
Mortality											
	Very High	0.0%	−36.4%	−37.5%	<Base	−3.3%	−6.2%	−2.9%	0.0%	0.0%	<Base
	High	0.0%	−9.1%	−18.8%	<Base	−1.3%	−2.5%	−1.1%	0.0%	0.0%	<Base
	Moderate	0.0%	18.2%	18.8%	>Base	0.9%	1.2%	0.7%	0.0%	0.0%	=Base
	Low	0.0%	27.3%	25.0%	>Base	1.3%	1.2%	1.0%	0.0%	0.0%	=Base
	Very Low	0.0%	27.3%	31.3%	>Base	1.6%	2.5%	1.2%	0.0%	0.0%	=Base
Selectivity											
	Very High	0.0%	0.0%	−6.3%	=Base	−5.2%	−6.2%	−5.2%	−4.5%	−4.9%	=Base
	High	0.0%	9.1%	0.0%	=Base	−0.4%	−1.2%	−0.5%	0.0%	0.0%	=Base
	Moderate	0.0%	13.6%	3.1%	=Base	0.0%	0.0%	0.2%	0.0%	0.0%	=Base
	Low	0.0%	18.2%	6.3%	>Base	0.9%	1.2%	0.8%	0.0%	0.0%	=Base
	Very Low	0.0%	27.3%	12.5%	>Base	1.4%	2.5%	1.3%	0.0%	0.0%	=Base
Mixed											
	Starting Overfishing UTLs	0.0%	−9.1%	−18.8%	<Base	−1.3%	−2.5%	−1.1%	0.0%	0.0%	=Base
	Overfishing UTLs	0.0%	−36.4%	−43.8%	<Base	−5.7%	−12.3%	−5.2%	0.0%	0.0%	<Base
	Starting Eutrophication	0.0%	27.3%	25.0%	>Base	*50.0%*	0.0%	*50.0%*	−9.1%	*50.0%*	>Base
	Eutrophication	0.0%	9.1%	−6.3%	=Base	*93.5%*	4.9%	*94.2%*	0.0%	*100.0%*	>Base
	Strong Eutrophication	0.0%	*−54.5%*	*−62.5%*	<Base	16.5%	−40.7%	17.1%	−39.4%	22.8%	=Base

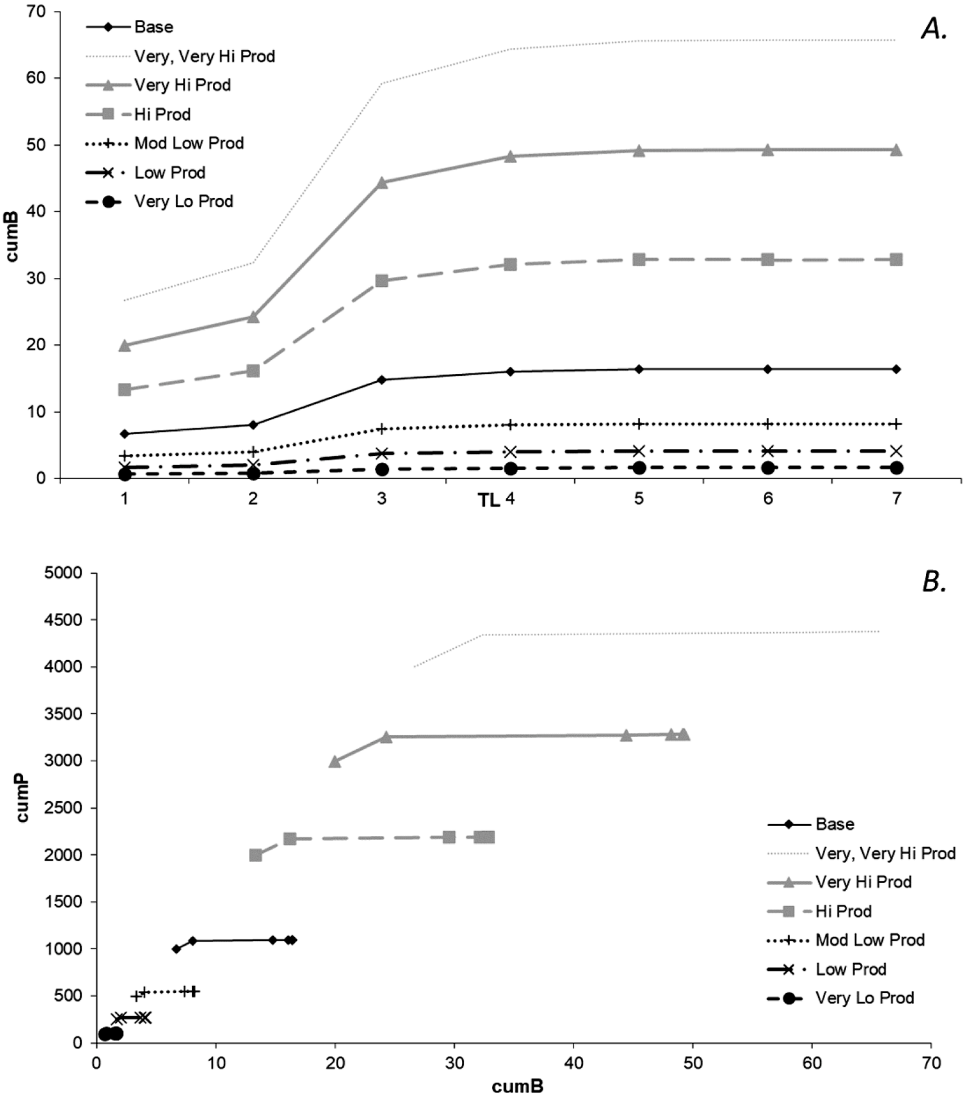

Fig. 2. A. The cumB-TL "S" curve across different levels of productivity. B. The cumP-cumB "hockey stick" curve across different levels of productivity. See Table 1 for parameter details of these bottom-up scenarios.

these production scenarios tended to show the largest departure from the baseline (Table 2), with changes much greater than ±100% (in many cases larger than 200%) from the base scenario.

In another bottom-up set of scenarios, changing the growth at various TLs has some seemingly counterintuitive results (Fig. 3). The "S" -shaped curve shows that an increase in growth for TL 1, 3 or across all TLs, the curve actually shrinks and flattens (Fig. 3a), similar to a lower production situation (Fig. 2a; Table 2). The opposite occurs for an increase in those TLs, with the "S" -shaped curve enlarging (Fig. 3a). The cumP-cumB curve effectively maintained the same shape, but the "blade" of the "hockey stick" begins at higher biomass levels with an actual decrease growth at TL 1, 3 or across all TLs (Fig. 3b; Table 2). Conversely, the blade shifts to lower cumulative biomass with higher growth rates at these various TLs (Fig. 3b; Table 2). The results for changing growth for TL 5 (or any higher TL, not shown) are effectively the same on both curves and don't fundamentally differ from the base case scenario (Fig. 3). Why lower (or slower) growth leads to an increase in the curves and opposite of what would be expected (Fig. 1) is likely deduced from the growth term (i.e., P/B) being in the denominator (EQ. (6)) when calculating biomass from production at each TL, and hence when integrated results in cumB being higher. The production and cumP do not fundamentally differ in these scenarios (Fig. 3b). We best understand this to be that faster (higher) growth rates tend to result in lower standing biomass, due to higher turnover rates of said biomass (Odum and Barrett, 1971; Gasol et al., 1997). These scenarios had very few instances that were greater than ±40% difference from the base scenario, except when changing growth at all TLs, i.e., the *All TL* scenarios.

Results from exploring transfer efficiency were as expected (Fig. 1g, h), albeit with an important nuance from either production or growth (Fig. 4). Lower TEs resulted in a flattened "S" -shaped curve (Fig. 4a; Table 2) and shorter, closer-to-the-origin cumP-cumB "hockey stick" curves (Fig. 4b; Table 2). And the opposite held; higher TEs results in larger "hockey sticks" (Fig. 4b; Table 2) and more pronounced "S" -shaped curves (Fig. 4a). The "S" -shaped curves in all three of these bottom-up (Figs. 2b-4b) scenarios could be effectively interchangeable. But the cumP-cumB curves in these scenarios are more distinct, with the curves at lower TEs shrinking and being both closer to the origin and with much less cumulative biomass (i.e., the handle of the "hockey stick" is shorter). Both the TE (Fig. 4b) and production (Fig. 2b) cumP-cumB curves shrink and have smaller cumulative production at lower levels, whereas the growth cumP-cumB curve (Fig. 3b) has the same amount of cumulative production and a much less pronounced decline in cumulative biomass. In the TE scenarios, with higher TE there is more production transferring to upper trophic levels, and the effect on the "handle" of the "hockey stick" is more noticeable (Fig. 4b; Table 2), with

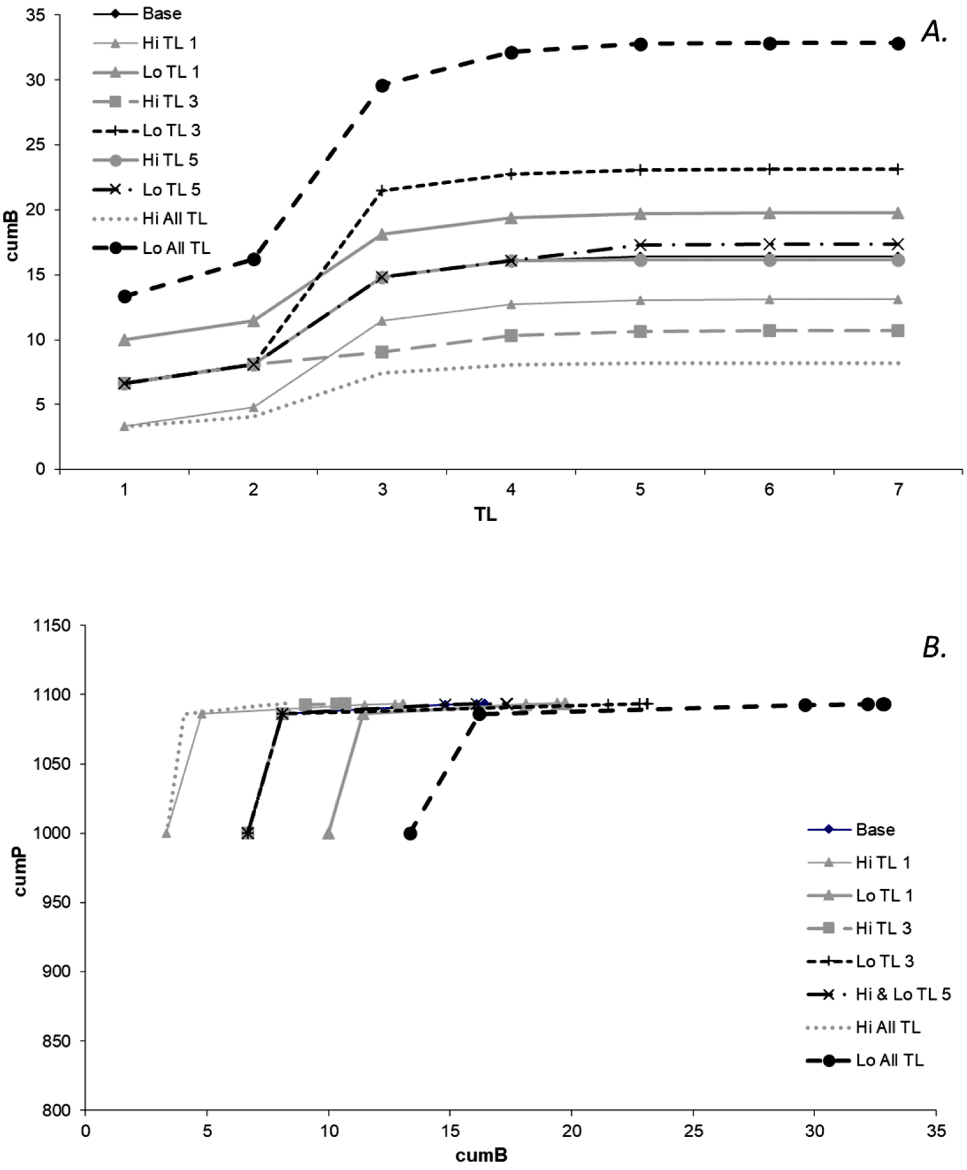

Fig. 3. A. The cumB-TL “S” curve across different levels of growth across various trophic levels (TL). B. The cumP-cumB “hockey stick” curve across different levels of growth across various TLs. See Table 1 for parameter details of these bottom-up scenarios.

the highest level of cumulative biomass among all of the scenarios explored. All the moderate-high or higher TE scenarios showed notable changes from the base scenario for the cumB-TL curve, but effectively no changes to the cumP-cumB curve (Table 2).

Shifting emphasis to more top-down considerations, the mortality scenarios (Fig. 5) match what would be expected with an increase in perturbation (Fig. 1g, h, , l-k). The “S” -shaped curves are more pronounced at lower mortality levels, and flatten out at higher mortality levels (Fig. 5a; Table 2). Although opposite in mechanism and hence sign (i.e., here the highest levels are the lowest curves), the “S” -shaped curves in these mortality scenarios (Fig. 5a) are qualitatively similar to the prior “S” -shaped curves noted (Fig. 2a-4a). That is, lowering mortality has the same response as increasing production or TE. The same holds true for the cumP-cumB curves (Fig. 5b). The “hockey stick” similarly enlarges or shrinks and moves toward the origin at lower and higher mortality levels, respectively (Fig. 5b; Table 2). The cumP-cumB curves do not fundamentally exceed a cumulative production, but those values do decline with higher mortalities (Fig. 5b; Table 2). The cumulative biomasses similarly decline with increased mortality (Fig. 5b; Table 2). These mortality scenarios show moderate changes from the base scenario for the cumB-TL curve, and very minor changes for the cumP-cumB curve (table 2).

The selectivity scenarios show similar but less pronounced responses (Fig. 6) as the mortality scenario curves (Fig. 5). There is less difference in the “S” -shaped curves (Fig. 6a; Table 2), and the scenarios that essentially test how much of a TL that is available for removal (e.g., mortality, fishing, etc.) has less of an impact. Again, higher effects across various TLs resulted in a shallower “S” shape, and vice versa (Fig. 6a; Table 2). The cumP-cumB curves (Fig. 6b; Table 2) similarly exhibited the same type of responses seen in the mortality scenario curves (Fig. 5b) but again were less pronounced. The difference in cumulative production across most of these scenarios was less than 5%. The exception is the highest selectivity effect, which had notably lower cumulative production. This effect resulted from allowing for availability to potential removal of both TL 1 and 2 in that particular scenario. Similar to the mortality scenarios, these selectivity scenarios had relatively minor differences to the base scenario (Table 2).

The final set of scenarios were meant to exemplify two common pressures facing marine ecosystems, i.e., overfishing and eutrophication. Both overfishing scenarios show a flattening and shrinking of the “S”

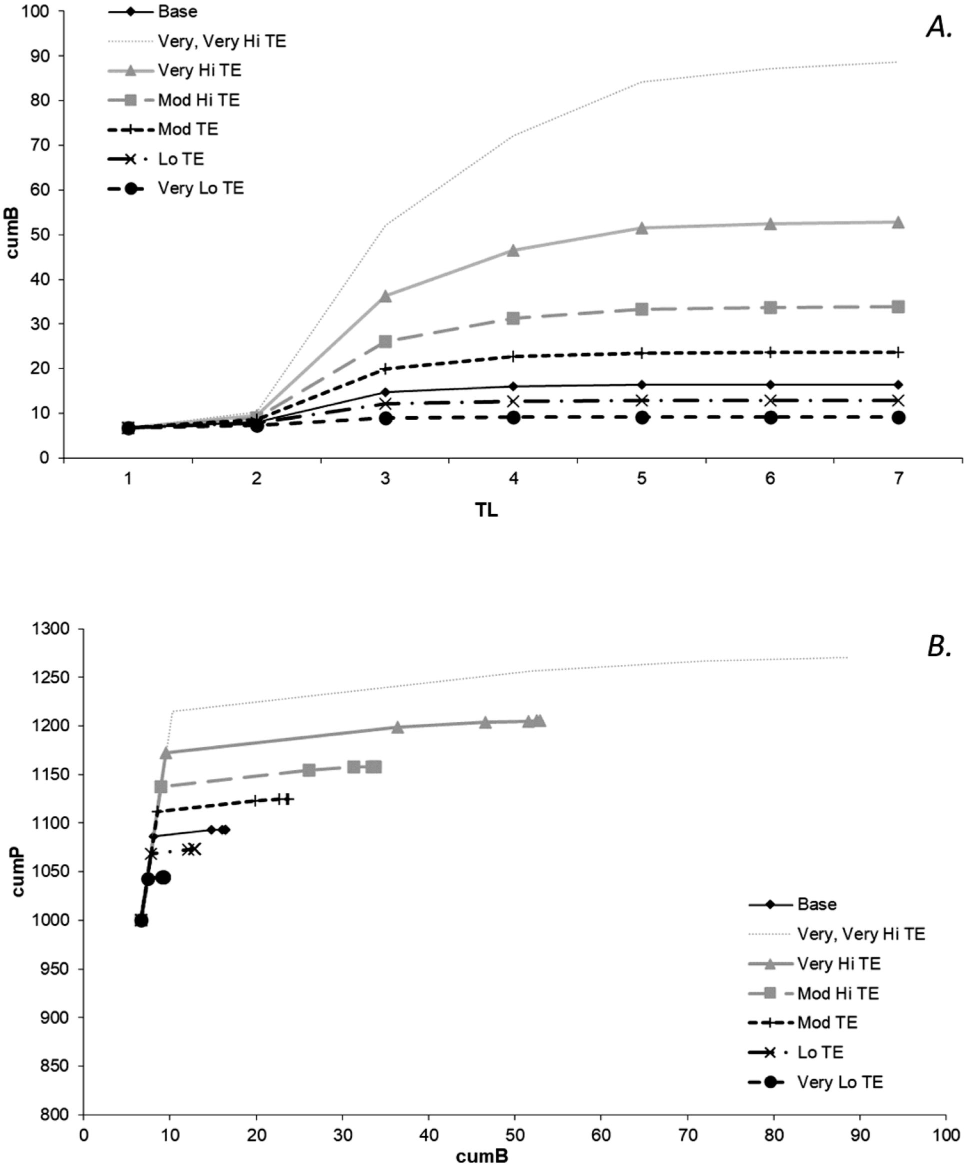

Fig. 4. A. The cumB-TL "S" curve across different levels of transfer efficiency (TE). B. The cumP-cumB "hockey stick" curve across different levels of transfer efficiency. See Table 1 for parameter details of these internal dynamics, efficiency scenarios.

-shaped curve relative to the baseline (Fig. 7a; Table 2), as would be expected (Fig. 1g, k). The cumP-cumB curves similarly show a shrinking and shortening of the "hockey stick," though the starting overfishing scenario (i.e., mild impacts) are relatively close to the base case scenario (Fig. 7b; Table 2). The full overfishing scenario had significantly eroded cumulative biomass, almost by a factor of two. The eutrophication scenarios are more nuanced. As eutrophication initiates, the "S" -shaped curve (Fig. 7a; Table 2) and cumP-cumB curve (Fig. 7b) shows an increase and even extension of cumulative biomass, consistent with an increase in production scenarios (Fig. 2). As eutrophication sets in, it actually flattens the "S" shaped curve (Fig. 7a; Table 2) and though it raises the cumP-cumB curve, does not increase available cumulative biomass (Fig. 7b, Table 2). At strong eutrophication, both the "S" -shaped curve (Fig. 7a; Table 2) and cumP-cumB curves (Fig. 7b; Table 2) exhibit patterns consistent with severe declines in production (Fig. 2) or increases in mortality (Fig. 5), reflective of the combined effects of severe eutrophication.

4. Discussion

Our model simulation results demonstrate that cumulative trophic theory can predict consistent and repeatable patterns in response to a range of common pressures facing marine ecosystems. These generally conform to a broad set of empirical observations (Pranovi and Link, 2009; Pranovi et al., 2012, 2014, 2020; Link et al., 2015, 2020; Libralato et al., 2019) and confirm the expected responses to positive (i.e., recovery) or negative (i.e., perturbation) conditions (Link et al., 2015; Libralato et al., 2019; Pranovi et al., 2020). That they arise from a relatively simple trophic transfer equation has high utility.

Across all these simulated scenarios, a few observations emerge. First is that the "S" and "hockey stick" -shaped curves are repeated across the various impacting mechanisms for this generic marine ecosystem. Although they did change shapes, no one scenario entirely obliterated these curve shapes, as expected from cumulative trophic theory (Fig. 1e, f). That the "S" and "hockey stick" -shaped curves were generally retained may be further evidence for the widespread utility of these patterns and the possible benefits of approaches that consider them. Second, the response of increasing top-down pressures or decreasing

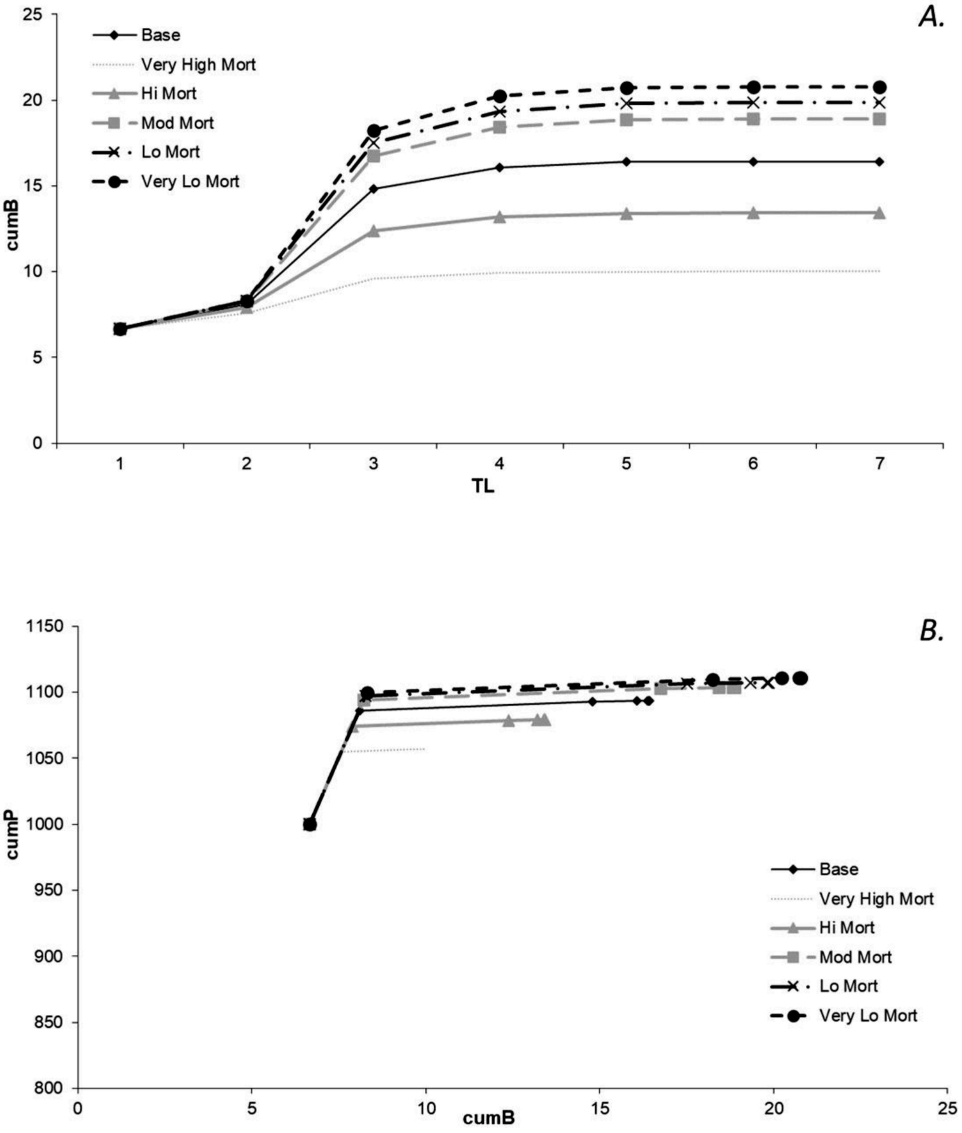

Fig. 5. A. The cumB-TL "S" curve across different levels of mortality. B. The cumP-cumB "hockey stick" curve across different levels of mortality. See Table 1 for parameter details of these top-down scenarios.

bottom-up factors generally resulted in responses on these curves consistent with perturbation (Fig. 1g-k). That the general responses shrunk, decreased and moved toward the origin regardless of specific mechanism of change demonstrates the common directional responses to perturbation, as well as the validity of the cumulative trophic theory. The converse holds as well; the response of increasing bottom-up factors and decreasing top-down pressures generally resulted in responses consistent with recovery of marine ecosystems. Another observation is that these scenarios demonstrate that they can accommodate nuances to a suite of conditions, as seen in the growth or eutrophication scenarios. That these curves are able to detect and present these nuances in eutrophication is useful.

Being able to address non-linear or at least non-obvious responses is requisite for a theoretical approach to be flexible enough to meet, and survive, "real-world" situations, even if they are simulated. These simulations resulted in predictable, repeatable, common and consistent patterns; that observation is not trivial. Flattening the "S" curve and shrinking the "hockey stick" under degrading scenarios, and vice versa, are in line with what one would expect from the cumulative trophic theory (Link et al., 2015; Libralato et al., 2019; Pranovi et al., 2020). That these patterns repeat under a wide range of simulated conditions and possible mechanisms is further evidence that this theory truly does describe major, emergent features of marine ecosystem dynamics.

Most pressures are relatively straightforward to understand, as are the cumulative curve responses. Increasing top-down or decreasing bottom-up factors (Micheli, 1999; Collie and DeLong, 2001; Lotze and Milewski, 2004; Frank, 2005; Hunt and McKinnell, 2006) results in readily observable perturbations to marine ecosystems. Conversely, increasing bottom-up and decreasing top-down factors (Lotze and Milewski, 2004; Myers and Worm, 2005; Hunt and McKinnell, 2006; Lynam et al., 2017) results in relaxation of these pressures, and even potential recovery, of marine ecosystems. Changes in bottom-up drivers responded as expected, as did changes in top-down pressures, but what about more specific cases? Selected TL removals that mimic apex predator reduction (Libralato et al., 2008) or fishing through the food web at lower to mid TLs (Essington et al., 2006) also had responses that would be expected. Given that the cumulative trophic theory was able to accommodate two examples of common pressures facing marine ecosystems—overfishing and eutrophication—that have more multi-faceted mechanisms, is also not trivial and a valuable outcome (e.g., Piroddi et al., 2021). Other common pressures that warrant testing in future studies include changing thermal conditions with particular

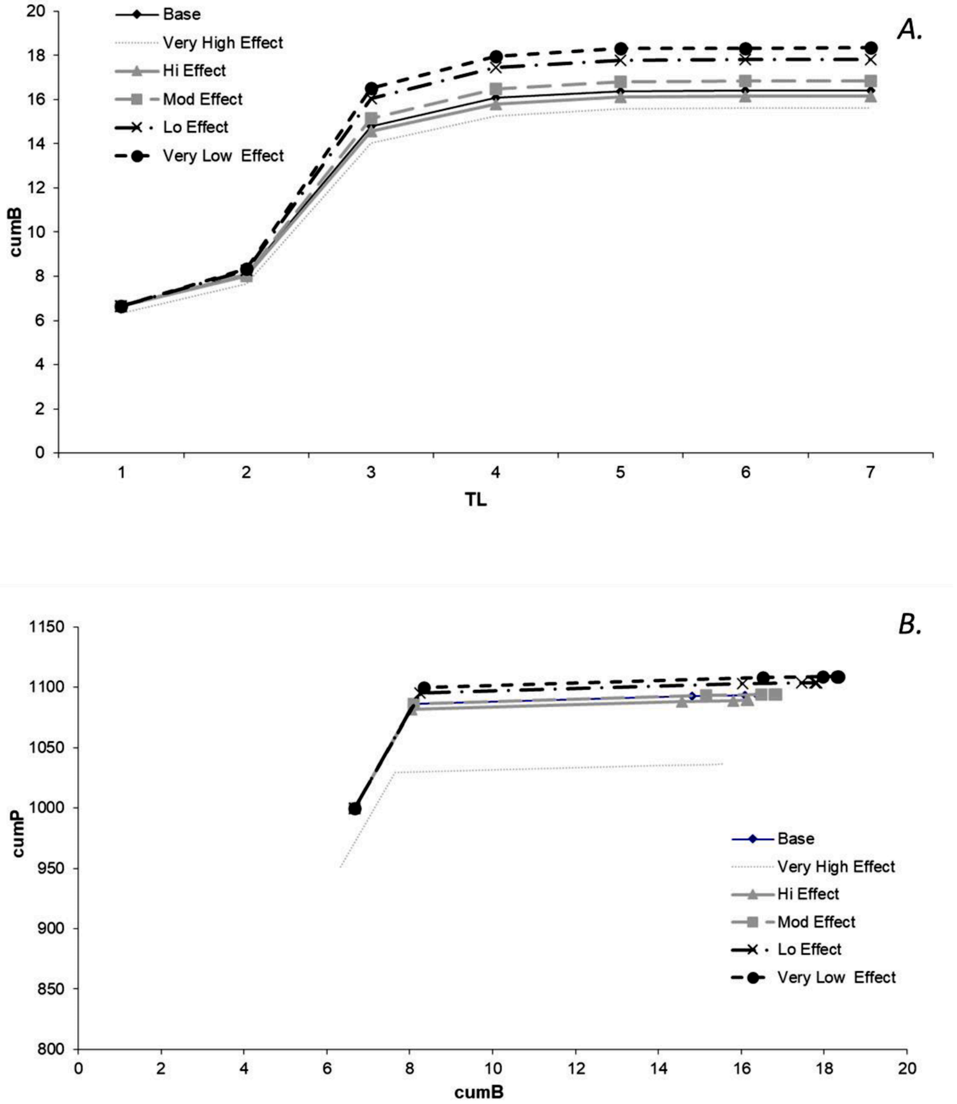

Fig. 6. A. The cumB-TL "S" curve across different levels of selectivity across various trophic levels. B. The cumP-cumB "hockey stick" curve across different levels of selectivity across various trophic levels. See Table 1 for parameter details of these top-down scenarios.

temperature links to growth or production (Libralato et al., 2015; Bentley et al., 2017; Serpetti et al., 2017), changes in acidification, pH and related chemical responses linked to mortality or growth (Zunino et al., 2021), changes in multiple ocean-uses across many sectors (Douvere and Ehler, 2009; White et al., 2012), efficacy of certain marine ecosystem management measures, including marine protected areas (Walters, 2000; Wood et al., 2008), food-web biomagnification of toxins, plastics and other chemicals (Kelly et al., 2007; Diepens and Koelmans, 2018), or even siting of offshore energy and impacts on ecological functioning (Gill, 2005), among others. Collectively this suite of scenarios demonstrates that the cumulative trophic theory, and the cumB-TL and cumP-cumB curves, can capture and predict the dynamics of marine ecosystems.

One seemingly counterintuitive response that warrants further exploration is the results seen from increasing growth. As treated here, we represented growth as P/B ratios (Shannon and Jarre-Teichmann, 1999; Heymans and Baird, 2000; Heymans et al., 2004). As a result of that term being in the denominator of some core equations to back-calculate biomass (EQ. (6)), increased growth resulted in a decline in overall standing biomass. Though this did not ultimately impact production and cumulative production, it did alter the accumulation of biomass along the trophic chain and thus the cumulative biomass. Again, we understand this to be indicative that faster (higher) growth rates tend to result in lower standing biomass, due to higher turnover rates of said biomass (Odum and Barrett, 1971; Gasol et al., 1997). Others have postulated that higher growth leads to higher standing biomass (Dortch and Packard, 1989; Gasol et al., 1997), and we understand that argument as well. Here we also accounted for removals of said biomass, so we suspect that is why our results align with those associated with the turnover rate explanation. Given that there is high standing biomass at intermediate trophic levels in marine ecosystems (DeYoung et al., 2004; Link et al., 2015) could also give undue weight to changes in growth for those organisms, at least in terms of cumulative responses. This is an area that merits further examination.

An important aspect of trophodynamics is the concept of trophic level (Lindeman, 1942; Libralato et al., 2014; Shannon et al., 2014). Here, we treat TL as an integer for simplicity in calculations. Certainly there is debate about what a non-integer TL means (Odum and Heald, 1975; Christensen and Pauly, 1992; Pauly and Watson, 2005; Shannon et al., 2014), and we appreciate that for a given taxa of marine species that the TL is not fixed across size, life history, seasonality, geographic location, etc. (Polis and Strong, 1996; Woodward and Hildrew, 2002; Layman et al., 2005; Hunt and McKinnell, 2006; Fort et al., 2010; Costalago et al., 2012). We suspect that integrating a more continuous

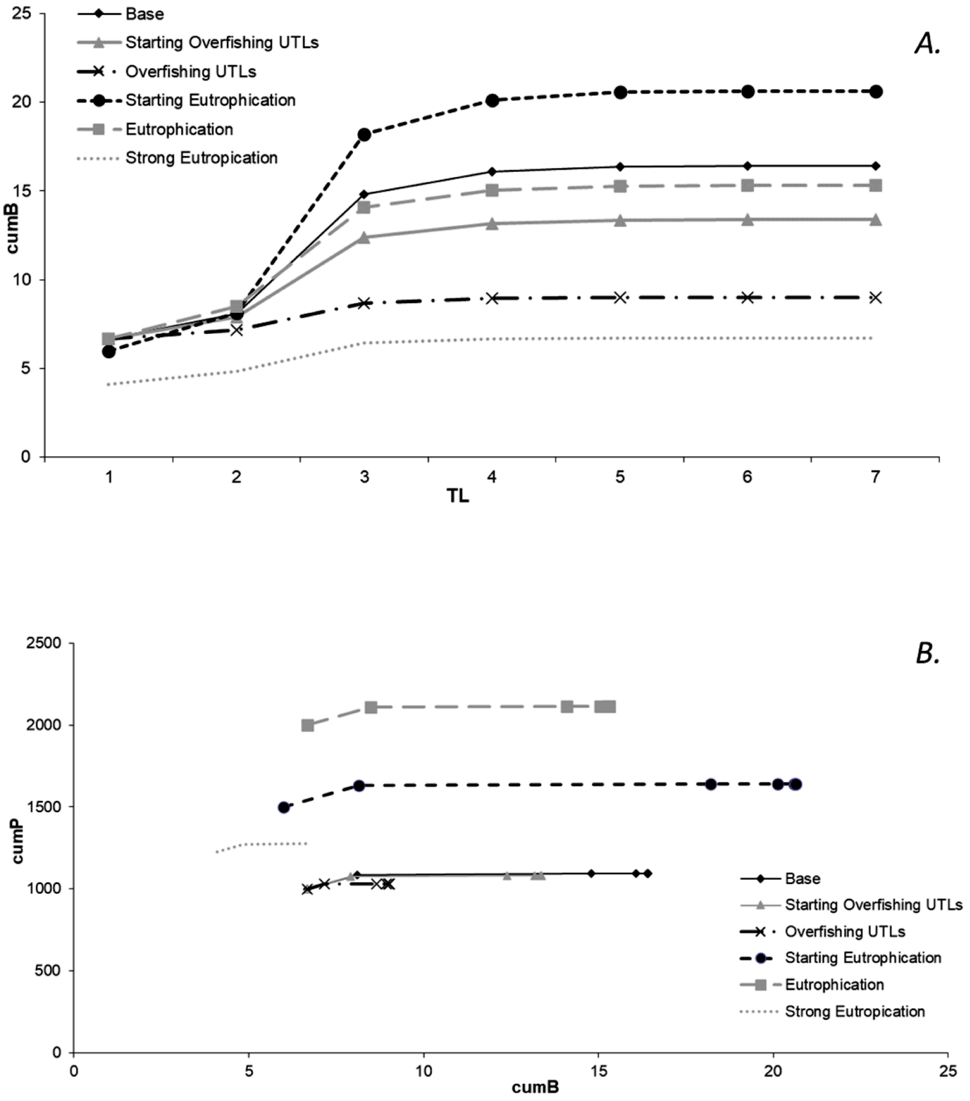

Fig. 7. A. The cumB-TL “S” curve across different levels of common pressures—over fishing and eutrophication—facing marine ecosystems. B. The cumP-cumB “hockey stick” curve across different levels of common pressures—over fishing and eutrophication—facing marine ecosystems. UTL = upper trophic level. See Table 1 for parameter details of these special, mixed-effects scenarios.

treatment of TL that also considers the pathways of interactions among species (e.g., O’Gorman and Emmerson, 2009) and pressures (e.g., Agnetta et al., 2019) in the food web that are more complicated than in a linear food chain will result in broadly comparable results, and preliminary examinations tend to confirm that suspicion. Future work examining a continuous treatment of TL beyond the discrete approach presented here is warranted, as well as the analysis using complex ecosystem models that might detect potential counterintuitive effects and also might provide further support to the cumulative theory (Link et al., 2015). They could also be used as tools to test thresholds (Libralato et al., 2019).

One intriguing, aspect of the core trophic transfer equation (EQ. (1)) is the value of the transfer efficiency itself. That term alone merits further consideration. Transfer efficiency is often central to the results in analyses like these (Link et al., 2015; Libralato et al., 2019; Pranovi et al., 2020; Eddy et al., 2021), as well as many marine food web and ecosystem models (e.g., Christensen and Pauly, 1992; Heymans and Baird, 2000; Pauly et al., 2000; Libralato et al., 2004). Typically TE is assumed to be approximately 10%, which came from very early studies (Lindeman, 1942; Odum and Barrett, 1971; May 1976; Pauly and Christensen, 1995), though more recent studies, reviews, and meta-analyses suggest that TE is somewhat higher (Libralato et al., 2008). There is no means to directly measure TE in a marine food web, at least across entire TLs, and thus the TE term is highly derived. Although what we present here spans the likely range of values (Colléter et al., 2014, 2015; Heymans et al., 2014; Eddy et al., 2021), it was obvious that the value of this TE term had large effects on model results. A prior sensitivity analysis (unpublished data) similarly demonstrated the impact of changing the TE term. In the current context, this hyper-responsiveness to changes in some TE scenarios is seen in the response of the cumulative curves. Thus, not only for this particular context but for trophic ecology more generally, we recommend further examination and exploration of the assumptions surrounding TE, as well as novel ways to estimate or measure it.

Odum (1969); Jorgensen, (2001) notes that ecosystems tend to optimize the use of energy by modulating their trophic structure along a continuum between high levels of energy flow (early development stages) and high levels of standing biomass (mature development stages). These ecosystem “development” stages seem to be well accommodated by the cumulative trophic theory and associated curves, with modifications to curve properties corresponding to the different ends of the ecosystem maturity continuum (Odum, 1969). For instance, the shrinking of the cumB-TL curve under perturbed conditions could very well be related to a reduction of the standing biomass, and hence increased energy flows, and even a reduced system capability to saturate the use of available energy (e.g., increasing losses and wastes of metabolic expenditures or the presence of bottle necks in the food web energy transfer). The cumulative trophic theory has not been developed without broader context, yet further exploration of how it is connected to other means of framing and understanding ecosystem dynamics is warranted. We particularly note that the cumulative trophic theory here has been explored in marine ecosystems; how applicable it is to other types of (non-aquatic) ecosystems remains an interesting question.

The value of any theory is often heightened in how it handles caveats, or nuanced circumstances. Here the cumulative trophic theory was able to accommodate those, especially in the growth, selectivity, and eutrophication scenarios. Recognizing that, for example, eutrophication is not linear nor uni-directional is important, and we were able to represent that nuance in this model construction. A relatively simple equation, when explored in multiple views with a particular emphasis on cumulative, emergent features, can provide a surprising amount of insight into marine food web dynamics. Testing any theory, no matter how simple, benefits from mathematical formulation, simulation, sensitivity analyses, and application to (near) real world conditions (Caswell, 1988; Jørgensen and Bendoricchio, 2001; Cariboni et al., 2007). Here we demonstrate that the cumulative trophic theory can be confronted with, and survive, those conditions.

The value of the cumulative trophic curves remains high, and is improved even further by this theoretical, simulated treatment of its features. The commonality of “S” and “hockey stick” -shaped curves is growing with each study that actually looks at cumulative biomass and production (Pranovi and Link, 2009; Pranovi et al., 2012, 2014, 2020; Link et al., 2015, 2020; Libralato et al., 2019), such that these patterns are observed in essentially every marine ecosystem that has been examined. Certainly, additional marine and aquatic ecosystems warrant cumulative curve examinations, as do terrestrial ecosystems, to verify the ubiquity and veracity of this theory and its predictions beyond the large marine ecosystem context. Yet the global observations from over 200 marine ecosystems (Link et al., 2015; Pranovi et al., 2020), from over 70 years of data (Libralato et al., 2019), and across a wide range of perturbations and histories is compelling evidence, suggestive that this cumulative trophic theory has continued merit. Our ability to predict and repeat the responses of these curves to common pressures via known mechanisms increases the utility of these cumulative, emergent properties of marine ecosystems. The application of cumulative trophic theory for the wise management of marine ecosystems has higher utility knowing we can more repeatedly and comfortably predict their responses to a wide range of conditions. Thus the applications that may follow might prove useful for the even wiser management of marine ecosystems (Link et al., 2015, 2020; Libralato et al., 2019; Pranovi et al., 2020). More so, that a relatively simple equation can depict, capture and predict such a wide range of marine ecosystem dynamics across a broad array of situations is not trivial, and further suggests the robustness of the cumulative trophic theory.

Author credit statement

All authors contributed to the conceptualization of this work, and its analyses, interpretation, writing, review, and graphics.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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