Food-density-dependent inefficiency in animals with a gut as a stabilizing mechanism in trophic dynamics

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Animals with a gut, when confronted with food supplied *ad libitum*, can elevate their ingestion rates and inefficiently use the material they ingest. As a consequence, assimilation efficiency (AE) declines, resulting in food-density-dependent inefficiency (f-DDI). A model describing these processes shows that f-DDI can dampen the consequences of oscillations in food abundance that may occur in response to external stochastic (e.g. climatic) forcing both with respect to production and timing. This response is illustrated with a simple planktonic food chain of a phytoplankton and two consumers. The assumption of a fixed gut transit time, consistent with the traditional model descriptions of a fixed AE, produces predator–prey oscillations. By contrast, simulations using a model showing f-DDI (behaving in accordance with the experimental data) cushion not only the impact of such oscillations but also the effects of the removal of intermediate grazers in the food chain. The operation of f-DDI affects other trophic interactions through changes in the nutrient regeneration and the voiding rates. The extent to which f-DDI operates in nature needs valuation, followed by the appropriate construction of consumer-based ecosystem models.

Keywords: assimilation efficiency; consumer growth dynamics; gut passage time; predation kinetics; food quality

1. INTRODUCTION

Factors that control the production at each trophic level and the transfer of elements between those levels are central to ecology. In classical Lotka–Volterra models, and variants thereof, the limits of production are set by simple parameters describing predator–prey interactions and carrying capacities. More mechanistically, trophic interactions may be controlled by resource acquisition (typically as hyperbolic functions of resource availability) coupled with stoichiometric variation and nutrient recycling (Hessen *et al.* 2002; Sterner & Elser 2002). Autoecological factors also control production, the most obvious being self-shading by phototrophic populations, while for higher trophic levels the behaviour of predators in crowded situations (e.g. cannibalism) can limit growth. The subject of this work concerns another factor that affects the trophic transfer, namely the food-density-dependent inefficiency (f-DDI) that is associated with the operation of the gut in consumers.

The optimal gut transit time (GTT) is a function of the time taken to initiate the digestive process (which will vary with the food type) followed by the liberation and recovery of assimilable chemicals (Sibly & Calow 1986). The maximum assimilation rate requires the maintenance of a high gradient of assimilable materials across the gut wall. While this does not require that the gut is full, it is aided by a high through flow of the material, with only a partial assimilation. The more material that is removed (assimilated), the lower the cross-wall gradient becomes, a situation compounded by changes in chemical composition of the

remaining material, which becomes increasingly difficult to digest. The theoretical implications of this operation and the repercussions for ingestion have been well explored (Sibly & Calow 1986; Penry & Jumars 1987; Jumars 2000; Yearsley *et al.* 2001; Illius *et al.* 2002). Mitra & Flynn (2007) linked, for the first time, a description of gut operation to the control of ingestion in a multielement dynamic model, showing how changes in ingestion rates, GTT, assimilation and voiding are coupled both for the situations of different food quantity and also of variable stoichiometric quality. Whereas simple consumer models employ fixed assimilation efficiencies ($AE = (\text{Ingested} - \text{Voided}) / \text{Ingested}$), the dynamic model of Mitra & Flynn (2007) shows how AE varies with food availability. Thus, the consumers with a gut display f-DDI at high food availability through the following chain of events: ingestion is elevated, GTT is decreased, voiding (of partly degraded material) is increased, and AE consequently decreases. The model allows the study of the emergent properties of such physiology upon ecosystem dynamics. Decreases in GTT with high food availability result in a deterioration of trophic transfer efficiency, and a linearization of the relationship between food availability and ingestion. These and the food-quality-stimulated changes in GTT are seen in invertebrates (such as zooplankton; Mullin & Brooks 1970; Tirelli & Mayzaud 2005), through to fishes (Horn & Messer 1992), mammals (Trumble & Castellini 2005) and birds (Afik & Karasov 1995), although not all animals show decreased AE with increased ingestion rates (Sibly & Calow 1986).

Variation in the physical environment is an important driver affecting matching and mismatching of trophic

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activities. In aquatic systems, one of the most important forcing factors acts through changes in the mixed layer depth that governs the depth of the photic zone for phytoplankton growth. Mechanisms that may cushion trophic dynamics against climate-related stochastic events are especially important for organisms with lifespans over several seasons; in the planktonic realm they are the meso-zooplanktonic (and higher) predators. The effects of voiding of excess material by consumers confronted by excess food are also important to other ecosystems (e.g. loss of material from photic zone to benthic systems). It is clearly important to understand these processes (e.g. [Jumars *et al.* 1989](#)), and others such as the impact of sources of mortality on trophic chain intermediates (including harvesting or fishing), and to simulate them appropriately. However, simple traditional models display oscillations through the food web in response to the stochastic variation in physical forcing because the linkage between trophic levels is stiff, operating with fixed transfer efficiencies, while one may expect considerable variation in AE with food availability and with quality.

Here, the implications of f-DDI in consumer activity have been considered by comparing the consumer model of [Mitra & Flynn \(2007\)](#) configured either with constant GTT or with GTT related to gut satiation. The ecosystem scenario is planktonic (the model of [Mitra & Flynn \(2007\)](#) having been tuned against the data for zooplankton activity), with growth of the phytoplankton controlled by the mixing depth, self-shading and nutrient availability. The operation of f-DDI can have important effects on the trophic activity; in particular, stabilizing against excess production at lower trophic levels.

2. MATERIAL AND METHODS

The model of [Mitra & Flynn \(2007\)](#) was used to describe two predatory consumers in terms of their carbon and nitrogen biomass, one (Z1) feeding on phytoplankton and the other (Z2) feeding on Z1. These consumer models were parametrized as per the configurations employed for the plots in fig. 4 in [Mitra & Flynn \(2007\)](#). These configurations had been tuned to the experimental results for Crustacea (copepods) assuming either a constant GTT or one in which GTT decreased with increasing gut satiation (this giving rise to increasing f-DDI as food availability increased). The alternative models are hereafter termed as non-DDI and DDI configurations, respectively, and displayed similar relationships between the food availability and the consumer growth rate ([Mitra & Flynn 2007](#)). The description of the phytoplankton employed a normalized carbon–nitrogen quota model, based on that employed by [Mitra & Flynn \(2007\)](#) in their fig. 6, but with inclusion of a photoacclimative component (variable Chl : C, as described by [Flynn 2001](#)). This trophic model was then placed in scenarios in which the initial concentration of dissolved inorganic nitrogen (DIN) was either low (10 μM ; 0.14 mg N l^{-1}) or high (200 μM ; 2.8 mg N l^{-1}), and in water columns of varied mixing depths. Mixing, at a rate of 0.01 d^{-1} (similar to that seen in the early summer mid-Atlantic) introduced fresh nutrients and removed the photic zone organisms, the nutrients and the voided material. The surface photon flux density was held constant at 750 $\mu\text{mol m}^{-2} \text{s}^{-1}$; this value equates to approximately 40 per cent full sunshine. The average photosynthetic rate varied with the Chl : C and nutrient status (indicated by

N : C) of the phytoplankton, with the phytoplankton biomass density and the mixing depth; the last two mentioned lead to increasing self-shading of the phytoplankton production as the biomass develops. Particulate nitrogenous materials voided by the consumers degraded to DIN at a rate of 0.05 d^{-1} . Thresholds for predation by Z1 upon phytoplankton and for Z2 upon Z1 were set at 0.05 and 0.005 mg C l^{-1} , respectively; they prevented extinction. The model assumed homogeneous mixing of all the populations throughout the mixed layer, with no patchiness. In order to further disturb the trophic dynamics, the intermediate predator Z1 was culled (simulating harvesting, fishing, as may be applied to krill). This cull was applied at a rate of 0.1 d^{-1} and was not associated with a balancing return of the elements removed in inorganic form to support new phytoplankton growth. The models were run on POWERSIM CONSTRUCTOR (Isdalstø, Norway), with dynamic risk analyses conducted using POWERSIM SOLVER v. 2.

3. RESULTS

In general, phytoplankton show a much higher biomass when grown at low mixing depths, before coming under nutrient, light and/or predatory control. Following the initial bloom, a second growth develops, the success of which depends on nutrient regeneration and the grazing activity by Z1 ([figure 1](#)). In comparison with the model configuration with fixed GTT (non-DDI), the model displaying DDI gives a more rapid decay of phytoplankton prey from the initial bloom, and a more modest and less variable growth of Z1 and Z2 populations. The differences between the non-DDI and DDI models are not so marked at greater mixing depth. Deeper mixing gives lower phytoplankton growth rates and lower phytoplankton biomass densities so that predator–prey coupling is closer. When an additional loss term is applied to Z1 ([figure S1](#) in the electronic supplementary material), simulating a continuous cull (harvesting) of these predators, again the DDI version shows less extreme oscillations both with respect to the peak biomass and also to its timing. By contrast, the non-DDI model has a more marked temporal shift in the peaks of Z1 and Z2 ([figure S2](#) in the electronic supplementary material).

The differences between the consumer model configurations (non-DDI versus DDI) are primarily due to differences in the ingestion rates and the assimilation efficiencies ([figure S4](#) in the electronic supplementary material), with the DDI configuration showing elevated ingestion coupled with a low AE for carbon (AE_C), which together drive a rapid consumption of prey without a *pro rata* increase in predator population. At greater mixing depths, where the phytoplankton growth is more light limited and hence matching between the predator and the prey is much closer, the model outputs are far more similar to each other. The prey stoichiometric quality (i.e. N : C) is lower in the shallow mixing-depth scenarios, where the phytoplankton growth is most rapid and the nutrients are exhausted; here, the DDI model describes a shorter period of low-quality prey (approx. 5–20 d, versus 5–30 d for non-DDI; [figure S3](#) in the electronic supplementary material). This has ramifications for subsequent predator growth as phytoplankton with low N : C support lower predator growth rates.

Figure 1. Low nutrient ($10 \mu\text{M N}$) model output showing the temporal development of (a,b) phytoplankton and two predators, (c,d) Z1 and (e,f) Z2, at different mixing depths (as indicated by each grey-shaded area). (a,c,e) The non-DDI model and (b,d,f) the DDI model configuration.

In the high-nutrient scenario (figure 2), the extended growth potential for the phytoplankton at shallow mixed depth systems is apparent. Again, the initial algal bloom terminates more rapidly in the DDI simulation, and the development of the predators, Z1 and Z2, is far more limited, not tracking that of the phytoplankton production. By contrast, the non-DDI model shows large predator population growth at shallow mixing depths. The differences between the model outputs are less apparent

at greater mixing depths because matching between the predator and the prey is closer. The affect of culling Z1 is less pronounced for the high-nutrient scenarios (figure S5 versus figure 2, cf. figure S1 versus figure 1).

The results from a dynamic risk assessment of the model outputs (figure S6 in the electronic supplementary material) show clearly that the DDI model exhibits greater stability both without (figure S6.1 in the electronic supplementary material) and with the inclusion of the

Figure 2. As figure 1 but for a high-nutrient system ($200 \mu\text{M N}$). (a,c,e) The non-DDI model and (b,d,f) the DDI model configuration.

additional cull (harvesting) of Z1 (figure S6.2 in the electronic supplementary material). Assessments with other altered parameters (e.g. initial phytoplankton biomass, regeneration rates of the voided material) confirmed the relative stability of the DDI configuration (not shown).

4. DISCUSSION

The fundamental mechanistic difference between the model configurations is seen with the greater variation in ingestion rate and assimilation efficiencies in the DDI

model (figure S4 in the electronic supplementary material). The DDI model configuration simulates the variation in GTT seen in animals when presented with food supplied ad libitum; this results in a more efficient gut operation (Jumars 2000) but a lower organismal AE. Traditionally, models assume fixed AE (specifically for the limiting nutrient) although it is recognized that food quality can affect this and other aspects of consumer activity (Mitra & Flynn 2005). While the DDI configuration behaves in accordance with the knowledge of gut dynamics, the non-DDI configuration is in closer accordance with the much-simplified description of the

consumer activity typically employed in ecosystem models. The non-DDI model used here had a fixed GTT, which dampens the variation in AE (Mitra & Flynn 2007), but does not eliminate it. Much of the variation in non-DDI AE_C (figure S4 in the electronic supplementary material) reflects the stoichiometric effects and the non-steady-state interaction between ingestion and assimilation rates. These differences have important implications for simulation and understanding of the trophic dynamics.

In the simulations presented here, without DDI the original phytoplankton bloom lasts much longer, especially at shallow mixing depth. By contrast, the DDI configuration shows a rapid decline in phytoplankton even though the predator is less numerous (figure 1); excess production is lost as voided material that would in a real system support detritivores (Jumars *et al.* 1989). There is also a marked temporal shift of predator production in the non-DDI model (figure 2; figure S2 in the electronic supplementary material), which reflects slower consumption of the phytoplankton in part associated with deterioration in the food quality (i.e. the phytoplankton N : C stoichiometric shift; figure S3 in the electronic supplementary material), that develops because predatory grazing cannot increase quickly enough to prevent phytoplankton exhausting the inorganic nutrient. This effect is most obvious for shallow mixing depths where phytoplankton growth is most rapid and the potential for mismatch thus greatest.

As a consequence of the DDI that results from the activity of predators in the presence of excess food (prey), the DDI configuration displays considerable stability in response to both the temporal and quantitative shifts in production. In the simulations used here, the mixing depth is a surrogate for climate-linked variability; shoaling of the mixed-layer depth is critical for the start of the plankton production cycle, and the resultant potential for mismatch between the primary and secondary production (phytoplankton to Z1 as simulated here) is considered as important for the subsequent trophic levels (Cushing 1995). However, in general, it appears that a fundamental operational characteristic of consumers with guts (Sibly & Calow 1986; Penry & Jumars 1987; Jumars 2000; Yearsley *et al.* 2001; Illius *et al.* 2002) can act to dampen the otherwise expected predator–prey oscillations. Behavioural traits prior to food ingestion, such as the so-called ‘messy feeding’ (Møller 2005), will only exacerbate such inefficiency in trophic transfer.

The rapid and enhanced *pro rata* grazing activity of predators confronted with high prey availability may also generate stability at a second level, because it lessens the likelihood of a stoichiometry-linked downregulation of grazing (Mitra & Flynn 2005). Without this downregulation, the phytoplankton becomes more nutrient deprived, N : C declines, and their poor food quality affects not only the growth of their immediate predators (Z1) but also the nutrient regeneration that would otherwise counteract the deterioration in the phytoplankton nutrient status. Mitra & Flynn (2006) showed how such a chain of events could lead to a positive feedback and the formation of harmful algal blooms by blocking elemental trophic transfer. The involvement of f-DDI, however, decreases the risk of such developments; the risk is likely to be decreased further if GTT is also decreased by the consumption of food low in quality (Mitra & Flynn 2007). The above-mentioned processes will contribute to the interplay between the

physical environment and the biological activity that are recognized as important factors in models describing climate and anthropogenic impacts upon the biodiversity and the population stability (Hsieh *et al.* 2005; Anderson *et al.* 2008).

In conclusion, f-DDI has the potential to stabilize the operation of predator–prey systems, with respect to quantity, quality and timing of production. In some instances with removal (e.g. harvesting) of both predator types, the production of Z2 is actually enhanced using the DDI model configuration. Dampening of the peaks and troughs associated with predator–prey mismatch results in more C actually flowing to the higher trophic levels (not shown). The proper description of such events is important. The risk assessment conducted on these simulations (figure S6 in the electronic supplementary material) suggests that both for events affecting primary production (e.g. stochastic, climate-related consequences, such as mixing depth; figure S6.1 in the electronic supplementary material) and predatory activity outside of the normal trophic interactions (simulated here by harvesting Z1; figure S6.2 in the electronic supplementary material), f-DDI cushions the impacts. The question is to what extent such processes affect the real systems, e.g. for how long may other losses (including those associated with human activity, such as fishing) be endured with no apparent damage before a tipping point is reached? While the consumer model used for this work is solidly grounded in animal physiology (Penry & Jumars 1987; Jumars 2000) and is consistent with what data are available not only for zooplankton but for other higher predators, there is a basic lack of the data upon which to fully parametrize the f-DDIs described here. Anderson *et al.* (2008) report how the selective harvesting of fishes, through the disturbance of age structure, magnifies fluctuations in fish abundance. At first sight, the implications of that study run contrary to that shown here. However, f-DDI will operate throughout an age-structured population affecting generations of predator and prey interactions. To study the full implications requires a coupled age structure–physiology model and quite likely also to consider the implications of chemical stoichiometry beyond elemental N : C. While these matters need addressing in the meantime, it is clear that doubt may be cast upon models describing trophic transferences that rely on fixed assimilation efficiencies.

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