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Assumptions about Trophic Cascades: The Inevitable Collision between Reductionist Simplicity and Ecological Complexity[1]

By

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Highlights

1. **Several trophic cascade assumptions and their logical outcomes are flawed.**
2. **Marine food webs cannot be controlled in the sense of the machine metaphor.**
3. **Loop analysis shows that sometimes the role of trophic cascades has been exaggerated.**
4. **Ecologists should apply complex system thinking in studying food webs.**

Abstract:
The assumptions ecologists make both influence and constrain their conclusions. Too often these assumptions are not explored or validated rigorously enough. The purpose of this paper is to critically review seven trophic cascade assumptions frequently used in the current literature and to identify whether their conclusions are compatible with results from loop analysis. Assumptions center upon food web conceptualization, food chain to food web extrapolations, constancy of food webs, role of driving forces or parameter inputs, top-down versus bottom-up phenomena, associated dichotomies, and the notion of food web control by keystone predators and parameter inputs. Data-fitted marine loop models involving about 500 species show how complex, biologically-reasonable food webs are qualitatively different from food chains as well as simple intuitive food webs. Both supporting and opposing views of other authors are contrasted in regard to loop analysis results. This review concludes that the roles of trophic cascades are sometimes afforded an exaggerated importance using over-simplified reductionist logic especially in marine pelagic food webs. It would be useful if these seven assumptions could be similarly analysed using other modelling methodologies to determine a more realistic role for trophic cascades and to facilitate consensus among ecologists. It would also be worthwhile to construct data-fitted loop models for more types of ecosystems. Regardless, biological reality should not be sacrificed for convenience.

Key Words: Trophic Cascade, Trophic Escalade, Marine Food Webs, Loop Analysis, Keystone Predator, Control

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[1] Abbreviations: ES(s) = Ecological Skeleton(s), KP = Keystone Predator, LA = Loop Analysis, PI(s) = Parameter Input(s), TC = Trophic Cascade, TCC = Trophic Cascade Concept, and TE= Trophic Escalade

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1.0 Introduction

Today, there is a massive literature on trophic cascades (TCs) (Hanley and LaPierre, 2015; Terbough et al., 2010). Ripple et al (2016) identified more than 2200 theoretical and empirical papers involving a TC focus published by 2015. There are also increasing numbers of applied studies using the Trophic Cascade Concept (TCC) for environmental management and conservation purposes (Ripple, et al., 2014, Mills, et al., 1993). Underpinning this extensive literature is a set of somewhat conflicting definitions and problematic concepts, many originating from the first research on the concept. The TCC has become so entrenched in current ecological thinking and research that we often do not review its conceptual base in detail, rather it is assumed to be fact or foundational. The purpose of this paper is to examine seven common TC assumptions and their conclusions using loop analysis (LA), a signed digraph network technique. This paper illustrates that many of these assumptions arose earlier in studies of food chains and simple food webs. While simplicity can be convenient, if too reductionist, it can obfuscate ecological reality and be counterproductive. Since the TCC is so central to food web ecology, it is important to clarify potential logical pitfalls in its assumptions.

Each investigator selects their preferred methods and tools to observe the natural world (Lane, 1986). Observing modes vary from intuitive constructs to formal models (differential equations, simulations, statistical analyses, etc.), to laboratory experiments, and field observations among others. This paper does not aim to praise or criticize other investigators and their observing modes, but only to identify how LA results either support or refute many of the working assumptions investigators currently apply in TC studies. While LA supports some assumptions and conclusions, beyond this partial agreement, the methodology provides a systematic methodology to evaluate all of the assumptions holistically.

To make the literature manageable, my objectives and methods are restricted. First, I limit my observations and remarks largely to pelagic marine food webs despite the frequent conclusion that identifying TCs is often difficult in the ocean (Hessen and Kaartvedt, 2014). Probably many results described here are also applicable to freshwater, terrestrial, and coastal marine ecosystems such as salt marshes, the rocky intertidal, and mangrove swamps. Although it is technically possible to construct data-fitted loop models for any ecosystem, to my knowledge these models are not presently available for other types of ecosystems. Even after restricting the ecosystem type, only a portion of the vast pelagic marine literature could be reviewed, and the examples used here are more illustrative than comprehensive. Second, it is beyond the scope of the paper to delineate the logic pathways from assumptions to conclusions employed by each author in minute detail as Murdoch (1966) did for the Green World Hypothesis of Hairston Smith and Slobodkin (1960). He essentially analysed each word. Thus, I simply lump these logic statements as either assumptions or conclusions, and point out both the logical and ideological leaps between them. Some conclusions serve subsequently as assumptions for further conclusions, but are treated independently here. Third, I limit the discussion to density-mediated TCs that are best handled by LA and ignore trait-mediated phenomena. Fourth, LA is a qualitative technique so I also ignore discussions of strong versus weak TCs. Whereas, loop models can in theory be made quantitative, these efforts have not yet been realized. Fifth, I do not examine the evidence for or against any specific TC; I assume TCs exist in nature, although perhaps not as frequently or as exactly as reported. Thus, my focus is on how we think about TCs and the ramifications of this thinking, if the observing mode is LA.

This paper is arranged in two parts. First, LA methodology, TC definitions, and field results using LA for Narragansett Bay are summarized in Section 2. Second, the seven assumptions and their conclusions are listed with representative opposing quotations from the literature, followed by a LA explanation with supporting quotations from authors not using LA, but who agree with its results (Section 3). These latter quotations illustrate that LA observations and explanations are well within current ecological thinking. All assumptions taken together provide a more coherent basis for subsequent TC studies, as well as more realistic expectations of what will be possible in management applications.

2.0 Loop Analysis and Field-Models

2.1 Loop Analysis Methodology

The mathematical basis underlying LA was created by Richard Levins (1973, 1975) and has been discussed by many authors and is not repeated here (Lane and Levins, 1977; Puccia and Levins, 1985; Lane, 1986; Wright and Lane, 1986; among others). Loop models include large circles to represent variables and signed (+,-) lines between pairs of variables two indicate interactions. An arrowhead touching a variable indicates a positive effect and a circle head represents a negative interaction on the variable it touches. The parameter input (PI) for a given model is illustrated as an enlarged, unconnected bold-face arrowhead (+) or circle head (-) on the variable it touches; this stressor originates outside of the network such as the driving forces in computer simulation models. All links for a single LA graph can also be illustrated in a matrix format similar to the Community Matrix of interaction coefficients (Levins, 1968; Vandermeer, 1990; and Mittelbach, 2012).

A loop diagram can be decomposed into its pathways and feedback loops. A pathway is a single route beginning at one variable and ending at another by entering and leaving each intervening variable one time each. Pathways can be of any length up to N, the total number of variables in the network. Pathways of zero variables (P_o) = +1 by convention. Pathways can be further divided into ‘operating ‘and ‘non-operating. To operate and have an effect on other variables, a pathway must have a valid complement, that is, all variables not on the path must be in at least one set of disjunct loops that do not share variables with each other. Feedback loops are closed pathways that return to the original variable, and like paths, can include up to the total number (N) of all variables in the network. Feedback of zero variables (F_o) = -1 by convention.

Signs of pathways and feedback loops are calculated by multiplying the links algebraically. Using traditional LA calculations, feedback can be calculated at each level of the loop model up to and including F_N, the total feedback of the whole system. In addition, LA includes specific equations that can be used to calculate the abundances of all variables in the network for each possible positive or negative PI. These results are placed in a square matrix termed the Community Effects Matrix, with each row giving the predictions for a single parameter input. For parameter inputs of different signs to the same variable, predictions of zero remain the same and the signs are flipped, that is, positive predictions become negative, and *vice versa.* To date, most loop models have been theoretical.

Lane (1986, 2016, and 2017, In Press) has developed a methodology for fitting loop models with field or laboratory data. Using this methodology, it is possible to determine the most likely operating pathway that produces changes in nutrient concentrations and biotic variable abundances from one date to the next. Thus, the predicted changes in abundances are compared to those that occurred in nature, and a loop model is constructed with the best fit possible using the most likely PI. Usually, this fit is 95% or better. This process is explained in Lane (1986, 1998, and 2016). For the Narragansett Bay study, abundance data were collected around an annual cycle for several dates and at several depths per date. This enabled the construction of several loop models (8-10 for the field) per year. Once the individual models are constructed, they can be summarized as an ecological skeleton (ES) consisting of the most frequent variables, links and PIs. The individual loop models essentially represent the minimal food web structure and main operating pathway that produces the observed changes in the variables from one date to the next for the best fitting PI in terms of its sign and location. Although presently only a conjecture, eventually it may be possible to prove that the links in these data-fitted diagrams are not only the most frequent, but also represent the strongest interactions in the food webs.

LA can also test for stability using the Routh-Hurwitz criteria (Puccia and Levins, 1985). These criteria include: (1) feedback at each level should be negative, and (2) negative feedback at lower levels should be stronger than at higher levels. Level is defined as the number of variables in a feedback loop up to N maximum. According to these criteria, the individual models in Figure 2 are stable, but not the ES in Figure 1, which constitutes a summary description of the variables and links that operate throughout an annual cycle. It is too interconnected to be stable and likely does not exist in nature.

For the purposes of this paper: a trophic cascade (TC) is defined as all or part of an operating pathway, including at least three adjacent variables, starting with a variable at or near the top of the food web and ending with a variable at the bottom, with all the links on the pathway representing predator-prey and consumer-resource interactions that produce a checkerboard pattern (+ - + or - + -) of changes in the abundance of the path variables. In addition, we also need to consider upward pathways. A trophic escalade (TE) is defined as all or part of an operating pathway, including at least three adjacent variables, starting with a variable at or near the bottom of the food web and ending with a variable at the top, with all the links on the pathway representing predator-prey and consumer-resource interactions that produce a uniform pattern of changes (+ + + or - - -) or that can sometimes include zeros on alternative levels of the pathway (+ 0 + or 0 + 0) or (– 0 – or 0 - 0). Depending upon the level of complication in a food web, there can be more than one TC and/or TE.

2.2 Loop Models of Narragansett Bay Plankton Community

Figure 1 illustrates the ecological skeleton (ES) for an annual cycle for a field study of Narragansett Bay involving a set of 10 cruises conducted at the Marine Ecology Research Laboratory (MERL) of the Graduate School of Oceanography, University of Rhode Island. Figure 2 compares the nine individual loop models constructed by fitting the cruise data that serve as the basis for the ES.

The food web structure of the Narragansett Bay plankton community is essentially a three-tiered lattice, as if three food chains were horizontally parallel to each other with some key cross-links. Models generally have ranged between 15 and 25 variables representing about 500 plankton species and nutrients. In marine food webs analyzed to date, predator-prey and self-damping links constitute the main loop types of one and two variables respectively. Non-trophic links, while infrequent, are important for the overall qualitative structure of these systems. A subsystem of small algae and other plankton is attached to the left of the main nutrient variable, N_1 (Lane, 2016). This subsystem is not fully described because of data inadequacies in taxonomy and sampling for this micro-community. Even smaller nano-plankton and pico-plankton species were not sampled in these studies as well as vertebrate predators. Refer to the original publications for more detail and explanation (Lane, 1986; 1998, 2016, 2017 In Press, Lane and Collins, 1985).

To date, no two loop models have been identical. 'When is one food web not like another?' can be a difficult question to answer (Polis, et al., 2000). In approximately 1000 loop models constructed to date for coastal planktonic food webs, both the three-tier lattice configurations and the species lists per variable have been highly similar across many different ecosystems and mesocosm experiments. Lane (2016) calculated the similarity coefficients for a set of field loop models and found they were on average 85% similar in terms of their variables and link types over an annual cycle. Thus, there is a certain amount of normal change in food web structure throughout the year, in this case, about 15%. This occurs because of the life history dynamics of the food web species, changes in predator-prey interactions, presence or absence of self-damping loops, migrations in and out of the community, varying physiological, behaviors, and other adaptations, etc. that occur over an annual cycle. These small structural changes are not, however, unnatural or irreversible.

Figure 1. Ecological Skeleton Constructed from Individual Data-Derived Loop Models Given in Figure 2 for Marine Plankton Communities in Narragansett Bay. Key to the variables: Si=silica, N_1=nitrogen/phosphorus ratio, N_2=organic nitrogen, A_1=diatoms, A_2=dinoflagellates, A_3 =luxury-consuming diatoms, A_4=miscellaneous algal group, A_5= micro flagellates and monads, A_6= silica flagellates, Z_1=copepod adults group 1, Z_2= all copepodites and nauplii, Z_3=copepod adults group 2, Z_4= cladocerans, P=polychaete larvae, M=mollusc larvae, C=cirriped (barnacle) larvae, D=decapods, S=*Sagitta* spp. (chaetognaths), G=gammarids, MD=medusa (coelenterates), and R=rotifers. Main parameter input is the disconnected positive arrowhead to N_1 .

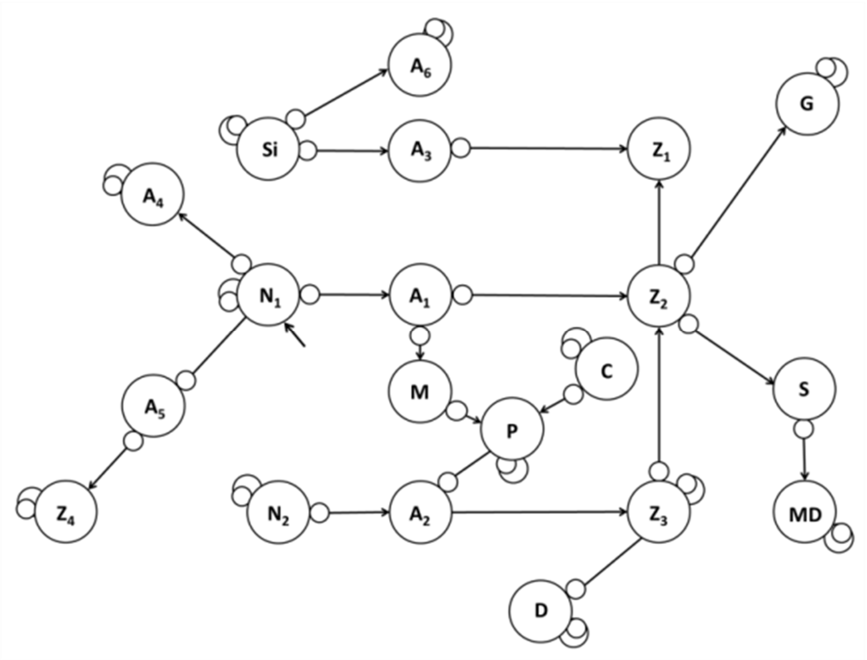
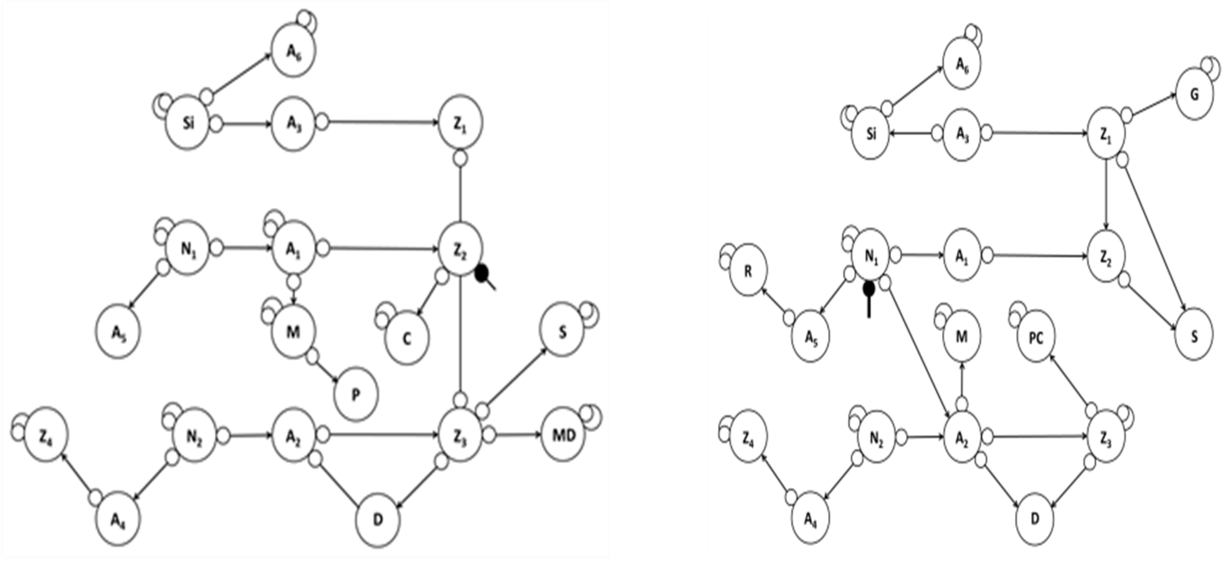


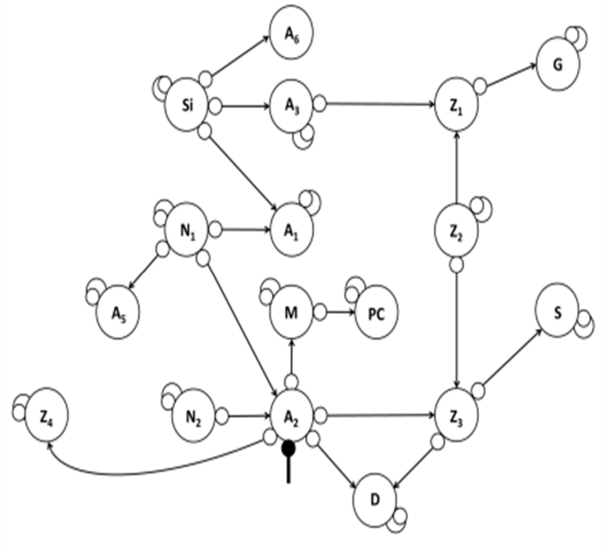
Figure 2. Nine Individual Field Loop Models of the Plankton Community in Narragansett Bay as a Succession Of Models from One Date to the Next for Dates 1-10. Parameter inputs are shown as arrowheads (+) or circleheads (-) in boldface type. Key to variables: Si=silica, N_1=nitrogen/phosphorus ratio, N_2=organic nitrogen, A_1=diatoms, A_2=dinoflagellates, A_3 =luxury-consuming diatoms, A_4=miscellaneous algal group, A_5= micro flagellates and monads, A_6= silica flagellates, Z_1=copepod adults group 1, Z_2= all copepodites and nauplii, Z_3=copepod adults group 2, Z_4= cladocerans, P=polychaete larvae, M=mollusc larvae, C=cirriped (barnacle) larvae, D=decapods, S=*Sagitta* spp. (chaetognaths), G=gammarids, MD=medusae (coelenterates), and R=rotifers. Main parameter input is the disconnected positive arrowhead or circlehead.



a. Date Change: 1-2

b. Date Change: 2-3

c. Date Change: 3-4



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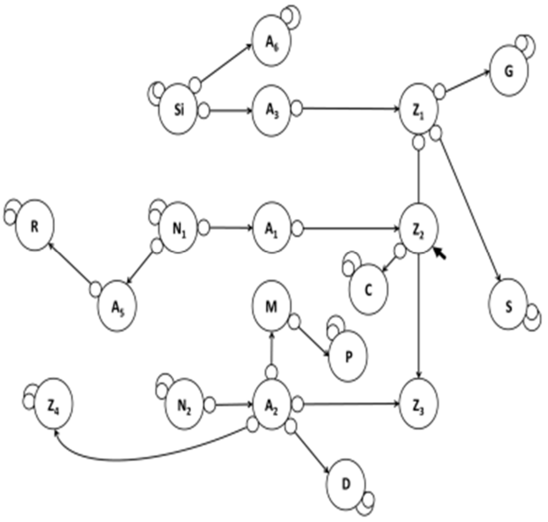
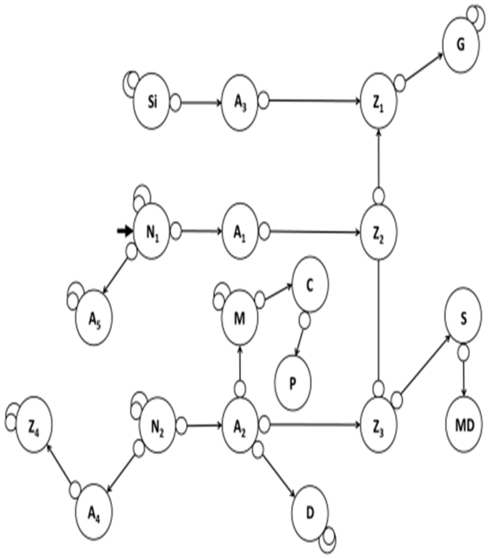


e. Date Change: 5-6



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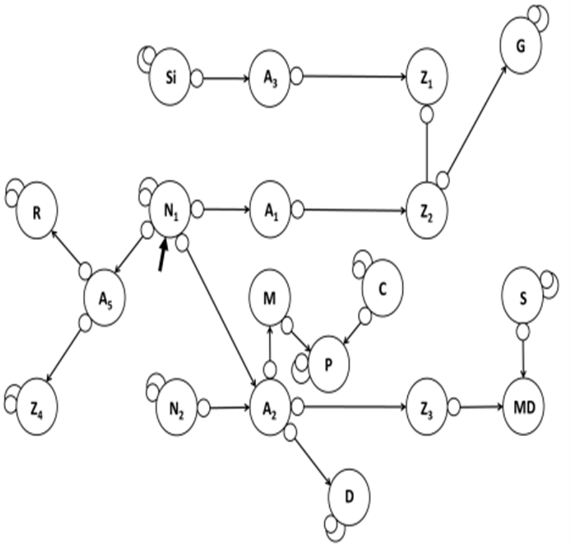
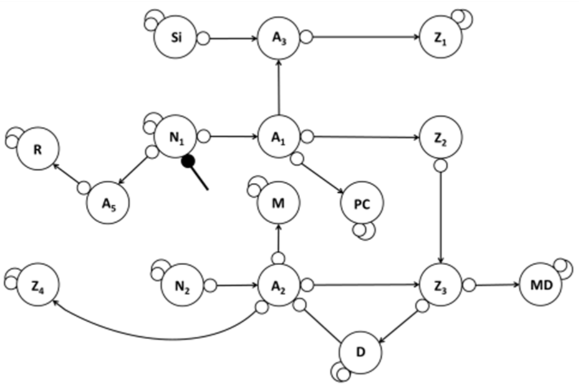
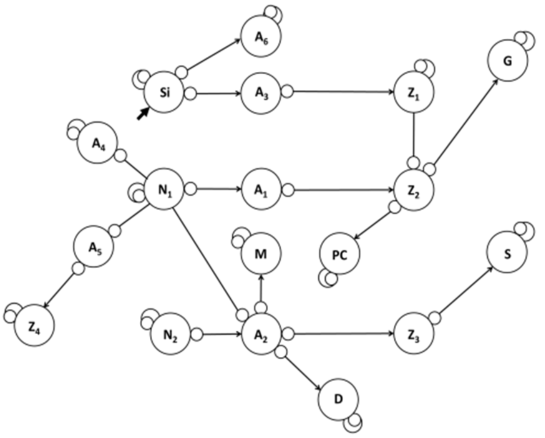


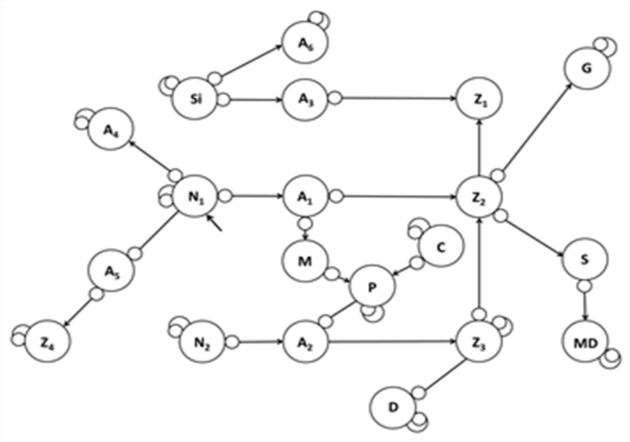
g. Date Change: 7-8

h. Date Change: 8-9





i. Date Change: 9-10



3.2 Seven Trophic Cascade Assumptions and Conclusions

Using the literature, seven common TC/TE concepts and assumptions with their associated conclusions are summarized in Table 1. For each assumption, some representative literature quotations are provided as well as my own additional comments, which are enclosed in square brackets. Then explanations using LA results are presented to explain how the assumptions and conclusions are viewed using LA. Each subsection concludes with quotations that support the LA explanation by other authors. It was not unusual to find the same authors who both agree and disagree with LA conclusions across the seven assumptions.[3]

Table 1. List of Trophic Cascade Concepts, Assumptions, and Conclusions Associated with Marine Ecosystems. Note: impact and effect (change) are used as synonyms in this paper.

CONCEPTS AND ASSUMPTIONS	CONCLUSIONS
A1. The food web of interest is understood.	C1. The food web conceptualization or model accurately depicts nature well enough to identify a TC and evaluate its role.
A2. Food chains function like simple food webs of a few trophic levels.	C2. Food chain results can be extrapolated directly to food webs and inform them without consequence.
A3. Food webs are constant during an annual cycle.	C3. Food webs have integrity that can be identified in any season or year unless so strongly perturbed as to transition to an alternative state (regime shift).
A4. A parameter input is unique and constant.	C4. If the PI can be identified, we can understand food web structure and function over time.
A5. Food webs respond either top-down (trophic cascade) or bottom-up (trophic escalade).	C5. A single food web is impacted either top-down or bottom-up continuously; top-down is considered more frequent and important than bottom–up.
A6. Trophic cascade approaches can be divided into several meaningful binary subcategories.	C6. Several dichotomies are real, operational, and useful: a) Direct versus indirect effects b) Species level versus community level effects c) Trophic cascades vs. apparent trophic cascades d) Odd vs. even number of trophic levels
A7. Variables and/or parameter inputs at the top of a food web have special roles in trophic cascades and food webs.	C7. Top predators, other keystones, and/or PIs, especially at the top of a food web, can 'control' food web structure and function.

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[3] I apologize in advance to authors for excerpting small quotations that were taken from their larger text. These excerpts were only used as examples for the various assumptions and not meant to be a criticism of the overall work.

Assumption 1: The food web of interest is understood.

Conclusion 1: The food web conceptualization or model accurately depicts nature well enough to identify a TC and evaluate its role.

Representative Quotations 1:

1. "[There are] three distinct approaches to constructing food webs, illustrated for the same set of species/functional groups found in marine intertidal zone of Tatoosh Island, off the coast of Washington State [as described by Paine, 1980]. (A) A connectedness web, based on observation of who eats whom. (B) An energy flow web, based on estimates of biomass consumption…and (C) A functional web, based on species removal experiments", (Mittelbach, 2012, p 202).

2. Based on the assumption that each trophic level acts as a single exploitative population, a model relating the trophic structure of ecosystems to their potential primary productivity is developed", (Oksanen, et al., 1981, p 258). [4 trophic levels: plants, herbivores, carnivores, top carnivores, and essentially all biological interactions can be subsumed within these few trophic levels. See also Persson, 1999].

3. "The US Northeast shelf ecosystem has a speciose, highly connected food web. [81 species, 1562 links]…The value for the mean number of interactions per species (linkage density, 19.3) confirms that this is a highly connected food web", (Link, 2002, p 3). [It seems unlikely that this complicated model, essentially a connectedness web, and the previous minimalist one in No. 2 are both biologically-reasonable].

LA Explanation 1: This is perhaps the most common and most problematic of all the assumptions; it is rarely addressed. Presently, there is such a plethora of food web models that clearly not all can be the 'best' or even satisfactory representations of nature. Probably most are not biologically-reasonable, that is, not likely to occur in nature (see also Winemiller and Layman, 2005 for a review of this issue). The food web in Quotation 2 above is extremely minimal, whereas the food web in Quotation 3 appears overly complicated. Lane (2016) discussed the perennial problem of identifying the Goldilocks' or 'just right' level of ecological complication in food webs. Thus, if the model employed to study TCs is poor, the results cannot be expected to be very useful. Food web descriptions have consequences.

In the food web conceptualization process, decisions are never-ending involving how much to lump or split variables, to use only biotic or a mix of biotic and abiotic variables, to use particular units (abundances, kilocalories or grams of carbon), or types of links to include (one-way, two-way, signed or unsigned, etc.). Some investigators even confuse the variables or links within the food web with the one-way driving forces or PIs that are external to the system. In addition, it is difficult to find papers in which authors critically evaluate their own models. One exception is Fedor and Vasas (2009) who tested for false positive and negative links in 26 food webs, but they did not evaluate the validity of variable aggregations, which are closely tied to link number and type. Persson (1999) suggested that trophic levels should be replaced with the new concept of variable aggregation based upon interactions so that species or groups of species that consume the same food or are resources for the same predators should be lumped together. This is essentially how variables are aggregated in LA.

There are many ways to be wrong when selecting and constructing models to conceptualize a food web, and probably only a few ways to be correct. Quotation 1 above includes the three main approaches discussed by Paine (1980) almost four decades ago. He termed them: (1) the connectedness or structural food web usually based upon presence-absence data; (2) the energy flow food web in which often the thickness of the bivariate links were proportional to the amount of energy flowing between the two variables; and (3) the functional approach based upon experimental manipulations of the food web, especially predator removal experiments (Mittelbach, 2012). These three basic categories have blurred, proliferated, and subdivided over time. The range of both empirical and modelling techniques has greatly expanded and user-friendly computer accessibility of these methods has greatly improved. For example, Williams and Martinez (2008) compared cascade, niche, and nested hierarchy models, whereas Fulton et al. (2003) contrasted several other types of models: multi-species, biomass size-spectrum, static aggregate, dynamic aggregate, and biogeochemical. It is beyond the scope of this paper to review these methods in detail and attempt a detailed categorization scheme, but I can provide a few comments about how LA relates to Paine's scheme, and in particular, to illustrate how his categories have become blurred.

At first glance, LA appears to be a highly flexible connectedness or structural food web methodology as per Paine's approach No.1. Using the intuitive approach, the investigator can simply decide on the presence or absence of the variables and links. Variables can be both biotic and abiotic and can include a vast array of disparate components with the proviso that these variables are interconnected and essentially 'moving' with similar temporal dynamics while PIs are either slower or faster. Similarly, in mathematics, parameters are treated as constants in relation to the co-varying variables. For example, Levins (pers. comm.) has used fishery managers and regulations as variables with fish and their food sources to study issues about managing fish populations. Since links encompass the full set of 9 qualitative types (+, -, and 0 or 3^2) that can possibly occur between two variables, LA can represent both food webs and ecological networks. Many structural food web models include only one type of link such as positive arrowheads to predators. This substantially reduces their capacity to embed information within the food web structure. LA also includes a set of calculations for predicting community effects as a function of PIs as well as measures of stability.

If loop models are data-fitted, however, then they can also represent Paine's approaches 2 and 3. For example, once the variables and links are known they can be quantified in terms of energy units using appropriate field and laboratory techniques for approach No. 2. With approach No.3, there is much more 'blurring '. This is an approach that has traditionally had an empirical foundation, in which manipulation experiments define function. Leaving aside how difficult and unnatural the experimental logistics can be in many environments, this is not the only way to arrive at functional understanding. At best, much of the empirical understanding is centred upon determining changes in population abundances, for example, of prey populations when their predator is removed. There is a lot more to food web function than changes in abundances. Theoretical approaches can also give us insight into function. For example, with LA we cannot only calculate changes in population abundance via the community effects matrix, but we can identify feedbacks and operating pathways and test for stability that also reveals a lot about food web function (Lane, 2016). Thus, loop models could be used to represent all three of Paine's (1980) approaches. In addition, a better understanding of food web function will provide improved understanding of ecological complexity beyond the mere enumeration of nodes and links in ecological complication.

A final concern is that by the time a food web has been conceptualized, perhaps formally modelled and data collected, a great number of arbitrary decisions have been made. For example, in LA, there are no absolute definitions, however, as to what is slow or fast, similarly there are no absolute definitions of how to determine a change in a food web model (+, -, or 0) or in an abundance value, or in the criteria we use to test for significance and difference using standard statistical methods. Many of these decisions involve a continuum of values. We make arbitrary decisions about cut-off points and thresholds so that science can proceed. Being arbitrary is usually not a choice, but how to be arbitrary, and to minimize the consequences, can be at least partially addressed. All of the assumptions discussed below exhibit some aspects of the 'arbitrary'.

In summary, many TC studies do not include a satisfactory food web conceptualization or model, which makes their results and conclusions suspect, and even when formal models are included, authors do not usually explain the assumptions and shortcomings of their models. We need to be more rigorous in identifying biologically-reasonable food webs before determining the role of their TCs.-

Quotations Supporting LA Explanation 1:

1. "Evaluating TCs in large, complicated ecosystems requires data that are difficult to collect and inferences about causality that are difficult to make reliably", (Peterson et al., 2014, p 339).

2. "In real food webs with 10^2 to 10^4 species, an astronomical number of direct and indirect, weak and strong, trophic and non-trophic, and positive and negative links operate… Only when we embrace complexity and variability will we truly understand natural systems", (Polis and Strong, 1996, p 833).

3. "Any single methodology including stable isotope ratios cannot provide a complete description of food web structure and function. Application of a variety of research methodologies, as well as a thorough understanding of the natural history of organisms and of species interactions, will lead to the most thorough understanding of food webs", (Layman, et al., 2007, p 46). [This is an example of the usefulness of Levin's' 'many roads to Rome' approach discussed in Section 4.0 Conclusions.]

4. "… Components of a large network may be aggregated so that they constitute a smaller web that is it easier to analyse… But the bias in biological content is potentially large and hard to understand (there are no clear aggregation rules and significant taxonomic biases)", (Jordan, 2009, p 1735).

5. "The construction of a trophic network is far from trivial and the definition of nodes and links largely rely on the author's possibilities and opinion. Apart from problems with the definition of nodes…the existence of trophic links in the network is usually based on the biomass and feeding habits of species rather than actual measurements… Due to these difficulties, more than one network can be constructed for describing the same communities, and these could be different from each other in the number of links that connect species", (Fedor and Vasas, 2009, p 372). ["More than one network" is an extreme understatement].

Assumption 2: Food chains function like simple food webs of a few trophic levels.

Conclusion 2: Food chain results can be extrapolated directly to food webs and inform them without consequence.

Representative Quotations 2:

1. "If we treat trophic levels as units, then, by definition, food chains are always linear and alternate utilizers cannot exist. Such an assumption also appears realistic enough to be potentially useful", (Oksanen, et al., 1981, p 242).
2. "We show that our conclusions, based on simple food chains, transfer to a more complex marine food web model in which cascades are induced by varying river nutrient inputs or fish harvesting rates", (Heath et al. 2014, p 101).

LA Explanation 2: A food web is usually not just a more complicated form of food chain. The latter is a causally-impoverished structure of interlocking predator-prey pairs with self-damping at the bottom of the chain and sometimes at the top. There are no loops longer than length 2, no positive loops, no lateral links, no omnivorous links, and no non-trophic links. Food chains have only a maximum of two pathways between each pair of variables. In contrast, food webs are much richer in their potential interactions. Food webs can also have any length of feedback loops up to and including N variables. For the MERL mesocosms, the average number of operating pathways varied from 27.4 for low enrichment tanks to 42.4 for high enrichment tanks (Lane, 2017, In Press). Likewise, the number of feedback loops on average also increased from 25 to 32. For the Delaware Bay field plankton community, there were 368 possible paths of which 317 were valid involving 26 feedback loops and 2,507 potential complements (Lane, 1986). Even one or two of these feedbacks can totally shift the behavior of the system and produce counterintuitive results. Thus, unfettered extrapolation from food chains to food webs is a risky procedure at best.

In summary, a food web is qualitatively different than a food chain, and the two often require different interpretations even when a food chain is part of a food web. These consequences are not trivial and remind us that when a food chain is embedded in the food web, it cannot be analyzed in isolation of its linkages to the rest of the system when seeking the total effect of one variable on another. While we can identify TCs as food chains or partial food chains, this does not constitute a complete food web analysis in the sense of LA.

Quotations Supporting LA Explanation 2:

1. "Linear food chain theory lacks appreciation of the breadth and diversity of phenomenon found in natural webs… omnivory, a ubiquitous contravention of the TCC, must be accommodated to understand community structure and dynamics", (Polis and Strong, 1996, pp 815-816).
2. "The trophic architecture of high-diversity ecosystems, in contrast to that of trophic cascades, is more like a complex web than a ladder. Trophic webs have a high fraction of omnivores and resource generalists, which defy discrete trophic levels. They have looping, the lack of compartmentalization, many species, long chains of interacting species, high conductivity, and a rarity of top predators", (Strong, 1992, p 752).
3. "A trophic cascade, especially as the ideas associated with Hairston et al. (1960) and Oksanen et al. (1981), is an intellectual construct born in an imaginary world of simple food chains governed by

equilibrium dynamics. By contrast, most ecosystems are uncontrolled and entail complicated, multi-causal food webs governed by nonequilibrium dynamics…, "(Peterson et al., 2014, p 339).

4. "Although these early models [GWH, EEH] can represent the dynamics of some systems, nature is more commonly constructed of complex food webs and not chains. In this context, trophic cascades are strong interactions within food webs that influence the properties of the system," (Pace, et al., 1999, p 484).

Assumption 3: Food webs are constant during an annual cycle.

Conclusion 3: Food webs have integrity that can be identified in any season or year unless so strongly perturbed as to transition to an alternative state (regime shift).

1. "Early food-web empiricism tended to make the implicit assumption that food webs can be envisioned as static entities (Cohen 1978). This approach was consistent with early theory that relied heavily on equilibrium assumptions (May 1973)", (McCann and Rooney, 2009, p 1789).

2. "Despite their complexity, the structure of natural food webs displays a number of remarkable regularities. The existence of these empirical regularities has prompted several researchers to develop simple models that aim to identify the mechanisms that underlie food webs. In particular, three recent "static" models, the niche model, the nested-hierarchy model, and the generalized cascade model predict key statistical properties of food webs from a variety of environments, including deserts, rain forests, lakes, and estuaries…Studies have suggested that by using species' mass or size, a food web can in fact be mapped to a single dimension. Furthermore, the placing of species onto a single dimension is a crucial ingredient in many models developed to describe food web structure", (Stouffer et al., 2006, p19015).

3. "Despite some intraspecific seasonal variability for some species, community trophic structure appeared relatively stable throughout the year", Albo-Puigserver, et al., 2016, p 27.

LA Explanation 3: Even superficial observations of a marine ecosystem belie Assumption 3. Variables and links can be present at one time of the year and not at another. Akin and Winemiller (2006) carefully documented how estuarine food webs varied seasonally by conducting detailed stomach analysis that informed predator-prey links. They found that summer food webs had more nodes, links, and connectivity than winter food webs. Some of these seasonal changes in food web structure are predictable. For example, each year pelagic marine diatoms exhibit a large spring bloom, but a smaller one in the autumn. As summer approaches, there is a reversal of luxury consumption of silica in the spring phytoplankton bloom to its eventual release after cell lysis as the algae die. The shift in their interaction produces different patterns of changes in abundances of the other variables with the same PI. [See Figures 2a. and 2b. for the change in links between Si and A_3 (luxury-consuming diatoms)]. Zooplankton nodes and links also change. For example, the marine cladocerans *Podon spp*. and *Evadne spp.* appear in coastal marine food webs in the summer months and disappear in fall. Many predators are also seasonal with predictable migration patterns. Less predictably, some species become locally extinct from predation or pollution. If a variable disappears, so do its links to the rest of the food web. In LA there are nine qualitative link types mathematically-possible for every variable pair and some pairs exhibit more than one link type in an annual cycle even as many as 4-5 (Figure 2). Other mathematical modelling techniques for food webs use fewer than nine link types; this limitation can compromise biological reality.

The ES essentially represents the most important variables needed for system integrity, the strongest bivariate interactions, and the most frequently-used pathways in a food web. Lane (1986) used a kaleidoscope analogy to illustrate how network configurations change over an annual cycle while maintaining a core structure in plankton communities. Thus, food webs can have a probabilistic integrity although the amount of ecological complication can be enormous and usually greatly underestimated (Lane, 2016). ESs in LA also provide sets or universes of networks that are empirically-based and biologically-reasonable. For example, the nine loop diagrams over one annual cycle, for Narragansett Bay (Z_2, Figure 2), produced a potential set of biologically-reasonable food webs termed the micro-universe that contains $1.4 \times 10^{10} – 5.9 \times 10^{13}$ networks (Lane, 2016). For the Delaware Bay plankton community, the micro-universe was 3.7×10^{15} (Lane, 1986).

All food web investigators have similar micro-universes of potential food web configurations to consider whether they are explicitly computed or not. Even if variable aggregation is successful, relying on intuition or the anecdotal feeding literature to identify links cannot be expected to be accurate given this level of ecological complication. Furthermore, using a brute force, trial and error approach, a single investigator does not have a long-enough life-time to analyse all of these probable (biologically-reasonable) food web configurations and identify their TCs for a single ecosystem. At present, there are no agreed-upon rules of construction for biologically-reasonable food webs regardless of modelling methodology and LA has its own limitations. Even when the predictions of a loop model match the field or laboratory data perfectly (100% correct), it is not possible to determine if that loop model is the only one with that number of correct predictions (Lane, 1986: 'The Uniqueness Problem'). To date, no detailed analysis has been conducted on the micro-universe. LA has proven useful, however, for reducing ecological complication to more manageable levels.

In summary, while food webs do not exhibit constancy of abundances, nodes, links, and operating pathways over an annual cycle, their overall structure appears to fluctuate close to their ecological skeleton or core food web. Nevertheless, in one year a community can potentially exhibit millions of different food webs with relatively small changes in their nodes and links making it highly unlikely that a single static food web model could ever be adequate to capture the community's annual dynamics.

Quotations Supporting LA Explanation 3:

1. "Both variation in TCs and the lack of expression of cascading effects are leading to a better appreciation of food webs as probabilistic not static structures", (Pace et al. 1999, p 484).

2. "…a growing body of complex systems theory has argued that some of the most fundamental aspects behind the persistence and functioning of complex systems, in general, may be their ability to adapt in the face of perturbations. While a very interesting general theory, it has proven somewhat elusive to concretely map this abstract set of ideas to specific food-web structures. This paper…argue[s] that variability (in space, time and food-web structure) and the ability to rapidly respond to such variation (i.e. organismal behavior) are critical to the maintenance of one of nature's most amazingly diverse and complex entities—the food web", McCann and Rooney, 2009, p 1790).

Assumption 4: A parameter input is unique and constant.

Conclusion 4: If the PI can be identified, we can understand food web structure and function over time. [Note: Assumption 7 examines PIs and their impacted variables and keystones in regard to the concept of control in food webs.]

Representative Quotations 4:

1. “Based on our evaluation of 45 biophysical variables, we conclude that upper ocean temperature is the strongest single factor explaining the observed spatial patterns of trophic control across marine ecosystems…Collectively these analysis indicate the temperature is the primary deterrent of spatial patterns in the type and strength of trophic control across marine ecosystems and that it operates both directly and indirectly, through its effect on other factors”, (Boyce, et al., 2015, pp 1006-7).

2. “A strong association is documented between variability of the North Atlantic Oscillation (NAO) and changes in various trophic levels of the marine ecosystems of the North Atlantic… The impacts of the NAO are generally mediated through local changes in the physical environment, such as winds, ocean temperatures, and circulation patterns”, Drinkwater, et al., 2003, p. 211).

LA Explanation 4: PIs or external drivers are quite diverse in their type, network location, mechanism, and timing. PIs also change sign and location frequently over an annual cycle in a single food web. Rocha et al. (2015) identified 54 drivers associated with 13 marine regime shifts to evaluate how “human action is transforming the biota, chemistry, and temperature of the world’s oceans at unprecedented rates”. Marine ecosystems are also known for their strong geophysical forcing. PIs can be both natural (temperature, currents, light, pH, etc.) or anthropogenic (harvesting, pollution, climate change, etc.) and each category can be further subdivided into biotic and abiotic factors. Drivers can be a one-time impact (pulse) or a continuous pressure (press) on the ecosystem. They can be linear or non-linear; cyclic or non-cyclic; predictable or unpredictable. Even if two PIs enter at the same variable with the same sign, the mechanisms of the two PIs are likely to be different. Impacts on the input variable also vary. For example, they can be physiological (e.g. increasing a metabolic rate) or ecological (e.g. decreasing a species’ abundance).

PIs such as nutrient enrichment or excessive harvesting may impact a single variable, whereas PIs like temperature and light impact most variables simultaneously. These environmental factors can also impart information including environmental cues. For example, a cool temperature and low light intensity can inform a species that winter is coming in the North Temperate Zone and it is time for accumulating fat reserves or entering diapause. Climate change presents a large challenge since it involves several PI mechanisms impacting virtually all variables simultaneously. PIs can be of opposite signs and life can become better or worse for the initially-impacted variable. Temperature might decrease a herbivore’s reproductive rate on one sampling date, and increase feeding rates on the next.

In pelagic marine ecosystems and mesocosms studied to date with LA, the location of the key PI impacting the food webs changed from sampling date to sampling date on a time scale of one to two weeks in the MERL experiments up to six to eight weeks in the field (Lane, 1986; 2016; 2017, In Press). It is impossible to know if PIs change more frequently in nature because no one has created loop models on a daily basis over an annual cycle. Resources needed to do this are prohibitive. Regardless, it is highly unlikely that there is a sustained single

PI over a single season and especially not over an annual cycle in nature. Since no single PI dominates for very long, this indicates that TCs can be expected to be somewhat ephemeral in nature, and to a lesser degree, TEs, because the bottom of a marine food web appears more responsive to PIs. Even when we manipulate a PI in the laboratory or observe a perturbation in the field, we should not assume that it is the dominant one without additional evidence. For example, in the MERL nutrient enrichment experiment as the nutrient additions increased from 1X (ambient level) to 32X in the mesocosms, the food webs became less than responsive to enrichment and the main PI moved from the nutrient level to higher trophic levels (Lane, 2016, 2017 In Press).

In summary, PIs by themselves do not provide a means to "understand food webs". Conclusion 4 is wholly unjustified. With LA, it appears that only one key PI dominates the other PIs at a time, at least one usually best explains the whole set of variable changes, but the PI changes frequently both in sign and location. While PIs tell us something about system behavior when a particular variable is impacted, what subsequently happens in the system is more a function of system configuration and feedback, and general resilience capacity to a set of ephemeral and external PIs. At present, ecological understanding for pelagic marine ecosystems is inadequate to predict how and why PIs change sign for specific variables, their locations over the annual cycle, and whether there is some type of foreshadowing that occurs between sampling dates in regard to a food web's sensitivity to particular PIs.

Quotations Supporting LA Explanation 4:

1. "Our results confirm the need to examine simultaneously a broad suite of ecosystem drivers…Claiming that only one or other type of driver is the only thing to worry about (or ignore as the case may be) in a management context seems imprudent", (Link et al. 2009, p 793).
2. The responses of marine biota to global ocean change is characterized by multiple environmental drivers that interact to cause non-linear changes in organismal performance…There is now a large body of evidence that drivers do not act independently…", Boyd and Brown, 2015, p 1).
3. "… Many relationships are nonlinear, where small changes in the driver prompt a disproportionately large ecosystem response…Overall we found that non-linearities are common in pelagic ecosystems, comprising at least 52% of all driver-response relationships. This is likely an underestimate… In pelagic systems, strongly non-linear relationships are often driven by climate and trophic dynamic variables, but also are associated with local stressors, such as overfishing and pollution", (Hunsicker, et al., 2016, p 651).

Assumption 5: Food webs respond either top-down (trophic cascade) or bottom up (trophic escalade).

Conclusion 5: A single food web is impacted either top-down or bottom-up continuously; top-down is considered more frequent and important than bottom-up.

Representative Quotations 5: Note: these quotes include the term or notion of 'control', which is discussed in more detail in Assumption 7 and is antithetical to LA and complex system analysis in general.]

1. “The pelagic food web as a whole is primarily bottom-up controlled”, (Heath, 2005, quoted in Mackinson et al. 2009, p 2980).

2. “… In exploited North Atlantic ecosystems, we found pronounced geographical variation in top-down and bottom-up trophic forcing”, (Frank, et al., 2007, p 236).

3. “Plants have obvious primacy in food webs: in particular, their primary productivity is the fundamental control of higher trophic levels”, (Power 1992, p 742).

4. “Aquatic grazing channels tend to be characterized by factors which facilitate high predator attack rates and thus, strong vertical transfers of energy… Rendering grazing channels prone to top-down control”, (Ward, et al. 2015, p 1195).

5. [Mackinson et al. (2009) studied the relative roles of fishing in primary productivity on nine marine food webs using eco-path/ecosystem models. They concluded:] “fishing effects more strongly influenced 6 of 9 of ecosystems, but primary production was more often found to be the main factor influencing the selective pelagic and demersal fish stock trends.” (p. 2972)

LA Explanation 5: food webs can be impacted from the top-down through predators at the top (apex predator) or near the top of the food web (meso-predator). Food webs can also experience bottom-up PIs causing TEs usually starting with PIs to nutrients and primary producers as well as in the middle of a food web. Marine ecologists such as Frank et al., 2007, Lassalle et al. (2012), and Pershing et al. (2015) have argued that the dominant driving forces or PIs have traditionally been recognized by oceanographers as entering at the bottom of marine food webs, thus, emphasizing feeding and competitive feeding interactions more than predatory ones. Hunter and Price (1992) suggested if food webs were analyzed with the null hypothesis, the template should be based upon ‘bottom-up forces’. Charles Elton (1927) observed, ‘food drives all animals’. Species spend enormous efforts in searching, capturing, and consuming food, which must be of the right type, size, amount, and nutritional quality with all the associated evolutionary adaptations that make nutrition accessible and adequate.

In the marine pelagic models prepared to date, approximately 85% of all PIs enter at the nutrient and algal levels, and not at carnivore levels. Top-down PIs seem to have been accorded disproportionate and often unwarranted attention. For the field-based loops of Narragansett Bay (Figure 2), 6 were at the nutrient variables and 1 at the algal level for a total of 78% whereas 2 were at a single zooplankton variable, Z_2, the immature copepods. No PIs entered at the large invertebrate predator variables. For the Delaware Bay food web represented by 12 fields loop models, all PIs entered at the nutrient and algal levels (Lane, 1986). At most, trophic cascades, initiated at the top, could not occur more than 15% of the time in these marine pelagic models. In nature, this would be less frequent since every PI at the top of the food web does not initiate a trophic cascade as defined here, and the 15% value includes all PIs entering all animal variables, which may be positioned at the top, but also in the middle of the food web. This result also has an inherent logic since food webs could not exist without the nutrient and energy inputs to primary producers as well as presence of detritus, largely constituted from the death and decay of the short-lived primary producers, to fuel food webs (Cebrian and Lartique, 2004). While predators can be important in re-assorting the taxonomic-nutrient-energy constituents among variables and sometimes changing links and therefore pathways, a food web cannot be sustained by predation. There must be enough energy flowing up from the bottom through TEs.

Although top-down TCs are not that prevalent in marine plankton communities, the remaining 15% of PIs that enter animal variables occur frequently enough to cause recognizable TCs in nature. Shurin et al. (2002) conducted a meta-analysis of TCs and said they were weakest in plankton communities and strongest in the benthos in marine ecosystems. Hessen and Kaartvedt (2014) pointed out that there has been a paucity of field evidence on the top-down effects of zooplankton on phytoplankton. Pershing et al. (2015) reviewed the evidence for TCs in marine systems, and agreed there are few examples in pelagic food webs. The LA results presented here support these observations and help explain the prevalent bottom-up causality of these systems. PIs can potentially enter all other ‘middle’ animal variables that are included in the 15% value (copepod variables as well as molluscan, cirriped, and polychaete larval variables in Figures 1 and 2. Top-down TCs could be initiated through larger invertebrate predators and their predators, but my data sets have not demonstrated this result.

TCs and TEs are simply particular kinds of pathways or partial pathways in food webs. Investigators find them interesting because of their recognizable patterns, but in terms of food web functioning they are not more or less important than all the other pathways that together produce the changes in variables that we observe. Furthermore, a TC or TE that is structurally present in a food web may not be operating. LA is a useful tool for distinguishing operating versus non-operating pathways; but more importantly, LA can calculate the effects of all pathways acting simultaneously, which produces the total system behavior.

In summary, claiming PIs either enter at the top or bottom of the food web is a false dichotomy. PIs can enter any variable. Whereas all variables in these loop models are not equally likely to receive PIs, there appears to be no good basis for believing their entry points are restricted to the top and bottom of the food web. Additional ‘either/or’ TC dichotomies are discussed under Assumption 6. Predator-prey links are the fundamental direct links of both TCs and TEs, but there is also no rule that the two phenomena are not interrelated. There are undoubtedly many cases in nature when a single PI can simultaneously cause a TC followed by a TE, and *vice versa*. In the three-tier models of Narragansett Bay (Figures 1 and 2), a pathway can go up and down via several routes.

Quotations Supporting LA Explanation 5:

1. “This [bottom-up primacy] emerges from the fundamental reality that the removal of higher trophic levels leaves lower levels present (if perhaps greatly modified) whereas the removal of primary producers leaves no system at all”, (Hunter and Price, 1992, p 725).

2. “A well-recognized problem with the concepts of ‘top-down’ and ‘bottom-up’ control is that they are difficult to separate in practice, and in many situations some form of resource (bottom-up) and predatory (top-down) control is operative. These terms also tend to be used in the context of equilibrium conditions, yet most natural food webs are probably rarely near equilibrium. Thus, although there is some descriptive value in the use of top-down or bottom up control this motif also creates a false dichotomy and is difficult to put into operation”, (Pace, et al. 1999, p 484).

3. “Bottom-up forces are ubiquitous and fundamental, and they are necessary to account for the responses of ecosystems to perturbations, but they are not sufficient. Top-down forcing must be included in conceptual overviews, if there is to be any real hope of understanding and managing the workings of nature”, Estes, et al., 2011, p. 13/22.

4. “The relative importance of top-down or bottom-up controls in continental shelf ecosystems is known to have important implications in the way ecosystems respond to perturbations caused by fishing activities and changes in the environment…Bottom-up processes were confirmed as the major control mechanisms operating over temperate continental shelves. Nevertheless, it is likely these are temporary phases of top-down control, depending to some extent on the exploitation level“, (Lassalle et al., 2012, pp 135 and 148).

5. “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”, (Conversi, et al, 2017, p 5)

Assumption 6: Trophic cascade approaches can be divided into several meaningful binary subcategories.

Conclusion 6: Several dichotomies are real, operational, and useful. [Note: one dichotomy has already been mentioned involving whether PIs enter a food web at the top or the bottom. See Assumption 5.]

Representative Quotations 6a-e:

6a) Direct versus indirect effects

“Although the importance of indirect interactions is recognized, their explicit consideration within a purely experimental approach is difficult. Most indirect interactions are weak, which seemingly justifies their being neglected”, (Libralato et al. 2006, p 154).

“Several configurations of these indirect effects have been described sufficiently often that they have been given their own names among them: keystone predation, trophic cascades, apparent competition, indirect mutualism or commensalism, and exploitation competition”, (Wootton, 2002, p 159). [Besides those quoted, Menge (1995) also included habitat facilitation, apparent predation, and indirect defence.]

6b) Species level versus community level effects

“The overriding point is that the environmental conditions must be right for full-blown, community level cascades to occur…thus, in my view, cascades that change the community-wide attributions of biomass are an exceptional event rather than universal or normal” (Polis, 1999, p 10).

6c) Trophic cascade versus apparent trophic cascade

“Subsidized predators [via detrital pathways] can increase so much that they depress herbivores, thus allowing plants to be more successful – an ‘apparent TC’ [is] apparent because energy sustaining high consumer densities is not from *in situ* productivity, but arises outside the focal habitat” (Polis, Anderson and Holt, 1997, p 302).

6d) Odd versus even number of trophic levels

"For food chains with odd numbers of trophic levels, increases in productivity at the lowest level led to increased biomass at odd-number trophic levels, but not at even ones" [also vice versa] (Heath et al. (2014, p 104).

LA Explanation 6a: Direct versus indirect effects Wooten (2002) reviewed indirect effects and divided them into density-mediated and trait-mediated. Only the former are discussed here. All binary links in a food web represent direct interactions. When a pathway travels past the second variable, *a priori* it involves one or more indirect effects. The causality inherent in the TCC *a priori* depends upon indirect effects, TCs are considered to be one of the most important types of indirect effects (Jordan, 2009). Thus, indirect effects are not exceptional; they are ordinary and pervasive in food webs.

Some of this confusion in distinguishing direct and indirect effects arises because we traditionally characterize biological interactions in two ways: first, by describing the biological mechanism or process of the interaction, and second, by determining the end result of the interaction, that is, ++, --, +-, etc. For example, we think of resource or exploitation competition as a direct two-species interaction in which each species exhibits a negative effect on the other (--), but this is usually an indirect effect by way of a third variable, the dwindling food resource, which both competitors are consuming. Similarly, when two species are consumed by the same predator, they can each have a negative effect on the other by way of the intervening predator species. This is called apparent competition, which Menge (1995) said is present in 25% of all food webs and one of the most frequent indirect effects, but in an evolutionary sense, it is the end result, which in this case is (--) that is most relevant to a species' success or failure. Ripple et al. (2016) used the term 'knock-off effects', which they defined as "cascading effects that are not trophically downward because they spin-off from the main interaction chain". Like the definition of a TC given here, this is an arbitrary termination of an operating pathway when it reaches the lowest variable on the pathway. It was done in the present paper to retain the clearest possible checkerboard pattern of effects that could be observed in the field.

Species biology and behavior is so diverse it has been impossible for ecologists to provide satisfactory and inclusive definitions for them, and this has led to modifiers like 'apparent' and 'indirect' when discussing interactions. Most of these terms are not helpful in LA, since these are small sub-sets of a few variables embedded in a larger food web. Sub-set outcomes can be misleading. When community effects are calculated for all operating pathways between any two variables, the outcome can be counterintuitive compared to a subset result. Consideration of the end results is usually less ambiguous, and even more convenient, but it does result in confusion in terms of biological processes and food web relationships.

As N, the number of variables, increases arithmetrically, combinations of indirect effects increase multiplicatively. The clear majority of effects in ecosystems, as the number of operating paths rises exponentially, are indirect and they can easily dominate direct effects. Menge (1995) found that indirect effects accounted for 40% of the changes in 23 rocky intertidal communities. It is also a common misconception that indirect effects are weaker than direct ones. Each indirect effect or pathway is constituted by two or more direct effects, thus depending on their strengths, the pathway can be stronger or weaker than any single direct link. Fox and Olson (2000) found increasing numbers of indirect pathways in ciliate-paramecium microcosms produced stronger not weaker predatory responses. It is generally true, however, that as pathways become longer, it takes more time for them to have an effect, but that does not necessarily weaken the final effect (Babcock et al., 2010), although Menge (1997) disagreed with this notion. Individuals can starve to death at the end of a long line of supply failures or from the direct effect of habitat flooding by a catastrophic event. Similarly, a person can be just as dead from a complicated indirect network of plague transmission as a single direct bullet. Furthermore, there is a more fundamental false dichotomy between the identification and definition of direct and indirect effects. Distinguishing direct and indirect effects is inherently arbitrary depending upon how much lumping and splitting there is in the creation of the variables.

In summary, 6a is a false dichotomy. While we can be arbitrary in some decisions we make about food webs, we must make sure that being arbitrary has some value or use, for 6a it does not.

Quotations Supporting LA Explanation 6a:

“We found in 40% of predator-prey interactions across nine food webs, predators had a positive (beneficial) net effect on their prey species [through indirect effects]… Ignoring indirect effects could lead to serious miscalculations of how perturbations affect natural communities”, (Montoya et al., 2009, p2429, p 2431).

“Food web complexity may have unanticipated consequences for the strength of indirect effects”, (Fox and Olson, 2000, p 219).

“Awareness of the potential ecological significance of indirect effects developed slowly… [then] became more important as theoreticians examined complex models of communities of more than two species… Empirical studies continued to demonstrate their existence and in most cases, to show that indirect effects could have a major impact on community structure”, (Menge, 1997, p 802).

LA Explanation 6b: Species level versus community level effects Polis (1999) first distinguished species level versus community level cascades. He defined these terms as follows: “It is important to distinguish two types of cascades: ‘species cascades’ occur in a subset of the community whereby changes in predator numbers affect the success of one to a few plant species; and ‘community level’ cascades occur whereby the distribution of the plant biomass changes substantially throughout the entire system”. He also believed that community level cascades would be more frequent in aquatic ecosystems than in terrestrial ones, but that generally they would be rare. Persson (1999) reviewed the evidence for community level TCs and concluded they were more prevalent in aquatic then terrestrial ecosystems. Polis (1999) gave no objective criteria for unequivocally distinguishing these two types of cascades although he concluded that community-level cascades would be more likely in ecosystems with a dominant plant species. This appears contradictory to his previous claim since marine pelagic ecosystems rarely have a dominant plant species. Investigators working in other types of ecosystems, however, have found the species- versus community-level distinction useful. The Green World Hypothesis (Hairston, Smith, and Slobodkin, 1960) and the Ecosystem Exploitation Hypothesis (Oksanen, et al., 1981) are two examples of community-level cascades, but they are based upon trophic levels not food webs. By definition, food webs exhibit community-level phenomena.

Whereas Polis (1999) and Polis et al. (2000) referred mostly to terrestrial food webs, a brief review of Figure 1 illustrates why 'community-level TCs' as defined by Polis (1999) would be rare in any food web. He based this concept largely upon whether all plant species were involved or not. With three connected food chains and two pathways there can be multiple ways to reach the plant and nutrient variables from the top (Figure 1). Some pathways involve reaching a bottom variable in one chain and then moving diagonally to the second chain and then down to the lowest variable in the first food chain. Using the TC definition given here, only three downwardly-connected variables need to exhibit a checkerboard pattern. As a food web increases in number of variables, there will be more operating paths of differing links with partial (<N) checkerboard patterns. Polis and Strong (1996) would term these effects: 'species cascades' since they can involve so few species. This exaggerates the dichotomy unduly. Depending on the exact network configuration, there could also be ambiguity in the results, which would be very difficult to discern in the field and could cancel each other out. In contrast, LA gives the changes in all variables in the network in the Community Effects Matrix for each PI. This is the set of real 'community level' effects. Why single out only changes in primary producers as 'community-level'?

In summary, the dichotomy between species-level and community-level effects is unwarranted at least for marine pelagic communities.

Quotations Supporting LA Explanation 6b:

"Mounting research reveals that top predators can have cascading effects that extend beyond their prey base to impact on ecosystem nutrient dynamics and then may feed upward to influence the biological productivity", (Schmitz, et al., 2010, p 1199).

LA Explanation 6c: Trophic cascade versus apparent trophic cascade Polis and Strong (1996) and Polis (1999) suggested that an upward detrital food chain could increase an apex predator and result in a downward TC in the parallel grazing food chain. They termed this the Apparent Trophic Cascade Hypothesis, which seems too restrictive in both understanding and application. The importance of this concept, however, is that it explains why a PI does not need to enter the top of the food web to initiate a TC. With LA, TCs can originate from any lower variable, travel upwards to a top predator and then cascade downwards. Whether the tiers are 'green' or 'brown' is also irrelevant as is the source of detrital inputs (autochthonous versus allochthonous matter). Figures 1 and 2 include up to six functional groups of primary producers, adding more confusion to the notion of 'community-level' as defined for the Apparent Trophic Cascade Hypothesis.

There are several ways to obtain a TC (Ward, et al. 2015) in LA with no requirement that the dominant PI must start at the top. Furthermore, why should 'authentic' TCs be limited to food chains and webs based only upon autotrophic production at the bottom and is this distinction even possible in marine ecosystems? Detritus and phytoplankton are totally intermixed in the photic zone. Many filter feeders in marine ecosystems consume ratios of algae to detritus in proportion to how they occur in nature. Moore et al. (2004) reported that most primary production is not directly consumed by herbivores and instead, forms detritus, and that more energy can flow through brown as well as green food chains. McCann et al. (1998) concluded that TCs involving detritus are more stable than those based only on autotrophs. Moore et al. (2004) described the diverse roles of detritus in ecosystems. Thompson et al. (2007) analysed 58 food webs containing 18-200 taxa. They observed there is a considerable amount of omnivory above the herbivore level, and it increases with the length of the food chain. Ward et al. (2015) concluded consumption of detritus is more likely as productivity increases in marine food webs. This also promotes long up-and-down pathways among food webs producing additional checkerboard patterns.

In summary, once detritus has been consumed by an animal, the distinction between detrital and autotrophic foods is irrelevant for the animal's predators and for the development of TCs. Thus, the word 'apparent' is not helpful.

Quotations Supporting LA Explanation 6c:

"Grazing in detrital food chains, which are dynamically coupled through generalist predators, nutrient recycling, and autochthonous production of detritus. Food web models that explicitly consider these linkages provide a more realistic template for understanding the regulation of ecosystem structure and function", (Attayde and Ripa, 2008, p 989).

"… Grazing and detrital-based channels were linked by predation and did not function as separate energy channels… Although apparent cascades may be propagated in either direction", (Ward et al., 2015, p 1192).

"The partitioning of communities into grazer and decomposer…Subsystems should move beyond its descriptive and heuristic value and work its way into the basic general ecological theory", (Moore et al., 2004, p 596).

LA Explanation 6d: Odd versus even levels

Odd versus even numbers of trophic levels have little meaning in a reticulate food web analysed with LA. The focus of this dichotomy is a function of how multiplying negative impacts (-1s) of each higher-level predator on its prey produces alternative signs (checkerboard pattern) especially in food chains. In addition, the origin of the checkerboard pattern based upon simple algebraic multiplication is more intuitive in LA. One can trace the pathways and multiply its signs directly on the graph.

Quotations Supporting LA Explanation 6d:

LA Explanation 6d:

"Early conceptual and theoretical analysis built around simple food chains of odd and even length are not applicable to most complex natural systems", (Pace, et al. 1999, p487).

"In 113 community food webs from natural communities, the average and maximum lengths of food chains are independent of primary productivity, contrary to the hypothesis that longer food chains should arise when more energy is available at their base", (Briand and Cohen, 1987, p 956). [This result negates the claim that odd-and even-food chains matter.]

"... There is no rule of thumb on the interplay between apex consumers and autotrophs in intact ecosystems. This is largely a consequence of natural variation in food chain length", (Estes, et al., 2011, p 7/22).

In summary, most food web dichotomies are more illusionary than real and many are essentially reductionist, which is counter to LA and unhelpful in understanding complex food webs.

Assumption 7: Variables and/or parameter inputs at the top of a food web have special roles in trophic cascades and food webs.

Conclusion 7: Top predators, other keystones, and/or PIs, especially at the top of a food web, can 'control' food web structure and function.

Representative Quotations 7:

1. "There is little doubt that predators have a fundamental influence on the structure and function of marine communities", (Heithaus, et al., 2008, p 202).
2. "Keystones are defined as relatively low biomass species with the structuring role in their food webs", (Libralato et al. 2006, p 153). [What is the structuring role?]
3. "This reduction in the abundance of apex predators has led to abnormally high densities of their former prey in a wide range of ecosystems… This has led some to conclude that large-bodied species are essential to the maintenance of ecosystem structure and stability (Hildrew, et al., 2007; Estes et al. 2011)", quoted in Frank, Fisher, and Leggett, 2015, p 32. [What does 'essential to maintenance' mean? Also, some keystones are not "large-bodied".]
4. Large-bodied species with a high trophic position in low numerical abundance are the most important for upholding the structure of rather intact communities, while species with high trait values for predation pressure, predation stress, dynamical and/or structural sensitivity could be keystone species in highly-degraded food webs", (Jonsson. et al., 2015, p 7). [What does 'upholding the structure' mean?]
5. "In most communities, several key species play a relatively large role if they have many links to others in the interspecific interactions network", (Jordan, 2009, p 1735). [Note: this author includes all mathematically-possible links and pathways in his food webs; many are not biologically-reasonable. Species with many connections can receive as many impacts as they transmit so how do they have a relatively large role?].

LA Explanation 7: The use of the term 'control' when discussing TCs and their role in food webs has a long and confused history (Heath, 2014), and perhaps is the single word that has muddled our understanding more than any other in trophic dynamics. For example, Lassalle et al. (2012) sought to explain the "mechanisms of control" in continental shelf ecosystems. There have been two major types of control mechanism proposed in trophic studies: (1) keystone species, especially predators, and (2) external parameter inputs (PIs) that drive food web dynamics.

First, for some authors, KPs assume an almost a mythic status as if they are divine puppeteers pulling the strings of all other species. Worm and Paine (2016) concluded: "The keystone concept…has also revealed the importance of mechanistic knowledge about interaction chains that transmit keystone effects to other species". Lassalle et al. (2012) distinguished KPs as species whose removal from a food web released prey species to increase in abundance as compared to the more traditional notion of 'key dominant species' who exhibited effects on their food web because of their high abundances or biomass. Despite its common use, the disparity in the abundances of predators and their prey is not a helpful criterion for distinguishing keystones from a LA perspective. *A priori*, predators decrease prey abundance and are themselves usually less abundant than their prey because of energetic considerations.

There has been a lot of disagreement over how to define a keystone. Originally, only predators were considered to be keystones especially in relation to TCs. Eventually, the term 'keystone' was applied to any species or group that had a disproportionately large effect on the abundances of other food web components relative to its own abundance or biomass. Libralato et al. (2006), using Leontief's input-output analysis, reported that keystone species can occur at the top, bottom, or middle of the food web, and that they do not even exhibit predominantly top-down effects contrary to the original KP Concept defined by Paine. Mills et al. (1993) also concluded that keystone species can occupy any trophic level and be involved in any biological interaction including habitat modification.

The role of the keystone predator has been generally overstated and often misused. Interestingly, even the originator of the concept, sought to dampen enthusiasm for its over-broad application. Paine (2010) concluded that the effects of KPs have more to do with the prey species and their varying competitive abilities then with the KP's superior prowess in consuming its prey. He often considered the KP simply an ordinary animal consuming whatever food it could, and in contrast, it was adaptations of the prey species that gave the appearance that the predator was something special. Yes, by definition, predators decrease the abundances of their prey directly, but they do so in relation to the rest of the food web structure and can even simultaneously increase their prey via indirect pathways. As Paine reported, the starfish, *Pisaster* spp., can be a keystone predator in one rocky intertidal area but not in another, thus, context matters.

Second, a PI can first impact a particular variable anywhere in a food web. Food webs are changing continuously in response to varying PIs resulting in density shifts of their component species. This impact does not imbue any special significance to that variable. Likewise, pathways travelling through that variable from other parts of the food web do not make it a keystone species. How a variable responds to a PI is a function of not only adaptations of that variable, but the embedding structure of the whole food web, in which pathways are operating – again context matters.

Both proposed control mechanisms, keystone species and PIs, rest upon the machine metaphor taken uncritically from physics and engineering. While useful in many applications such as simple inanimate physical systems, is not as relevant to the impredicate or self-referential, complex systems of biology (Poli, 2017). This is not to say that living systems do not have some mechanistic and predicative components and subsystems, but as whole systems they are essentially not amenable to simple mechanistic models and concepts such as control and optimization (Henning and Scarfe, 2013; Poli, 2017). According to Robert Rosen, a theoretical biologist, "if one accepts the machine metaphor, which is one of the primary underpinnings of contemporary reductionism in biology, then an organism [ecosystem] becomes a piece of engineering [that is, a simple system] albeit without an engineer"…a system is simple if all of its models are computable or simulable…Another name for simple systems is mechanisms [machines]…The terms 'computable' or 'simulable' … refer precisely to what such machines can do... Something is simulable or computable, if it can be expressed as software to the hardware of the machine…The class of simple systems is the reductionist paradise; the basic assertion of reductionism is that every material system is simple," (Rosen, 2000, pp 297-8, 303, 305). Food webs are not simple machines. New thinking, about life not being a mechanism, is at the center of the current Complexity Revolution in the biological sciences

(Henning and Scarfe, 2013). If this paradigm shift is fully-realized, much will change in ecological thinking far beyond TCs.

In summary, a considerable portion of the work on trophic cascades and KPs has involved reductionist approaches including the concept of rigid food web structure that can be controlled. There is neither a rule that says there is only one KP, if any at all, nor one that claims a KP is necessary to produce a TC. In both Figures 1 and 2, there were no discernible KPs. Furthermore, one external PI or one variable, keystone or not, in a food web has nothing to do with 'control' as it is traditionally defined in science and engineering. A PI, *a priori*, is not even a component of the food web. Control is a term that is obsolete in food web studies since a food web is neither a machine nor mechanism.

Quotations Supporting LA Explanation 7:

1. "Increasing predator diversity can induce surprising changes in community structure and food web dynamics. The consequences of changes in predator diversity are difficult to predict due to the many complex interactions that occur in diverse food webs and are likely highly context-dependent", (Bruno and O'Connor, 2005, p 1052) .
2. "An alternative usage [of top-down control] refers to mechanisms or processes within food webs, specifically self-limitation processes or density-dependence, which lead to alteration in the per capita rate of change in a population, as a direct function of its abundance… We use the term 'regulation' to refer to density-dependent processes within food webs, and 'forcing' to refer to exogenous factors which drive changes", (Heath et al., 2014, p 103).
3. Assumption 7-LA: "Food web structure is the primary determinant of ecosystem response to perturbations", (Layman, et al., 2005, p 2534).
4. "Diverse and complex food webs have the potential for buffering changes by structural rearrangements. Therefore, such webs are as well, less amenable to the attempts of external control by specific manipulations. This behavior contrasts strongly with the one observed for food chains, which due to their rigid structure exhibit a high sensitivity to structural changes and fluctuations in the environment", Pahl-Wostl, 1997, p. 120).
5. "There is a sense in which complex systems are infinitely open; just as with any infinite thing, we cannot exhaust their interactive capacities by attempting to control their parameters one at a time", (Rosen, 2000, p 307).

4.0 Conclusions

This paper has identified and reviewed seven common trophic cascade assumptions with their associated conclusions regarding TCs from a LA perspective, and contrasted authors who both agree and disagree with LA interpretations. This tangle of ideas and logic flows represents a kind of Gordian knot, which has consumed ecologists' attention and literature space for several decades. LA methodology helps to unravel this Gordian knot with a single, systematic methodology using a holistic approach. Many of these traditional assumptions do not appear valid for marine pelagic food webs, and probably other ecosystems, yet they have been applied often uncritically to a variety of food web models and conceptualizations. There is also an inescapable historical context of these ideas and approaches to trophic dynamics whereby earlier, and increasingly invalid assumptions, still permeate our thinking (trophic levels, two species interactions, food chains, keystones, notions of regulation and control, etc.)

and are used in unwarranted extrapolations from the simple to the complex. This stifles a more contemporary complex systems approach to our conceptualization and modelling of TCs.

Model validity is a somewhat slippery slope. Many ecologists knowingly use models with invalid assumptions. The prime example is the timeworn Lotka-Volterra model, which assumes all individuals are equal in their likelihood of being born, reproducing, and dying; everything happens instantaneously with no time lags in density responses; competition is density-independent, there are no other species interactions, all parameters (r, K, and alpha) are constant and independent of population size; no immigration or emigration; etc. No population has been identified that validates these assumptions. The same is true for food webs based upon TC assumptions. While it is possible to dismiss invalid assumptions associated with our models, after a while these invalid assumptions can begin to obfuscate meaning and understanding. I believe ecologists are at this point when TC assumptions need some review and updating.

Every tool and observing mode provides new information, and LA is no exception. It was possible to find authors who support the main LA results, illustrating that these ideas are neither unique nor radical, but they are presently fragmented with obscure foundations across the literature. Ideally, if investigators, using methodologies and observing modes distinct from LA, would evaluate this set of assumptions as is done here, ecologists could more efficiently characterize similarities and differences across approaches. This could help provide a more robust consensus in terms of model validation then has been achieved to date, which would be helpful for future studies. This is suggested *in sensu* of Levins' (1968) notion of the desirability of 'the many roads to Rome' approach in creating robust theorems. He claimed that "a theorem which can be proved by means of different models having in common the aspects of reality under study, but differing in the other details, is called a robust theorem. Therefore the presentation of alternative proofs for the same result is not merely a mathematical exercise – it is a method of validation". Complex systems, by their very nature, defy a complete and satisfactory description via a single observing mode (Rosen, 2000).

There is also more work to be done with LA. First, data-fitted loop models are needed for terrestrial and freshwater ecosystems as well as other types of marine food webs (polar and tropical areas, coral reefs, shore, and benthic communities), and more types of organisms: micro-organisms, large invertebrates, and pelagic vertebrates of all kinds. Second, the loop models need to be quantified and pathway strengths compared. This could be a much more efficient process then quantitative modelling from scratch, since LA provides a reduced set of relevant variables and links requiring quantification. The 'measure everything' approach has always been less-than-satisfactory, if not self-defeating, in ecology. Complete specification is not possible for complex systems; all ecologists are doomed to muddle through with incomplete data and imperfect conceptualizations. Of course, that is also the challenge of this fascinating discipline.

Although TCs and TEs have been reviewed here to clarify their use and popularity in ecological studies, I have done this without a firm conviction that their study and identification will greatly advance our understanding of marine food webs or provide useful insight needed for management. I cannot share the enthusiasm for TCs that Terbough et al. (2010) espoused: "we regard TC as a universal property of ecosystem functioning, a law of nature as essential and fundamental to ecology as natural selection is to evolution". This is incorrect. First, natural selection is not a law of nature *in sensu* of the Law of Gravitation or the Law of Mass Action, both of these laws are based upon rigorous observable invariant relationships with very small error terms. Food webs have not been distinguished by small error terms, and if they occur, they are well-hidden. Second, TCs begin with PIs at the top of the food web less than 15% of the time and often do not dominate other simultaneously-operating pathways starting at the same variable. This precludes uniqueness, dominance, importance, and invariance. When the concept of control is appropriately relegated to machines and not food webs, the importance of TCs shrinks further.

Many ecologists hoped that better understanding of TCs could lead to management options that we could simply use to 'save' the world ocean. That was a yesterday of fifty years ago and although some diehards still exude optimism as they 'fly to the sun' (Worm and Paine, 2016), today we face a dire reality of a rapidly-deteriorating planet. More species are lost each year than we can even document. This urgency demands a clear and practical appraisal of TCs and not wishful thinking.

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