



Sensitivity of secondary production and export flux to choice of trophic transfer formulation in marine ecosystem models



Thomas R. Anderson ^{a,*}, Dag O. Hessen ^b, Aditee Mitra ^c, Daniel J. Mayor ^d, Andrew Yool ^a

^a National Oceanography Centre, University of Southampton, Waterfront Campus, Southampton SO14 3ZH, UK

^b University of Oslo, Department of Biology, CEES, P.O. Box 1066 Blindern, 0316 Oslo, Norway

^c Centre for Sustainable Aquatic Research, Wallace Building, Swansea University, Swansea SA2 8PP, UK

^d Institute of Biological and Environmental Sciences, Oceanlab, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, UK

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ABSTRACT

The performance of four contemporary formulations describing trophic transfer, which have strongly contrasting assumptions as regards the way that consumer growth is calculated as a function of food C:N ratio and in the fate of non-limiting substrates, was compared in two settings: a simple steady-state ecosystem model and a 3D biogeochemical general circulation model. Considerable variation was seen in predictions for primary production, transfer to higher trophic levels and export to the ocean interior. The physiological basis of the various assumptions underpinning the chosen formulations is open to question. Assumptions include Liebig-style limitation of growth, strict homeostasis in zooplankton biomass, and whether excess C and N are released by voiding in faecal pellets or via respiration/excretion post-absorption by the gut. Deciding upon the most appropriate means of formulating trophic transfer is not straightforward because, despite advances in ecological stoichiometry, the physiological mechanisms underlying these phenomena remain incompletely understood. Nevertheless, worrying inconsistencies are evident in the way in which fundamental transfer processes are justified and parameterised in the current generation of marine ecosystem models, manifested in the resulting simulations of ocean biogeochemistry. Our work highlights the need for modellers to revisit and appraise the equations and parameter values used to describe trophic transfer in marine ecosystem models.

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1. Introduction

Zooplankton are key players in the biogeochemical cycling of carbon and nutrients in marine ecosystems, especially in their roles in linking primary producers to higher trophic levels including fish (Beaugrand and Kirby, 2010; Beaugrand et al., 2010) and in the export of organic matter to the deep ocean (e.g., González et al., 2009; Juul-Pedersen et al., 2010). Parameterising zooplankton in models is however far from straightforward (Carlotti and Poggiale, 2010). Quantifying prey selectivity and ingestion is an important starting point given the role of zooplankton in top-down control of biomass stocks and so the functional response has received considerable attention (Gentleman et al., 2003; Mitra and Flynn, 2006). Once ingested, food items are used for growth, with associated losses via faecal material and respiration/excretion. The role of food quality in trophic transfer provides an additional dimension which has been the subject of numerous experimental studies that have investigated the roles of nutrient elements (Augustin and Boersma, 2006; Jones et al., 2002; Siuda and Dam, 2010) and biochemicals such as essential

fatty acids (Burns et al., 2011; Mayor et al., 2009a) as factors limiting growth and reproduction. Food quality may interact with food quantity (in terms of carbon), yet C may often be in stoichiometric excess when present in the food of herbivorous zooplankton to the extent that “leftover C” must be disposed of via faecal material or increased metabolic activity and respiration (Hessen and Anderson, 2008). These pathways for disposal have important implications for C cycling and C use efficiency of food webs as a whole (Hessen et al., 2004).

The theoretical basis of ecological stoichiometry has advanced considerably in recent years. Early models, with zooplankton as their focus, examined the potential for limitation by carbon versus nutrient elements, usually assuming that the latter can be used for growth with high efficiency whereas C is necessarily consumed in maintenance. Elemental ratios in grazer and food are used to calculate threshold elemental ratios (TERs) that, by definition, are the crossover from limitation by one element to another (Anderson, 1992; Hessen, 1992). In freshwater systems, phosphorus was identified as the element limiting the production of zooplankton, notably cladocerans, whereas nitrogen was generally believed to be limiting in marine systems (Elser and Hassett, 1994). A case can, however, be made for limitation by carbon if the energy requirements for maintenance are sufficiently high (Anderson and Hessen, 1995). Since these early

* Corresponding author. Tel.: +44 23 80596337.

E-mail address: tra@noc.ac.uk (T.R. Anderson).

models, stoichiometric theory has been extended to include biochemical compounds (Anderson and Pond, 2000), improved representation of bioenergetic costs such as protein synthesis and turnover (Anderson et al., 2005), analysis of maternal biomass (in addition to food) as a source of nutrition (Mayor et al., 2009b), and Dynamic Energy Budget approaches for describing how competing substrates are utilised subsequent to absorption by the gut (Kuijper et al., 2004). As well as considering how food quality impacts on zooplankton growth, stoichiometric models for use in ecosystem scenarios also need to consider the fate of nonlimiting elements. The main choice to make in this regard is whether elimination of substrates in stoichiometric excess occurs pre- or post-absorption by the gut. In the former case (e.g., DeMott et al., 1998), excess substrates are packaged within faecal material which may sink out of the euphotic zone and thereby contribute to export flux to the deep ocean. Conversely, post-absorptive regulation (e.g., Anderson et al., 2005) favours recycling in dissolved form.

In the past, most marine ecosystem models, and particularly those running in general circulation models (GCMs), employed a single base currency (usually N or P) and, when necessary, converted to other currencies (notably C) by applying the Redfield ratio (e.g., Six and Maier-Reimer, 1996; Slagstad and Wassmann, 2001; Yamanaka and Tajika, 1997). With the realisation that many processes in marine food webs do not strictly conform to this ratio (especially for carbon versus nutrient elements, e.g., Anderson and Pondaven, 2003), models today often employ non-Redfield stoichiometry. For example, whereas a C:N ratio of 6.625 (Redfield) may be assigned to phytoplankton, alternate values are more appropriate for other state variables such as zooplankton, bacteria and the detritus. Appropriate parameterisations are then required to describe trophic transfer that take into consideration stoichiometric imbalances between predator and prey and how substrates in excess are dealt with. A wide range of such parameterisations is used in contemporary marine ecosystem models, begging the question as to whether predicted biogeochemical cycling is sensitive to this choice and, if so, the extent to which different choices can be justified in context of the experimental/observational literature.

Here, we compare the performance of four different trophic transfer formulations within two settings: (1) a simple steady-state ecosystem model, and (2) a 3D biogeochemical GCM (Yool et al., 2011). The four trophic transfer schemes are taken from: AH95 (Anderson and Hessen, 1995), ERSEM (European Regional Seas Ecosystem Model: Blackford et al., 2004), HadOCC (Hadley Centre Ocean Carbon Cycle model: Palmer and Totterdell, 2001) and Pah08 (Pahlow et al.,

2008). The latter three are ecosystem models while the first, AH95, is the trophic transfer scheme used in the recently published MEDUSA (Model of Ecosystem Dynamics, nutrient Utilisation, Sequestration and Acidification) ecosystem model (Yool et al., 2011). Each has thus been implemented within ecosystem models and, as such, may be considered to be representative of the current state-of-the-art in this field. There is considerable variation in the assumptions underpinning the chosen transfer schemes (Section 2) and, as a consequence, in the resulting predictions of transfer to higher trophic levels and carbon export (Sections 3, 4). Our aim is to highlight these differences and discuss them in context of the existing observational/experimental literature and the need for reliable parameterisations of non-Redfield stoichiometry in the next generation of marine ecosystem models.

2. Trophic transfer schemes

The metabolic budget of organisms, including different anabolic and metabolic requirements and how these are met from available substrates, needs to be taken into consideration when constructing trophic transfer formulations for use in ecosystem models. Rules are required to govern the absorption of ingested substrates across the gut, limitation of growth in the face of variable elemental composition in food with associated losses via respiration and excretion, and for how remaining substrates in stoichiometric excess are dealt with. In this respect, the four trophic transfer formulations studied here, AH95, ERSEM, HadOCC and Pah08, vary markedly in their assumptions (Fig. 1). Note that basal metabolic costs are not met directly using ingested substrates in any of these formulations but rather, when implemented in ecosystem models, a biomass-specific term is included as an additional loss rate. Within other, more recent, trophic transfer schemes (Acheampong et al., 2012; Anderson et al., 2005; Mitra, 2006) ingested food is first and foremost allocated to basal metabolism, taking priority over other functions including growth. We considered including these formulations in the analysis here but, due to the radically different way that basal metabolism is represented, chose not to do so because it is difficult to achieve a fair comparison. Also, none of the four constructs used here consider the more complex issues of food quality and quantity discussed by Mitra and Flynn (2005, 2007) and Flynn (2009). Although undoubtedly important, the aim here is specifically to consider simpler model structures currently in use in marine ecosystem models, to illustrate how even minor differences can have significant impacts on the overall simulation. Our focus is thus on investigating model sensitivity to

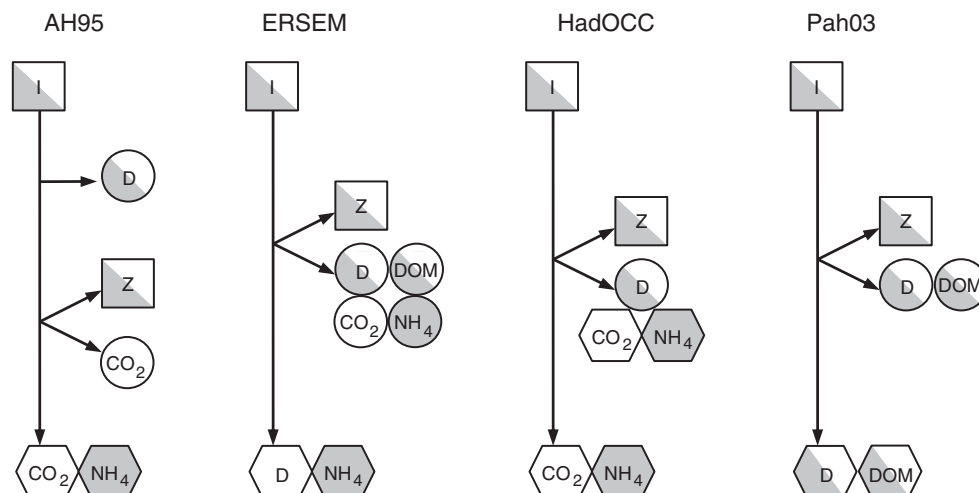


Fig. 1. Flow pathways of the 4 trophic transfer schemes. Ingested food (I) is allocated to zooplankton biomass (Z), faecal material (detritus: D), dissolved organic matter (DOM), CO₂ and inorganic N (NH₄). C flows unshaded, N flows shaded. Release of substrates in stoichiometric excess is shown in hexagons.

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