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Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: A plea for PREBAL

Jason S. Link*

NOAA NMFS NEFSC, 166 Water Street, Woods Hole, MA 02543, USA

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ABSTRACT

The widespread use of ecological network models (e.g., Ecopath, Econetwrk, and related energy budget models) has been laudable for several reasons, chief of which is providing an easy-to-use set of modeling tools that can present an ecosystem context for improved understanding and management of living marine resources (LMR). Yet the ease-of-use of these models has led to two challenges. First, the veritable explosion of the use and application of these network models has resulted in recognition that the content and use of such models has spanned a range of quality. Second, as these models and their application have become more widespread, they are increasingly being used in a LMR management context. Thus review panels and other evaluators of these models would benefit from a set of rigorous and standard criteria from which the basis for all network models and related applications for any given system (i.e., the initial, static energy budget) can be evaluated. To this end, as one suggestion for improving network models in general, here I propose a series of pre-balance (PREBAL) diagnostics. These PREBAL diagnostics can be done, now, in simple spreadsheets before any balancing or tuning is executed. Examples of these PREBAL diagnostics include biomasses, biomass ratios, vital rates, vital rate ratios, total production, and total removals (and slopes thereof) across the taxa and trophic levels in any given energy budget. I assert that there are some general ecological and fishery principles that can be used in conjunction with PREBAL diagnostics to identify issues of model structure and data quality before balancing and dynamic applications are executed. I humbly present this PREBAL information as a simple yet general approach that could be easily implemented, could be considered for further incorporation into these model packages, and as such would ultimately result in a straightforward way to evaluate (and perhaps identify areas for improving) initial conditions in food web modeling efforts.

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1. Introduction

The use of ecological network models has been notably expanding in recent years. In a contemporary review of food web depictions, the vast majority were energy flows, and of those the majority used ecological network and energy budget models (Link et al., 2005). One such model is Ecopath with Ecosim (EwE), a widespread and easy-to-use software package with several laudable characteristics (Christensen and Pauly, 1992; Kavanagh et al., 2004; Walters et al., 1997). Econetwrk (Ulanowicz and Kay, 1991; Ulanowicz, 2004) is another easy-to-use ecological network software package; these two models, along with similar network models, have proved capable of providing valuable insights into energy budgets and food web dynamics (Allesina and Bondavalli, 2003; Dame and Christian, 2006; Heymans and Baird, 2000). Having seen a veritable explosion of the use of these models, it has been recognized that the content and use of them has spanned a range of quality. The ease-of-use and resulting ubiquitous applications of these network models have resulted in their increasing use directly in the provision of advice and information for resource management in general and living marine resource (LMR) management in particular.

As the use of these ecological network models in general and EwE in particular continue to be increasingly used in a LMR management context, review panels and other evaluators of these models would benefit from a set of rigorous and standard criteria from which the basis for all network models and related applications for any given system (i.e., the initial, static energy budget) can be evaluated. As has been noted, using any model outputs in a resource management context poses some extra challenges (Townsend et al., 2008). Namely, for model outputs to be used in an LMR management context, there is an extra level of rigor in terms of quality control and assurance that is required. Aside from being good science and a best practice for ecological modeling in general (FAO, 2008; Plaganyi, 2007), this extra level of rigor is needed for enhanced confidence in the model (and model behavior and model

* Tel.: +1 508 495 2340.
E-mail address: Jason.Link@noaa.gov.

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results) by the myriad stakeholders involved in LMR management contexts.

Thus, for experts serving on a wide array of international review panels, reviewing a vast range of numerous journal manuscripts, or developing particular applications of these models, there is an obvious need for a set of standardized and rigorous criteria for the "approved" use of these network models (EwE, Econetwrk, etc.) in a LMR context. What is proposed below is a first step towards establishing such a set of common diagnostics that modelers and reviewers alike can use to ensure that best practice standards are being met for the applications of these models. I note the caveat that the type of ecosystem I am typically thinking of in an LMR context is often of the type of larger marine ecosystems at the scales at which fisheries operate, for both demersal or pelagic habitats. Certainly these diagnostics could be pertinent to other types of aquatic ecosystems such as estuaries, lakes, and rivers, or smaller-scaled systems, or more specialized systems (e.g. coral reefs, kelp forests), but my primary emphasis here was largely on those systems most typically associated with LMRs and their management.

In establishing feasible diagnostics (which can be calculated separately in spreadsheets or developed as a module directly in these network software packages), one can both draw on general ecological and fishery principles to ensure both theoretical and practical rigor. All of these diagnostics should be done before balancing a network (termed PREBAL) such that using these diagnostics can help to head off problems in initial network balancing before subsequent dynamic applications (e.g. Ecosim in EwE; Pauly et al., 2000). As much of the dynamic applications are known to be constrained by departures from equilibria established in a static network (Link et al., 2009), a solid assurance of reasonable balance as checked by a pre-balancing protocol is clearly merited as a starting point for further uses of an ecological network.

2. Proposed diagnostics

The intent of the present work is to provide a set of guidelines for both modelers and reviewers. Not every item on the proposed list needs to be met, but a clear understanding of why a particular model application departs from these proposed guidelines is warranted in any particular case. These guidelines are presented as a "checklist" of sorts for a model developer or reviewer to step through, thereby ensuring that any potential and major problems are captured before network model outputs are used in an LMR context.

The set of criteria fall into one of five general classes. These include: biomasses across taxa and trophic levels (Table 1); biomass ratios (Table 2); vital rates across taxa and trophic levels (Table 3); vital rate ratios (Table 4); and total production and removals (Table 5). After a brief description of each, some simple rules of thumb and associated graphic examples for exemplary diagnostics are noted. Examples presented are either hypothetical (but loosely and anonymously based upon several models the author has reviewed) or based upon a system that has undergone some PREBAL diagnostics (and which is familiar to the author; Link et al., 2006, 2008, 2009).

2.1. Biomasses across taxa and trophic levels

Where biomass is apportioned in a food web has significant implications for the functioning, structure and dynamics of an ecosystem. The allocation of biomass into various groups is indicative of how an ecosystem is ultimately processing and sequestering production (Lindeman, 1942, sensu Elton, 1927). Particularly across trophic levels, there is generally an expected decline in biomass reflective of the lower abundance of larger-sized organisms at upper trophic levels (Sheldon et al., 1972; Thibeaux and Dickie, 1993). Much empirical work has confirmed these general relationships (e.g. Jennings et al., 2001, 2002; Jennings and Mackinson, 2003; Brose et al., 2006; Blanchard et al., 2009). These general patterns of biomass allocation, particularly the trophic decomposition with increasing trophic level, can be used in a diagnostic sense. Thus, I propose a few rules of thumb for biomasses across taxa in network analyses (Fig. 1; Table 1).

First, the range of biomass should span 5–7 orders of magnitude (i.e., *y*-axis log scale in Fig. 1). That an individual marine organism can span 4–5 orders of magnitude in biomass across its life history (e.g. larval tuna to adult bluefin) is illustrative of the scale seen in marine ecosystems (Steele, 1985; Link et al., 2005). If biomass

Table 1
Food web model diagnostics, rules of thumb for their appropriate application, expected values or other possible values of the diagnostics, and a description of what the diagnostic is symptomatic of if not met. Expected values in bold.

Class of diagnostic: Biomasses across taxa/TLs		c.f. Fig. 1
Rule of thumb	**Expected** values of diagnostics	Symptomatic of:
Biomass should span 5–7 orders of magnitude		
	Reasonable	
	Too many	Runs risk of underparameterizing groups, maybe too much taxonomic or age-structured splitting
	Too few	Too centric on certain TLs; else maybe estuarine, lacustrine or similar, non-LME ecosystem
Slope (on log scale) should be ∼5–10% decline		
	Normal biomass decomposition	
	Middle heavy	Should not have ups and downs, likely too centric on fishes compared to other spp.
	Top heavy	Maybe overestimating upper TL biomass
	Bottom light	Likely underestimating lower TL biomasses; reminder to not use PP from other systems
Taxa notably above or below slope-line may need more attention		
	A few may be OK	Most are most probable candidates for change in balancing exercise
	None to very few is preferable	
	Too many, see above re slopes	
	Too "up and down"	B estimates may be way off, check units; merits revisiting data sources and initial estimates
Detritus does not count in the sloping, but worth including for context		
	On order of PP	

Biomass diagnostics. Presented as a possible set of guidelines for constructing or reviewing a network model prior to balance or to ensure best practices have been followed for balancing. TL: trophic level, B: biomass, C: consumption, P: production, R: respiration, PP: primary producers, ZP: zooplankton, HMS: highly migratory species.

Table 2
Food web model diagnostics, rules of thumb for their appropriate application, specific examples, expected values or other possible values of the diagnostics, and a description of what the diagnostic is symptomatic of if not met. Expected values in bold.

Class of diagnostic: Biomass ratios			c.f. Fig. 2
Rule of thumb	Specific examples	**Expected** values of diagnostics	Symptomatic of:
Compared across taxa, predators biomass should be less than that of (1 relative to) their prey			
Number of zeroes indicates potential trophic difference between predators and prey			
	Demersal and medium pelagic piscivores: small pelagics		
	Small pelagics: Zooplankton		
	Zooplankton: phytoplankton		
	Small pelagics: phytoplankton		
	Demersal: benthic Invertebrates		
	Sharks and HMS: small pelagics		
	Marine mammals and birds: small pelagics		
	Whales: Zooplankton		
		Ratio OK	
		Ratio approaching 1	Possibly too much predation pressure on prey, potential imbalances in system structure, may need to drop pred or increase prey initial estimates
		Ratio > 1	Likely too much predation pressure on prey
		Zeroes OK	
		Zeroes too many	Predators may not be feeding enough, or over-connected food web
		Zeroes too few	Possibly too much predation pressure on prey, may have predators feeding at too low of TL
Compared across taxa, ratios indicate major pathways of trophic flows (e.g. benthic vs pelagic)			
	Demersal: pelagics		
	Flatfish: roundfish		
	% of group: all fish		
	Small pelagics		
	Medium pelagics		
	HMS		
	Sharks		
	Demersals		
	% of group: all invertebrates		
	Macroinvertebrates		
	Meiofauna		
	Gelatinous ZP		
	Shrimp and micronekton		
	Other Zooplankton		
	Zooplankton: benthos		
	Benthivores: piscivores		
	Benthivores: planktivores		
	Planktivores: piscivores		
	<TL3:TL4+		
		Ratio OK	
		Ratio too high	Potential imbalances in system structure, may need to revisit initial estimates of some groups; likely to show up against B vs trend line above
		Ratio too low	Potential imbalances in system structure, may need to revisit initial estimates of some groups; likely to show up against B vs trend line above

Biomass ratio diagnostics. Presented as a possible set of guidelines for constructing or reviewing a network model prior to balance or to ensure best practices have been followed for balancing. TL: trophic level, B: biomass, C: consumption, P: production, R: respiration, PP: primary producers, ZP: zooplankton, HMS: highly migratory species.

ranges across a wider magnitude, that may be indicative of excessive taxonomic or age/size structured splitting, resulting in a wider range of groups and biomasses to estimate. This would run the risk of being an underparameterized model. Conversely, if the range of biomass is too narrow in magnitude, it may be that the model is too focused on particular groups in a limited band of trophic levels. The exception is that a narrow range of biomass magnitude may in fact be indicative of the model being an estuarine, lacustrine, or non-marine system, in which case this diagnostic may not be as critical an item to meet in an LMR context. Another, intentional exception might be the conscious choice of a model builder to construct a partial or subset of a food web, focusing on only certain facets of an ecosystem's biota and excluding or not fully treating others. If that is the case, such a model may be in fact quite rigorous but care is warranted for not overlooking some limitations of model output interpretation in such an instance (i.e., using the model beyond its stated intent and scope). Fulton et al. (2003) further discuss the tradeoffs in appropriate levels of grouping, noting that too much or too few may lead to bias in model outputs.

Second, the slope (on log scale) should be on the order of a ~5–10% decline with increasing trophic level, across all taxa (Fig. 1). This trophic decomposition is again loosely following a size spectra, with known general declines in total biomass at larger-sized organisms (Sheldon et al., 1972; Thibeaux and Dickie, 1993; Jennings et al., 2001, 2002; Jennings and Mackinson, 2003; Brose et al., 2006; Blanchard et al., 2009). Taxa with biomasses notably above or below the slope-line will likely need more attention in the network balancing process, so this is a useful step to flag groups for increased attention (see group in middle of Fig. 1A). Certain specialist (e.g. parasite or some benthic oriented systems) or partial food webs may not entirely follow this rule of thumb, but most should generally follow this pattern. If a biomass spectra has too many ups and downs, it is likely too focused on particular groups at the expense of others at a similar trophic level, likely resulting in underparameterization or misestimation of initial biomass. If a biomass spectra has too much biomass in the middle trophic levels, it is also likely too focused on particular groups of species (usually fish taxa) and the slope will flatten out (Fig. 1B). If a biomass spectra has too high

Table 3
Food web model diagnostics, rules of thumb for their appropriate application, specific examples, expected values or other possible values of the diagnostics, and a description of what the diagnostic is symptomatic of if not met. Expected values in bold.

Class of diagnostic: Vital rates across taxa/TLs			c.f. Fig. 3
Rule of thumb	Specific examples	**Expected** values of diagnostics	Symptomatic of:
Exception for homeotherms at upper TLs			
	C/B		
	P/B		
	R/B		
		Normal biomass decomposition	
		Middle Heavy	Should not have ups and downs, likely too centric on fishes compared to other spp.
		Top Heavy	Maybe overestimating upper TL biomass
		Bottom light	Likely underestimating lower TL biomasses, do not use PP from other systems
Taxa notably above or below trend merit further attention			
		A few may be OK	Even though most are candidates for change in balancing exercise
		None is preferable	
		Too many, see above re slopes	
		Too “up and down”	Rate estimates may be way off, check units; merits revisiting data sources and initial estimates
Detritus does not count, but worth including for context			
		On order of PP	

Vital rate diagnostics. Presented as a possible set of guidelines for constructing or reviewing a network model prior to balance or to ensure best practices have been followed for balancing. TL: trophic level, B: biomass, C: consumption, P: production, R: respiration, PP: primary producers, ZP: zooplankton, HMS: highly migratory species.

of estimates at upper trophic levels, or if it has too low of estimates at lower trophic levels, the slope will similarly flatten out (Fig. 1C). If the former, it likely indicative of overestimates of upper trophic level biomasses and an overemphasis thereon. If the latter, it is likely indicative of underestimating primary producer groups, often by using values from other “comparable” ecosystems as proxy values, when in fact doing so is inappropriate. This is especially not now necessary given the copious and easily accessible satellite-derived estimates of primary producer biomass and production for most of the world’s oceans (Platt and Sathyendranath, 1988, e.g. http://www.nodc.noaa.gov/SatelliteData/OceanColor/).

I also note that detrital groups should not be used in calculating or establishing these slopes, but are certainly worth including graphically for context. If detrital biomass estimates are much more than the same order of magnitude as primary producer biomass estimates then the network model configuration runs the risk of being dominated by detritus. The exception to this would be those systems that are particularly dependant upon detrital energy (e.g. estuarine, lotic, or some benthic oriented webs), but not most of the ecosystems typically associated with LMRs. Conversely, if those estimates are much lower than those of primary producer biomasses, it may be that the network model is not fully accounting for metabolism (i.e., respiration and waste) in some groups.

2.2. Biomass ratios

The ratios of biomass among various taxa groups has been repeatedly identified as a major indicator of marine ecosystem functioning (Fulton et al., 2005; Link, 2005). As a general rule, one would expect more total biomass of prey in ecosystems (particularly aquatic ones) than biomass of predators (Lindeman, 1942; Elton, 1927; Jennings et al., 2001; Jennings and Mackinson, 2003;

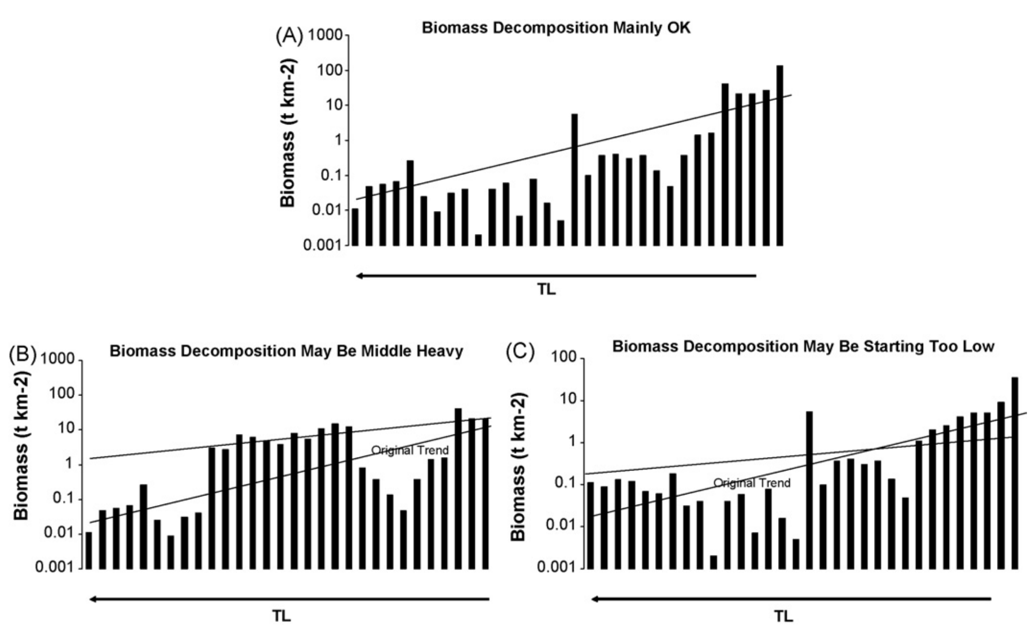

Fig. 1. Examples of trophic decomposition (trend line), showing variously declining levels of biomass with increasing trophic level. TL: trophic level. TL increases from right to left. The trend line in A is seen as comparable trend line in B and C, with those figure trendlines diverging from the original and generally with a lower slope.

Table 4
Food web model diagnostics, rules of thumb for their appropriate application, specific examples, expected values or other possible values of the diagnostics, and a description of what the diagnostic is symptomatic of if not met. Expected values in bold.

Class of diagnostic: Vital rate ratios			c.f. Figs. 4 and 5
Rule of thumb	Specific examples	**Expected** values of diagnostics	Symptomatic of:
Compared across taxa, predators should be less than 1 relative to their prey			
Number of zeroes indicates potential trophic difference between predators and prey			
	C/B		
	P/B		
	R/B		
	Demersal and medium pelagic piscivores: small pelagics		
	Small pelagics: Zooplankton		
	Zooplankton: phytoplankton		
	Small pelagics: phytoplankton		
	Demersal: benthic invertebrates		
	Sharks and HMS: small pelagics		
	Marine mammals and birds: small pelagics		
	Whales: Zooplankton		
		Ratio OK	
		Ratio approaching 1	Likely misparameterized at least one of C, P or R; possibly too much predation pressure on prey, potential imbalances in system structure, may need to change initial estimates of rates
		Ratio > 1	Certainly misparameterized at least one of C, P or R; likely too much predation pressure on prey
		Zeroes OK	
		Zeroes too many	Likely misparameterized at least one of C, P or R; predators may not be feeding enough, or over-connected food web
		Zeroes too few	Likely misparameterized at least one of C, P or R; possibly too much predation pressure on prey, may have predators feeding at too low of TL
Relative to PP approximate TL			
	P/B		
		No taxa should have a P relative to PP >, or even close, to 1	
		Taxa low P relative to PP	Mostly fine, but should not be too many zeroes as that might indicate too many trophic connections/inefficiencies
		Taxa higher P (∼ or >1) relative to PP	Strongly indicative of imbalance, check for too much subsidization by detritus or imports
Compared across vital rates; P/Cs or P/Rs near 1 merit reevaluating			
	P/C (all taxa)		
		P should not exceed C	Cannot make more out of what is not eaten
		P approximately C	Possibly misparameterized at least one of C, P or R; potential for imbalance, may need to check for subsidization by detritus or imports; merits revisiting/reevaluating rates
		P greater than C	Likely misparameterized at least one of C, P or R; highly indicative of imbalance, may need to check for subsidization by detritus or imports; most definitely merits revisiting/reevaluating rates
	P/R (all taxa)		
		>1	
		Near 1	Potential for imbalance, may need to check for subsidization by detritus or imports; might merit revisiting/reevaluating rates or maybe OK, but worth checking
		<1	Likely misparameterized at least one of P or R; highly indicative of imbalance, most definitely merits revisiting/reevaluating rates

Vital rate ratio diagnostics. Presented as a possible set of guidelines for constructing or reviewing a network model prior to balance or to ensure best practices have been followed for balancing. TL: trophic level, B: biomass, C: consumption, P: production, R: respiration, PP: primary producers, ZP: zooplankton, HMS: highly migratory species.

Brose et al., 2006), with perhaps the exception of bacteria and primary producers which have lower standing stock biomasses than their terrestrial counterparts (Steele, 1985; Link et al., 2005). One would also expect that biomass of organisms summed at a given trophic level to be higher than that at the next higher trophic levels (Elton, 1927; Lindeman, 1942). Again, the exception might comparable standing biomasses of trophic level II zooplankton to trophic level I phytoplankton. Similarly, in marine ecosystems one would expect the relative allocation of biomasses among habitat or functional groups to reflect the relative degree of energy flows within an ecosystem (Fulton et al., 2005; Link, 2005; Lindeman, 1942). From these general community principles, I propose a few rules of thumb for biomass ratios across taxa in network analyses (Fig. 2, Table 2).

First, compared across taxa, total predator biomass should be less than that of their prey (Fig. 2A–D). If the ratio approaches 1, then there may possibly be too much predation pressure on the prey groups, indicative of some potential imbalances in system structure. Zooplankton feeding upon phytoplankton may be a reasonable exception to this diagnostic given the high productivity and low standing stock biomass of these primary producers. Yet generally speaking, if this diagnostic approaches 1, it may be that a network model would need to either lower predator or increase prey initial biomass estimates. If this ratio is greater than 1, then it is highly likely that predation pressure is too excessive on a prey group, indicating that initial biomass estimates should be revisited prior to balancing or some form of migration needs to be considered directly in the model (e.g. Bustamante et al., 1995).

Second, the number of zeroes in these ratios indicates the potential trophic difference between predators and prey (Fig. 2A–D). Given that transfer efficiencies between trophic levels range from 5 to 20% (with 10% the usual assumption; e.g. Pauly and Christensen, 1995; Lindeman, 1942; Slobodkin, 1962), a predator should have at least a decimal point in a ratio to prey at an immediately lower trophic level, and additional zeroes if compared to even lower trophic levels (Link et al., 2008). If there are too many zeroes, it may be that predators are not feeding enough or the food web is

Table 5
Food web model diagnostics, rules of thumb for their appropriate application, specific examples, expected values or other possible values of the diagnostics, and a description of what the diagnostic is symptomatic of if not met. Expected values in bold.

Class of diagnostic: Total production and removals			c.f. Fig. 6
Rule of thumb	Specific examples	**Expected** values of diagnostics	Symptomatic of:
Total, scaled values should again follow a decomposition with increasing TL			
	Production		
	Consumption		
	Respiration		
		Normal biomass decomposition	
		Middle heavy	Should not have ups and downs, likely too centric on fishes compared to other spp.
		Top heavy	Maybe overestimating upper TL biomass
		Bottom light	Likely underestimating lower TL biomasses, do not use PP from other systems. . .especially with satellite info
Consumption of a taxa should be less than production by that taxa			
Consumption by a taxa should be more than production by that taxa			
Total human removals should be less than total production of a taxa			
		<1	Cannot remove more than what is produced, or at least should not; likely will not lead to imbalances
		Near 1	Cannot remove more than what is produced, or at least should not; might lead to imbalances
		>1	Cannot remove more than what is produced, or at least should not; will lead to imbalances; merits revisiting estimates
Total human removals should be compared to consumption of a taxa			
		<1	Reasonable to have more energy flowing within a system than out of it
		Near 1	Potential indication of system imbalance
		>1	Probable indication of system imbalance, warrants revisiting/reevaluation of estimates

Production and removal diagnostics. Presented as a possible set of guidelines for constructing or reviewing a network model prior to balance or to ensure best practices have been followed for balancing. TL: trophic level, B: biomass, C: consumption, P: production, R: respiration, PP: primary producers, ZP: zooplankton, HMS: highly migratory species.

at danger of being overly connected (i.e. too many spurious interactions relative to what is typical for most marine ecosystems; c.f. Link, 2002). If there are too few zeroes, it is possible that there is too much predation pressure on prey, predators may be feeding at too low of a trophic level (usually a holdover from diet data taken from the literature and not obtained within a particular ecosystem), or there is a high degree of omnivory (feeding at multiple trophic levels). These diagnostics may or may not suggest particular remedial action, but will certainly flag taxa groups warranting closer examination once the network balancing routines are initiated.

When compared across taxa, these ratios indicate major pathways of trophic flows (e.g. benthic vs pelagic; Fig. 2D and E). Ratios close to 1 indicate an equitable apportionment of biomass for comparable trophic level groups in an ecosystem. If the ratios of these groups are too high or too low, it is indicative of potential imbalances in the system structure, implying the need to perhaps revisit or verify initial biomass estimates of some groups. If this diagnostic shows up as noteworthy for a set of groups, it will likely confirm an individual taxa's biomass estimate being distinctive from the trend lines noted above.

Proportional representation also helps to characterize any potential imbalances within a network (Fig. 2F and G; sensu the FIB index, Pauly et al., 2000). For example, if a large percentage of all invertebrate biomasses are allocated to one of the major groups, such as gelatinous zooplankton (a commonly occurring problem), it is highly indicative of major imbalances in system structure. As a fraction of all invertebrate biomass, a particular group should probably not be much over approximately 70–80%, with the exception of benthos in general (and particularly in estuarine ecosystems) due to their known higher standing biomass than most other groups (Jennings et al., 2002; Brose et al., 2006; Link et al., 2008; Blanchard et al., 2009). As a fraction of all fish biomass, a particular group should probably not be much over approximately 70–80%, with the exception of small pelagics in upwelling ecosystems. These approximations may change as more rigorous models of more types of aquatic ecosystems are presented, but they should serve as useful diagnostic checks in a pre-balancing exercise. Again, this diagnostic may or may not suggest particular action, but will certainly flag taxa groups warranting closer examination once the network balancing routines are initiated.

2.3. Vital rates across taxa and trophic levels

The vital rates of organisms are reflective of, and an amalgamation of, an entire suite of physiological processes. The bioenergetics of an individual (Winberg, 1956; Kitchell et al., 1977), including the processes of consumption (C), production (P) and respiration (R) represent the balance of energy consumed and used by an organism. These rates can be scaled up to a population level. As such these factors are often presented as ratios to biomass, C/B, P/B, and R/B and are critical parameters in ecology and network models (Odum, 1956; Margalef, 1963; Odum, 1985; Pauly, 1980, 1989; Choi et al., 1999; Ulanowicz, 1986, 1997). As these vital rates are strongly related to body size and biomass (Odum, 1956; Pauly, 1980, 1989; Brey and Clarke, 1993; Denney et al., 2002), they tend to follow some of the same properties as noted above for biomass estimates. The exception would be for homeotherms, which tend to have lower production by higher metabolic and hence consumptive demands per unit body mass (Peters, 1983) than poikilotherms. I propose a few simple rules of thumb for vital rates (Table 3, Fig. 3).

First, there needs to be a general decline with increasing trophic level, with a similar trophic decomposition as in the biomasses (Fig. 3; Jennings et al., 2001; Denney et al., 2002; Brose et al., 2006). The exception is for C/B and R/B for homeotherms at upper trophic levels, which tend to have higher values than the trend line, and P/B for the same groups of organisms which tend to have lower values than the trend line. Otherwise, as in the biomass estimates, taxa with vital rates notably above or below the slope will likely need more attention in the network balancing process, so this is a useful step to flag groups for increased attention. Also, as per the

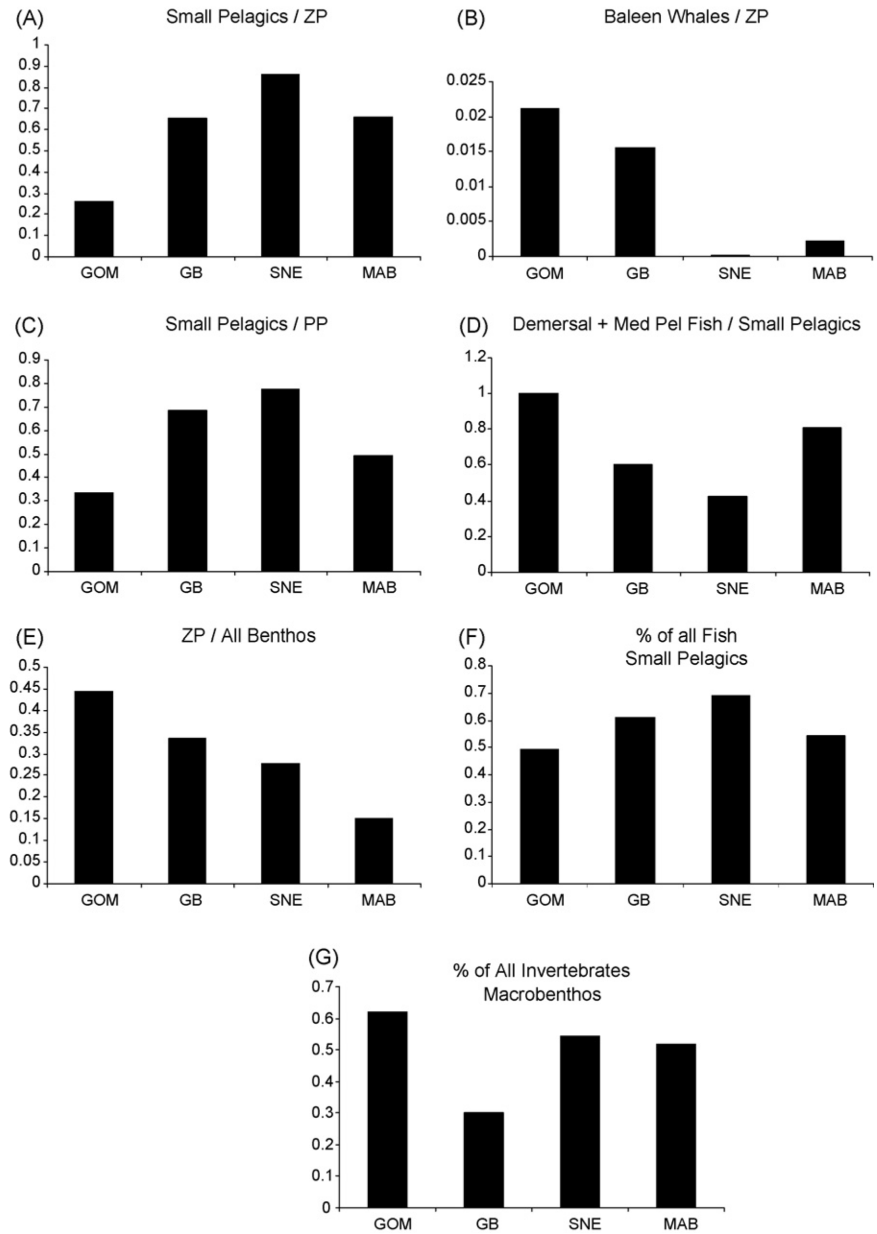

Fig. 2. Examples of biomass ratios, either of groups to groups (A–E) or as percentages of total for a broad taxonomic or functional group (F and G). *X*-Axis codes refer to different models of Northwest Atlantic ecosystem. GoM: Gulf of Maine, GB: Georges Bank, SNE: Southern New England, MAB: Mid Atlantic Bight, PP: primary producers, ZP: zooplankton.

biomass estimates, if values for vital rates are too high (relative to a more normal slope) at upper trophic levels it is likely indicative of overestimates (and overemphasis) for upper trophic levels. Similarly, if values for vital rates are too low (relative to a more normal slope) at lower trophic levels it is likely indicative of underestimating primary producer groups, again commonly from using values from other "comparable" ecosystems as proxy values. This seems unwise, when obtaining system-specific estimates is readily feasible given the copious and easily accessible satellite-derived sources now available for primary production (Platt and Sathyendranath, 1988, e.g. http://www.nodc.noaa.gov/SatelliteData/OceanColor/). Very simply, taxa notably above or below a trend merit further attention once the network balancing routines are initiated, with the exception of homeotherms.

As a further diagnostic, vital rates in tropical ecosystems should, on the norm, be slightly higher than those in temperate or boreal ecosystems (Brey and Clarke, 1993). This is due to the warmer waters (and hence effect on vital rates, at least for poikilotherms) typically experienced by organisms in the tropics. Similarly, one would expect lower rates for polar ecosystems (Brey and Clarke, 1993).

Additionally, using first principles as a sort of reality check, most fish consume on the order of ∼0.5–1% body weight per day (sensu Pauly, 1980, 1989). Extending that algebraically to an annual basis, most fish should thus have C/Bs on the order of 2–4 or less, with P/Bs and R/Bs scaled accordingly.

2.4. Vital rate ratios

As with the biomass ratios, ratios of vital rates can provide further insights beyond just the absolute values of these rates. These ratios elucidate the differences of various processes across taxa, bioenergetic constraints within taxa, and the relativity across vital rates (Link, 2005; Fulton et al., 2005). I particularly note that the

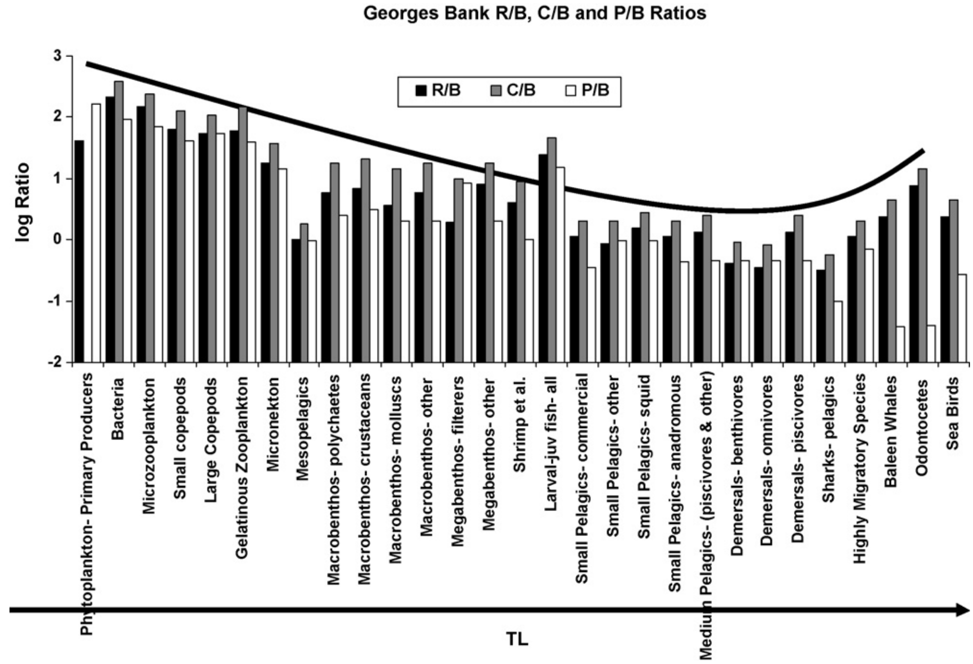

Fig. 3. Examples of vital rates from Georges Bank, that also expresses trophic decomposition (trend line) with the exception of consumption and respiration for homeotherms. TL: trophic level, B: biomass, C: consumption, P: production, R: respiration, and ratios thereof. TL increases from left to right.

primary production of an ecosystem forms the basis (accounting for caveats of first trophic level production, including influx of other sources of primary production, use of detritus, microbial loop, recycling of nutrients, etc.) from which all other productivity, and hence energy flows, are derived (Lindeman, 1942; Odum, 1956; Slobodkin, 1962; Margalef, 1963; Odum, 1985; Pauly, 1980, 1989; Pauly and Christensen, 1995; Choi et al., 1999; Ulanowicz, 1986, 1997). There are five proposed rules of thumb for vital rate ratios (Table 4, Figs. 4 and 5).

First, as with the biomass ratios, when compared across taxa predator vital rates should be less than that of their prey (Fig. 4A–D; Jennings et al., 2001; Brose et al., 2006). If the ratio approaches 1, then there is likely a misparameterization of at least one of C, P or R. This diagnostic may also be indicative of possibly too much predation pressure on prey or potential imbalances in system structure. As such, this diagnostic likely indicates a need to change the initial estimates of some rates. If this diagnostic exceeds 1, it is almost a certainty that some rates are misparameterized among at least

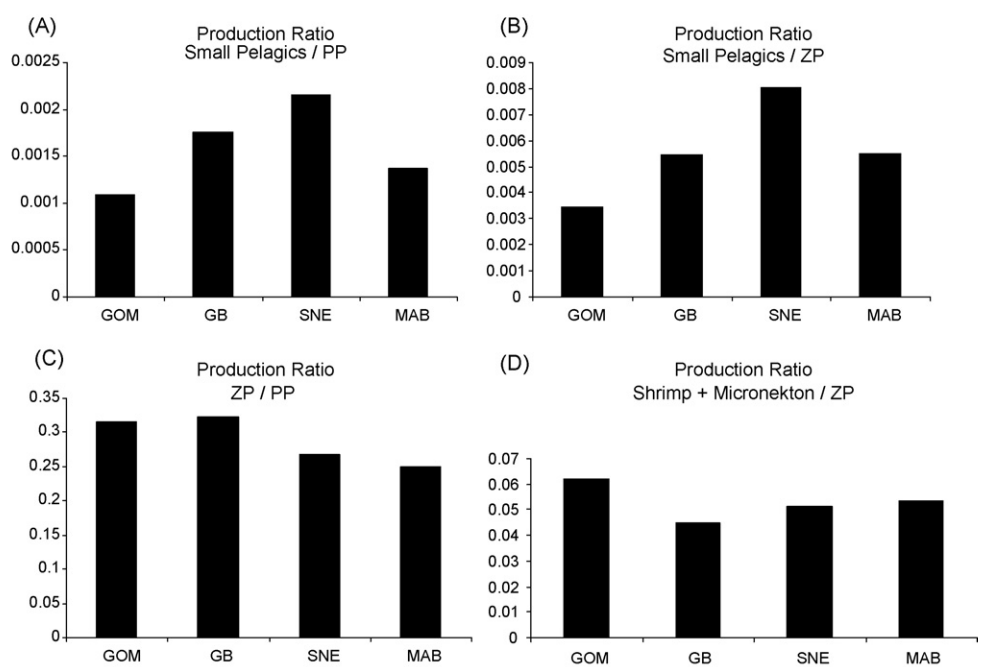

Fig. 4. Examples of vital rate ratios, comparing the rates of specific groups. *X*-Axis codes refer to different models of Northwest Atlantic ecosystem. GoM: Gulf of Maine, GB: Georges Bank, SNE: Southern New England, MAB: Mid Atlantic Bight, PP: primary producers, ZP: zooplankton.

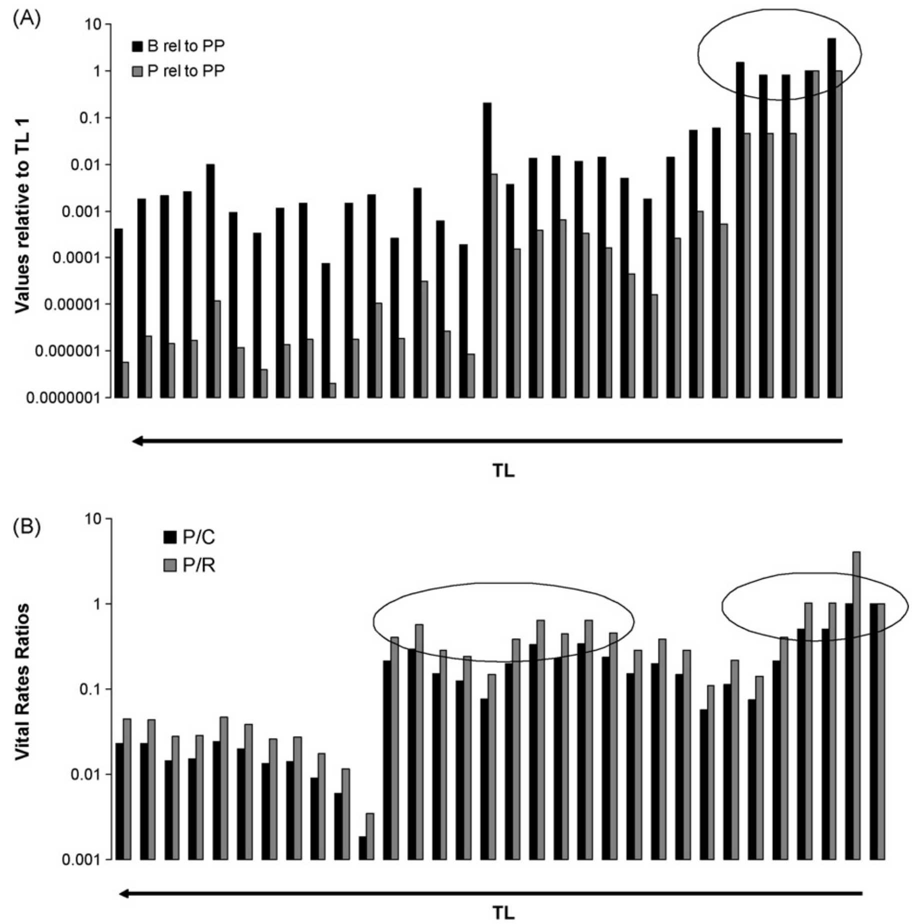

Fig. 5. Example of vital rate ratios, as compared to the primary producers (A) or as compared across rates for each taxa (B). TL: trophic level, PP: primary producers, B: biomass, C: consumption, P: production, R: respiration, and ratios thereof. Circled areas represent species groups of interest relative to these diagnostics. TL increases from right to left.

one of C, P or R. This may also indicate that there is too much predation pressure on particular prey. Or that migration would need to be directly considered (Bustamante et al., 1995). The value of this diagnostic would be a strong indicator that some rates merit reevaluation prior to the network balancing routines.

Similarly, as with the biomass ratios the number of zeroes indicates potential trophic difference between predators and prey (Fig. 4A–D). Again, given that transfer efficiencies between trophic levels range from 5 to 20% (with 10% the usual assumption; Pauly and Christensen, 1995; Lindeman, 1942; Slobodkin, 1962), a predator should have at least a decimal point in a ratio to prey at an immediately lower trophic level, and additional zeroes if compared to even lower trophic levels (Link et al., 2008). If there are too many zeroes, it may be that predators are not feeding enough or the food web is at danger of being overly connected. If there are too few zeroes, it is possible that there is too much predation pressure on prey, predators may be feeding at too low of a trophic level (usually a holdover from diet data taken from the literature and not obtained within a particular ecosystem), there is a high degree of omnivory (feeding at multiple trophic levels), or one of the vital rates is inappropriate for use on the taxa in question (common when using literature values of C/B or P/B from other ecosystems). These diagnostics generally indicate some misparameterization of vital rates that warrant reevaluation prior to the network balancing routines.

A third diagnostic is that no taxa should have a P/B rate relative to PP P/B rates (and as a corollary, B estimates as well) greater than, or even close, to 1 (Fig. 5A). If taxa exhibit a low P/B ratio relative PP, that is mostly fine, but it likely should not be too many zeroes as that might indicate too many trophic inefficiencies. If taxa exhibit a ratio even approximating 1, and certainly for any taxa greater than 1, this is strongly indicative of network imbalance and highlights the need to check for excessive subsidization by detritus or migrating imports. A diagnostic of greater than 1 will certainly flag taxa groups warranting closer examination once the network balancing routines are initiated.

When compared across vital rates (for each taxa), P should not exceed C (Fig. 5B). This P/C ratio is also known as gross efficiency (GE) which has been used in some software programs (Christensen and Pauly, 1992). The simple logic is that from an energetic perspective (2nd law of thermodynamics), a taxa group cannot produce more than what is eaten. If P approximates C, then there is likely some misparameterization, at least for C/B or P/B. This indicates a strong potential for imbalance and may also suggest a need to check for subsidization by detritus or imports (unless it is known to be an ecosystem largely dependant upon those imports). If this ratio approaches 1, then this diagnostic likely merits reevaluation of these rates prior to the network balancing routines. If P is greater than C, then this diagnostic most definitely indicates a reevaluation of those vital rates.

Just as P/C should be less than 1, similarly P/R should be greater than 1 (Fig. 5B). If P approximates R, that may be indicative of potential network imbalance. It could very well be that this diagnostic approaching 1 is acceptable, but would highlight taxa groups that merit further examination once the network balancing routines are initiated. If this ratio is less than 1, then this is highly indicative

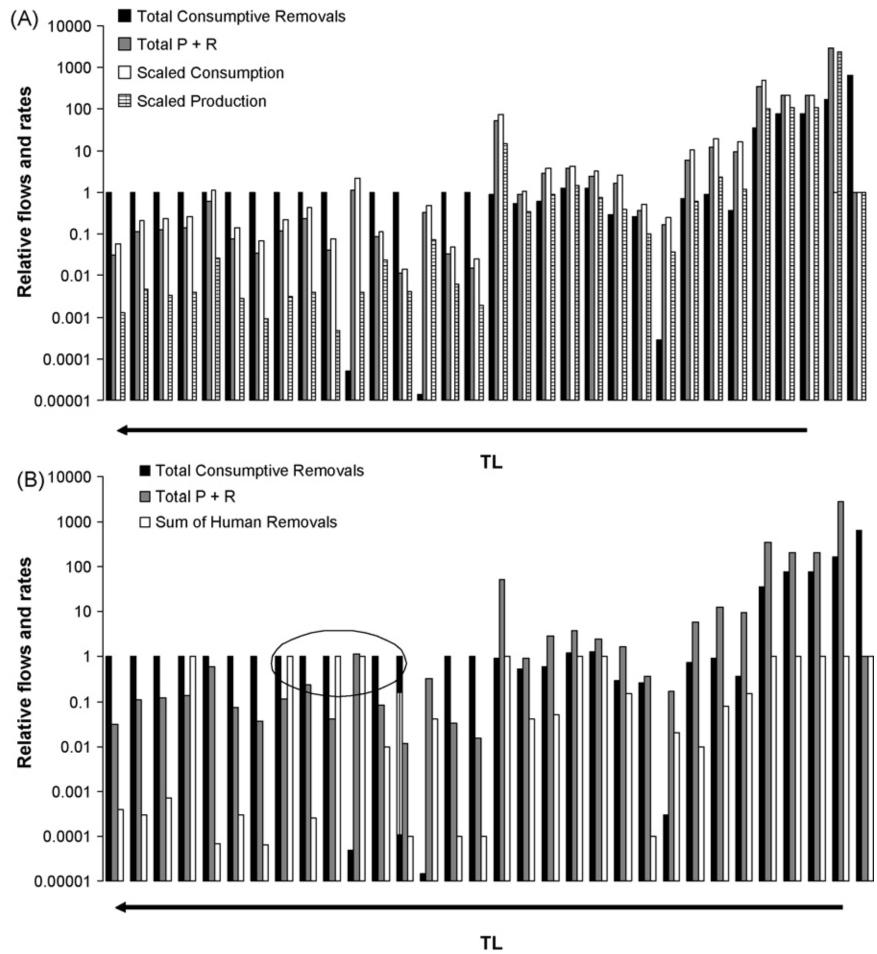

Fig. 6. Examples of total production and removals, scaled to the full ecosystem, comparing internal flows (A) and flows relative to external removals (B). TL: trophic level, P: production, R: respiration. Circled areas represent species groups of interest relative to these diagnostics. TL increases from right to left.

of imbalance and definitely merits reevaluating for either of these vital rates (P/B, R/B) for a taxa so identified.

2.5. Total production and removals

How much and where energy flows through, to and from a system is critical to understanding the dynamics of any network, particularly aquatic food webs (Ulanowicz, 1986, 1997). Assessing the relativity among those flows, in absolute amounts, is thus paramount to identifying and triaging among the most important processes in a system. Further, doing so is critical for evaluating how much exploitation a system can sustainably support (Libralato et al., 2008; Link, 2005; Pauly and Christensen, 1995), which is a critical consideration when using network models in an LMR context. These diagnostics represent the rates (or removals) scaled up by the magnitude of biomasses for each group to denote absolute amounts (per the units being used) in a network model. A few proposed rules of thumb then follow for total, scaled-up estimates (Table 5, Fig. 6).

First, total, scaled production (and consumption and respiration) should again follow a decomposition with increasing trophic level (Fig. 6A). Presumably this should be have been flagged in evaluations of biomass or P/B above, but scaling up to total, absolute amounts is yet another check to ensure initial estimates for both biomasses and vital rates are reasonable.

Second, consumption *of* a taxa should be less than production by that taxa (Fig. 6A). This is equivalent of saying that the Ecotrophic Efficiency (EE) should be less than 1 (Christensen and Pauly, 1992; Walters et al., 1997). If total consumptive removals are greater than scaled production, this may not necessarily have been highlighted in the vital rate or biomass diagnostics above. What this diagnostic indicates is that there is more demand on a group than what the group is producing; as such the network will be notably imbalanced and C/B, P/B, diet compositions, biomasses, or some combination thereof should be reevaluated. Even if this ratio approaches without exceeding 1, it would suggest revisiting some of the initial estimates prior to the network balancing routines.

Third and similarly, consumption *by* a taxa should be more than production by that taxa (Fig. 6A). Although this should have been identified in the P/C ratio diagnostic above, it is worth evaluating at a scaled-up level to ensure that the ratio is observably less than 1 to account for respiration, trophic transfer efficiencies, and other metabolic losses of consumption. If less than 1 this diagnostic will certainly flag taxa groups warranting parameter reevaluation prior to initiating the network balancing routines.

Fourth, total human removals should be less than total production of a taxa (Fig. 6B). Although obvious to the point of being a truism, arguably this has been largely ignored – or at least not entirely acted upon – by fisheries decision makers for many individual fish stocks during much of the modern era of LMR science (Graham, 1943; Smith, 1994). Heeding this removal to production ratio credo is even more germane for an entire system (Pauly and Christensen, 1995; Pauly et al., 2000; Libralato et al., 2008). This is because although systems may have more stability and resiliency than individual populations, once eroded system level redundancies are far less flexible than for functional groups comprised of multiple species (Auster and Link, 2009). The same diagnostic logic applies as per the consumptive removals and production diagnostics above. If this ratio is near or greater than 1, a network imbalance is highly probable and reevaluation of initial estimates is most likely warranted prior to network balancing.

Finally, total human removals should be compared to total consumptive removals of a taxa (Fig. 6B). If this is less than 1, then it seems generally reasonable to have more energy flowing within a system than out of it (Ulanowicz, 1986, 1997; Odum, 1985). However, if this ratio is near or greater than 1 this diagnostic is indicative of possible system imbalance. The exception to this diagnostic is that some apex predators with minimal predation upon them might be removed from a system primarily due to human factors. Regardless, diagnostic values at or near 1 warrant further evaluation as the network balancing routines are initiated.

3. Discussion

I assert that there are some general ecological and fishery principles that can be used in conjunction with PREBAL diagnostics to identify issues of model structure and data quality before network model balancing and dynamic applications are executed. These largely follow the partitioning of biomass and production as one ascends trophic level (e.g. Elton, 1927; Lindeman, 1942; Odum, 1956; Sheldon et al., 1972; Pauly and Christensen, 1995; Jennings et al., 2001; Denney et al., 2002; Jennings et al., 2002; Jennings and Mackinson, 2003; Blanchard et al., 2009) or as one expresses exploitative or eutrophic pressure relative to systemic and taxa-specific production (Fulton et al., 2005; Link, 2005; Libralato et al., 2008).

The PREBAL information presented is a simple yet general approach that could be easily implemented and thus should ultimately result in a straightforward way to evaluate (and perhaps identify areas for improving) initial conditions in food web modeling efforts. They can also help navigate the difficult choices of structural tradeoffs in model development (Fulton et al., 2003). Some of these diagnostics are already extant in some of the software (e.g. EE and GE flags for P and C ratios; Christensen and Pauly, 1992). Again, the diagnostics here are presented as suggestions to ensure that any modelers or reviewers associated with any particular application have improved assurance as to the quality of any network model output. Whether they are done in simple spreadsheets (one is available from the author; pers. comm.) or as another module in these software packages is not critical. Rather, the important point of the plea herein is to actually do a PREBAL in any network modeling exercise.

The PREBAL diagnostics are presented as a means to not only ensure confidence and quality in model design, parameterization, and implementation. These diagnostics are also a means to further elucidate the understanding of key ecosystem processes that might otherwise be overlooked by proceeding to the dynamic phase of food web modeling without pausing to rigorously evaluate these diagnostics. As network modeling exercises are being increasingly demanded, the heuristic value of such modeling efforts should not be overlooked.

For experts serving on a wide array of international review panels, reviewing a vast range of numerous journal manuscripts, or developing particular applications of these network models, I trust that the proposed diagnostics will serve as a useful set of standardized and rigorous criteria for determining the “approval” status of a network model. This is particularly so for those network models used in a LMR context. I also trust that the proposed diagnostics will serve as the first step towards ensuring that best practice standards (FAO, 2008; Plaganyi, 2007) are being used for the applications of these network models, especially in a LMR context. A solid assurance that reasonable practices have been employed to achieve a balanced network will lead to further confidence in the future use of these models.

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