



INTRODUCTION

Trophodynamics in marine ecology: 70 years after Lindeman

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ABSTRACT: The seminal work of Lindeman (1942), 'The trophic-dynamic aspect of ecology' (Ecology 23:399), has been an important starting point for the holistic view of ecosystem trophodynamics, but it was initially seldom applied to marine ecosystems. Over the past 70 years, research on marine trophodynamics has become more widespread, producing a variety of analytical methods, and increasing our understanding of marine ecosystem functioning. Yet difficulties remain in transforming this body of knowledge into operational management of marine ecosystems and marine resources. This Theme Section on 'Trophodynamics in marine ecology' documents recent advances and lessons learned over the past 70 years, and provides an opportunity to reflect on future directions for marine research.

KEY WORDS: Trophodynamics · Food webs · Food chains · Ecosystem indicators · Trophic level · Food web models

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BRIEF HISTORY

Trophodynamics, by regulating the cycling of mass, energy and nutrients, determines how marine ecosystems function and respond to both internal and external pressures, as food web pathways adapt to facilitate ecosystem resilience and persistence. The first reference to the term 'food chain' was in 1718, and the first graphical depiction of a food web was attempted by Camerano (1880; c.f. Egerton 2007; Table 1). The pioneer of the food chain concept was Elton (1927) in his now classic book 'Animal ecology'. With Lindeman's (1942) classic paper 'Trophic-dynamic aspect of ecology', however, researchers really began to

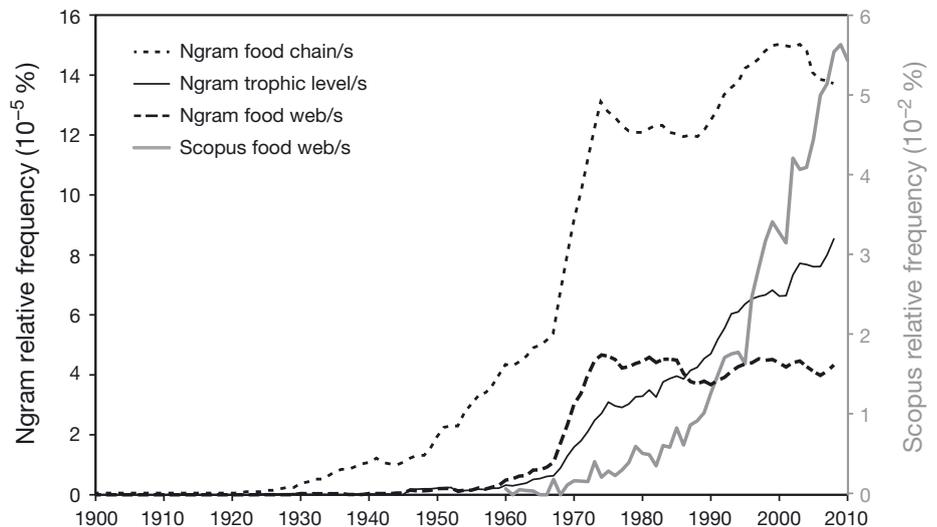
explore and understand the dynamics of ecosystem processes and functioning (Mann 1969; but see also Egerton 2007 and references therein). Lindeman (1942), in fact, examined ecosystem energetics as an integrated whole, positing the concept of trophodynamics, from whence food web thinking advanced (Fig. 1). Later, Clarke (1946) described a marine food web and Hairston et al. (1960) built on Lindeman's work by examining how populations of plants, herbivores and carnivores are regulated at distinct trophic levels.

Successively, trophodynamic concepts have been applied to link changes in primary production to commercial fish production (Ryther 1969, Vollen-

Table 1. Seminal publications on trophodynamics, extracted from an advanced search on Google Scholar (<http://scholar.google.it/>; search conducted on 15 August 2014) for books and articles containing at least one of the following terms: 'food web(s)', 'food chain(s)', 'food-chain(s)', 'trophodynamic(s)', 'trophic dynamics', 'trophic-dynamics', 'trophic level(s)', 'trophic pyramid(s)', 'ecological pyramid(s)', 'pyramids of numbers'. Search did not include patents and citations embedded in documents

Reference	Contribution	Cites	
		No.	Rank
Camerano (1880) ^a	First graphical depiction of food web	41	–
Pierce et al. (1912) ^a	Graphical description of food web	70	–
Shelford (1913) ^a	Graphical description of food web	410	–
Petersen (1915) ^a	Graphical description of food web	24	–
Summerhayes & Elton (1923)	Description of the herring food web	171	–
Hardy (1924)	Description of the herring food web	233	–
Thienemann (1926) ^a	Nutrient cycles and lake food webs; introduced to limnology the terms 'producers', 'consumers', and 'reducers'	66	–
Elton (1927)	Pioneer of ecology, analysed ecosystems by pyramids of numbers at different trophic levels	2309	9
Lindeman (1942)	Introduction of the trophodynamics concept	2422	8
Hairston et al. (1960)	Ecosystem description simplified as plant, herbivore and carnivore trophic levels	2481	6
Paine (1966)	Importance of predation in shaping the intertidal rocky shore community	3904	3
Odum (1969)	Definition of measures, also related to food webs, for assessing the development stage of an ecosystem	4316	2
Ryther (1969)	Food chain dynamics and primary productivity as main drivers of fish production	1338	17
Odum et al. (1971)	Food webs as central in ecology for a holistic view of ecosystems	9846	1
Vollenweider (1971)	Eutrophication affecting food chain in lakes	1605	12
Pomeroy (1974)	Changing the paradigm of linear food chain to complex food webs in the ocean	1052	23
Menge & Sutherland (1976)	Crucial role of predation in shaping the structure of communities	930	26
Price et al. (1980)	Trophic interactions in terrestrial ecosystems	1746	11
Paine (1980)	Importance of food web interaction strength in shaping community structure	1343	16
Oksanen et al. (1981)	Holistic vision of ecosystems and the effects of exploitation on food webs	1261	19
Pimm (1982)	Fundamental theory and analysis of food webs	1462	14
Landry & Hassett (1982)	Trophic role of microzooplankton in marine food webs	851	29
Azam et al. (1983)	Role of bacteria in the biogeochemical food webs of marine systems	3820	4
Minagawa & Wada (1984)	Nitrogen isotopic fractionation per feeding passage is independent of habitat	2447	7
Pimm (1984)	Relationship between complexity and stability through food web indicators	1506	13
Schoener & DeNiro (1984)	Stable isotope data for marine and terrestrial organisms highlight food web relationships	923	27
Carpenter et al. (1985)	Trophic interaction allows ecosystem changes to cascade through the food webs	2028	10
Odum (1985)	Responses of ecosystems to stress, including effects on structure, matter cycling and energy flows	890	28
Menge & Sutherland (1987)	Trophic structure of communities depending on environmental factors, competition and predation	1093	22
May (1988)	Comparing food web structure to highlight common patterns in food webs	1132	21
Polis et al. (1989)	Importance of including cannibalism and intraguild predation in food webs	1298	18
Decho (1990)	Polymers excreted by microbial organisms have an important role for lower marine food webs	1030	24
Polis & Strong (1996)	Central role of omnivory in food web dynamics	1363	15
Polis et al. (1997)	Importance of spatial processes for food web structure and dynamics	1172	20
Pauly et al. (1998)	Use of trophic level to assess the effects of fishing on marine communities	3318	5
Williams & Martinez (2000)	Properties of niche model are very similar to true food webs	843	30
Vander Zanden & Rasmussen (2001)	Stable isotopes for delineating trophic interactions and trophic levels	952	25
^a From Egerton (2007)			

Fig. 1. Frequency of trophodynamic terms in the literature. Ngram: searches in the corpus of digitized books extracted using the Ngram Google (<http://books.google.com/ngrams>) for level+Trophic level+trophic levels+Trophic levels, food web+food webs+Food web+Food webs and food chain+food chains+Food chain+Food chains (percentage of a phrase appearing in the books, compared to the total all phrases having the same number of words). Scopus: proportion of articles indexed in Scopus (www.scopus.com) containing 'food web(s)' in the title, abstract or keywords (percentage of all papers indexed); search conduct on 12 August 2014



weider 1971). Ecologists built upon the simplified model in Hairston et al. (1960) by introducing the concept of continuous trophic levels and by developing critical energetic descriptors and indicators (Odum 1969, Odum et al. 1971). These and the experimental work on rocky intertidal communities by Paine (1966) were the most influential publications on trophodynamics (Table 1) and seminal in fostering theoretical analyses and discussions on food web properties (e.g. De Angelis 1975). Within this context, two other important contributions emerged, notably Pomeroy's (1974) work, 'The ocean's food web: a changing paradigm' and Pimm's (1982) classic book on food webs. All of these built upon Lindeman's efforts.

Although trophodynamic analyses started in aquatic ecosystems, most of the ensuing work during the mid-20th century was focused on terrestrial or freshwater systems, and the concept was not widely applied to marine ecosystems until the last 2 decades of the 20th century (e.g. Polovina & Ow 1983, Baird & Ulanowicz 1989). The plea for methodological standardization (Pimm & Ow 1991, Cohen et al. 1993) and inclusion of system dynamics (Paine 1988) in food web analyses guided Christensen & Pauly (1990) to develop a tool, Ecopath, which facilitated the expansion of marine food web compilations on the basis of common standards, promoting comparative analyses (Pauly & Christensen 1995). The increasing attention of the scientific community to food webs and trophodynamics in marine ecosystems is reflected in the frequency of use of the term in peer-reviewed publications for 1960–2014 (Fig. 1, Scopus data), where aquatic/marine journals have an increasing role.

Since Lindeman's original contribution, new measurements have become routinely accessible to better define trophic relationships among and across trophic

levels, trophic level itself has been used as an index of perturbation, particularly in aquatic ecosystems, debates on the efficiency of energy transfer across trophic levels have arisen, and trophodynamic models have become widely available. These advances have led to the definition of ecosystem health indicators (Ulanowicz 1986, Costanza & Mageau 1999), and ultimately to the setting of reference points for ecosystem-based management.

TOPICS IN THIS THEME SECTION (TS)

We invited marine ecologists to submit papers on general patterns and processes of trophodynamics in marine ecosystems, combining theoretical, empirical, experimental and comparative studies that address (1) novel approaches to trophodynamics in marine ecosystems, (2) common properties of marine food webs, and (3) trophodynamics as a basis for management.

Novel approaches

Trophodynamics elucidates who eats whom, a difficult task in marine systems. Stomach content analysis in aquatic vertebrates has been the main method used for a long time, but the method has restricted spatio-temporal resolution (e.g. Paine 1988). In addition, it is complicated by digestibility of prey, and the abundance of unidentifiable material makes quantification of prey difficult (Pinnegar & Polunin 1999). N and C stable isotope analysis (Minagawa & Wada 1984) is now extensively used for the identification of food web pathways (Vander Zanden & Rasmussen

1999). However, unequivocal quantification of food linkages is especially difficult in the case of omnivory, which is common in marine systems (Pimm et al. 1991). The use of the isotopic method needs to move beyond integrating or averaging feeding habits over longer time scales, and additional analysis methods are needed for determining food preferences.

In this TS, Soares et al. (2014) and Corbisier et al. (2014) exemplify the state of the art in the use of the stable isotopes to delineate ecosystem processes off the Brazilian coast. Both studies explore the application of the isotope method for disentangling ecosystem functions such as biophysical processes related to upwelling and benthic-pelagic coupling. Other tracers can also be used for the determination of trophodynamic linkages: Pethybridge et al. (2014) analysed the fingerprint of fatty acids for small pelagics and their planktonic prey in the NW Mediterranean, showing the strong potential of this method for delineating food preferences. Conversely, Muto et al. (2014) showed that mercury biomagnification can be used to trace trophic positions in species of the northern Brazilian continental shelf. As an example of how to integrate such information, Prato et al. (2014) built a food web model of the NW Mediterranean using field-derived information. They show the effects of biological articulation on food web indicators and identify taxa of little commercial interest but high trophodynamic importance.

Ecosystem indicators

A number of indicators derived from key food web features have been proposed to describe ecosystems (e.g. Pimm et al. 1991: structure properties of webs; Pauly & Christensen 1995: food web flows; Ulanowicz 1986, Link 2002: food web network analyses). Although some of these indicators worked better for theoretical insights (De Angelis 1975, May 1988) and others were applied towards ecosystem assessment (Costanza & Mageau 1999), there is no clear border between the two (Rossberg 2013). Within this context, one reliable approach to better understand the functioning of marine ecosystems and to identify key indicators is inter-ecosystem comparison of food web properties (sensu Murawski et al. 2010). Ecosystem indicators must be tested before they are used for assessing the impacts of natural and anthropogenic change. More than 70 years after Lindeman, the use of transfer efficiency as an indicator continues to be an interesting topic. The fact that old and new indi-

cators are not fully tested, however, should not be seen as a limit for their application. Some papers in this TS show the potential of these applications and comparisons.

In this TS, Jordán et al. (2014) measured asymmetrical trophic relationships in a food web to identify key species for ecosystem management. Plagányi et al. (2014) used a multispecies food web model to define indicators of ecosystem shifts. Shannon et al. (2014a) used trophic level based indicators derived from models and catch data to detect structural changes induced by fisheries. Niquil et al. (2014) tested 4 metrics—food chain length, detritivory/herbivory ratio, average transfer efficiency, and transfer efficiency by TL—by comparing 6 models of estuarine ecosystems at different degrees of disturbance. Finally, using trophic relationships and biomass data from Ecopath models, combined in Ecospace with primary production and habitat preferences for the world oceans, Christensen et al. (2014) obtained a worldwide spatial distribution of fish biomass over more than a century, showing the large decline of fish biomass, in particular of top predators.

Management

Complex evolutionary and ecological interactions emerge only if species are studied in the context of food webs, and not in isolation (Cohen et al. 1993), but only on few occasions has this approach been used to quantify impacts of human activities and to address management strategies (Pauly et al. 1998, Plagányi 2007, Fulton et al. 2011). The uncertainty associated with the trophodynamic approach is often considered an important limitation (Hilborn 2011), but in multi-species fisheries, food web information can account for indirect (e.g. compensatory) effects ('tradeoffs' in Link 2010). Insights derived from trophodynamic analysis have provided context for single species fishery management (Tyrrell et al. 2011), and their use shows promise. In this TS, some contributions provide evidence in favor of the use of trophodynamics for management purposes (cf. ICES 2014).

Morello et al. (2014) explored food web Models of Intermediate Complexity for Ecosystem assessments (MICE) that demonstrated how measures based on trophic interactions can control outbreaks of the crown-of-thorns starfish. Kleisner et al. (2014) correct the mean trophic level of fisheries catches by considering a fishery's geographic expansion; corrected catches confirm the fishing down the food web (Pauly

et al. 1998) phenomenon. Analyzing the pattern of biomass accumulation across trophic levels, Pranovi et al. (2014) develop a new method to assess ecosystem changes after major perturbations; from a theoretical point of view, a perturbed ecosystem should lower the stored, cumulative biomass and 'stretch out' across TLs (Pranovi et al. 2014). Shannon et al. (2014b) analyzed the outputs of 5 ecosystem models for the southern Benguela Current to communicate with stakeholders and reach consensus on management decisions.

DISCUSSION

Quantifying trophodynamics is not easy

Current field data mainly include biomass of fishes and large invertebrates, some growth and turnover rates, and some fish food habits. These data are used for the construction of conceptual food web and ecosystem models, i.e. we build ecosystem descriptions using reductionist pieces. Thus, 70 years after Lindeman, we are still building the large picture by compiling pixels here and there, usually referring to a species that we target and eat. What can be done in the near term? (1) Metadata collections that facilitate integration and comparison of available information such as FishBase (www.fishbase.org, Froese & Pauly 2014) for fish and SeaLifeBase (www.sealifebase.org, Palomares & Pauly 2014) for non-fish marine taxa, should receive routine support. (2) Community ecologists must collect field measures with key trophodynamic information (e.g. efficiencies and rates) on crucial components (e.g. key species). Preliminary food web analyses can help to identify key factors that can be determined at low cost.

This TS shows the usefulness of isotopic enrichment, lipid fingerprints and contaminants in providing trophodynamic information. Other methods, such as molecular and genetic approaches, should also be more broadly considered for informing. We are far from having a trophodynamics tool similar to the satellite information on ocean primary production; ideally, we should have continuous, comprehensive and synoptic information on all trophic levels higher than TL 1. Sensitivity and uncertainty analysis (e.g. Pranovi et al. 2014, Prato et al. 2014) can test the robustness of trophodynamic models and identify key ecosystem elements (food web nodes, aggregation level; e.g. Jordán et al. 2014) on which data collection needs to focus.

A gap between theory and reality

Although there is asymmetry in trophic interactions, (something we do not fully understand), food web descriptions are often based on steady state assumptions in trophic flows and transfer efficiencies; since these are difficult to determine in the field, analyses are usually based on rates estimated from empirical formulas (e.g. consumption per unit of biomass; Palomares & Pauly 1998) or extrapolated from other models. This does not always allow us to discriminate between artefacts and real patterns.

We need more detailed analyses of productivity, transfer efficiencies, and flux measures at all trophic levels (Niquil et al. 2014). Additionally, novel and simple ways to quantitatively represent the marine food web should be developed; this can be achieved by losing taxonomic resolution, but may provide better assessments of system energy flow. Comparative studies across ecosystems are required for evaluating trophodynamic theory, identifying common patterns as well as differences, and suggesting ecosystem indicators.

Use of trophodynamics for management

Fisheries regulation, pollution abatement, pest control and other management activities benefit from trophodynamic inputs, as required by Europe's Marine Strategy Framework Directive (EU 2008; cf. ICES 2014) for defining the environmental status of marine ecosystems. Trophodynamics can provide a strategic framework for embedding traditional approaches such as single species targets. The various ecosystem aspects (e.g. structure, function, resilience, stability) require a set of indicators for applications in management (ICES 2014). Indicators that have been extensively tested, (e.g. mean trophic level of catch: Pauly et al. 1998; primary production required: Pauly & Christensen 1995), are the most promising. However, there will always be a need for new indicators that might perform better in terms of sensitivity to environmental change, accuracy, simplicity of monitoring and ease of comprehension (e.g. Coll et al. 2008, Libralato et al. 2008, Pranovi et al. 2014).

Perspectives

This TS includes contributions on marine trophodynamics that (1) provide an exemplary view of the state of the art, (2) provide evidence on current

limits, advantages and potential of trophodynamic measures, and (3) stimulate discussion across marine and terrestrial facets of trophodynamics research. This TS also shows that ideas continue to grow from the seminal work of Lindeman (1942), with the recent extension to marine ecosystems. Despite controversies, uncertainties and information gaps, trophodynamics as an organizing theme is robust and valuable for marine ecological research. Although trophodynamics concepts and methods are not fully operational in terms of marine ecosystem management, this TS exemplifies that trophodynamics remains a useful area for both theoretical and applied research.

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