

HORIZONS

Predator–prey interactions: is ‘ecological stoichiometry’ sufficient when good food goes bad?

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The dietary value of a prey type varies with its nutritional status and hence with its C:N:P content. However, while stoichiometric differences between a heterotroph and its food must affect growth efficiency (GE), and thence trophic dynamics, other factors related to food quality may act as powerful modulators of predator–prey interactions. Thus, minor changes in prey stoichiometry can be associated with more significant changes in prey quality (production of toxins, mucus, thicker walls etc.) that may have a disproportionate effect on predation rates and GE. We term the predator response to such events, ‘stoichiometric modulations’. Often these modulations are negative, decreasing predation and assimilation rates. We suggest that due consideration should be given in the construction of multinutrient-based models of predators to the processes of prey selectivity, ingestion and digestion as functions of food quality with quantity.

INTRODUCTION

The term ‘ecological stoichiometry’ has been coined recently to describe the role of stoichiometry (typified by C:N:P) in controlling trophic processes and has even been proposed as a new branch of ecology (Sterner and Elser, 2002; Andersen *et al.*, 2004). It has long been known that stoichiometric imbalances between predator and prey affect trophic interactions and ecosystem function. Those who have studied multielement predator–prey interactions have appreciated such implications [e.g. for plankton (Goldman and Caron, 1985; Caron and Goldman, 1988; Davidson *et al.*, 1995a)], as have theoreticians (e.g. Reiners, 1986). Indeed, in a mass-balanced multinutrient predator–

prey model it is impossible *not* to invoke stoichiometric-driven trophic events such as changes in growth efficiency (GE) and nutrient regeneration. However, there are additional food-related factors of at least equal importance shaping predator–prey interactions.

The dietary value of prey varies with the bulk elemental (e.g. C:N:P) stoichiometric relationship between predator and prey and also with finer biochemical differences, such as fatty acid content (Jónasdóttir, 1994). The former, prey quality, is a function of nutrient status (e.g. N or P limitation), and the latter is largely a function of prey type (e.g. diatom versus dinoflagellates). Together, prey quality and prey type have a powerful effect on prey

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selection, consumption and trophic transfer efficiencies (Flynn and Davidson, 1993; Flynn *et al.*, 1996; Jones *et al.*, 2002; Jones and Flynn, 2005). Such studies show that changes in prey nutrient status can result in very different predator behavioural responses to those expected from simple stoichiometric interactions. We discuss the nature of these responses and consider to what extent, as a consequence, stoichiometric imbalances alone should be considered as the primary driving factor in multinutrient models of planktonic systems. (Here ‘predator’ and ‘prey’ are used as generic terms for phagotrophs or higher heterotrophs and living or dead particulate food, respectively. Variation in prey quality refers to differences in composition *within* a prey type associated with its nutritional status; not to differences between prey types, e.g. diatoms versus dinoflagellates.)

We use the term ‘stoichiometric modulators of predator–prey interactions’ to describe the modification of predator behaviour associated with a disadvantageous stoichiometric disparity between the predator and its prey. The default expectation is that set solely by simple stoichiometric constraints; this is termed neutral modulation. In this instance, the kinetics of capture, ingestion and digestion of the prey are unaffected by food quality. Hence, for example, ingestion of the limiting nutrient (X) decreases in line with the decrease in prey content of X as indicated by declining prey X:C. Retention of ingested X remains the same as indicated by a constant gross growth efficiency for X (GGE_X), with no impact of prey quality on digestion and assimilation. Alternatively, the predator may attempt to overcome the dietary inadequacy by increasing ingestion rate and/or GGE , and hence improve its growth beyond the neutral status; this is termed positive modulation. On the contrary, the response of the predator may exacerbate the effect of poor food quality with a deterioration in ingestion and/or assimilation rates; this is termed negative modulation.

The question is whether the simplest response, neutral modulation, best represents the norm in plankton systems or indeed in any ecosystem. Whether it does or not will likely be a function not only of the ecophysiology of the dominant predator but also of the type of limiting nutrient. It is noteworthy that much of the work that has been the source of inspiration for ecological stoichiometry for plankton has been on *Daphnia*, considering the consumption of P-limited prey [(Andersen *et al.*, 2004) and references therein]. *Daphnia* is primarily a filter-feeder and thus exhibits limited prey-capture selectivity. It also has a relatively high P requirement (Steiner, 2004). Additionally, P is an element that can be readily recycled internally (as PO_4^{3-}), unlike N which during catabolism is released as toxic NH_4^+ and thus voided. One may question whether ecological stoichiometry, which

accords primarily with what we term neutral modulation, would be considered to be such a driving force if all these studies had been undertaken on a raptorial organism and/or involving limitation by an element other than P [e.g. copepods feeding on N-limited prey (Jones *et al.*, 2002)].

FEEDING AND GE

There are three important processes associated with feeding—(i) ingestion (prey selection and capture), (ii) digestion (liberation of material from the ingested prey in a form suitable for further incorporation) and (iii) assimilation of the material made available through digestion into predator biomass. Of these, the most important potential point of interaction is ingestion, followed by digestion. At the extreme, if nothing is ingested or if what is ingested is indigestible then the predator will not benefit from the presence of the potential prey. The third and comparatively least important process is also the primary point of pure predator–prey stoichiometric interactions. The ways in which these three processes are modulated in response to food nutrient status will impact not only directly on predator–prey dynamics, but also indirectly on the ecosystem through the nature of material that is voided by the predator. Material that is not digested is voided primarily as particulate and dissolved organics suitable for the support of other heterotrophic activity. In contrast, material voided after assimilation (i.e. respired or regenerated) is primarily inorganic and most likely to support photoautotrophic activity.

There are various potential problems caused by the presence of excess C (i.e. low X:C) in the food. It should be noted that ‘X’ need not be an element but could represent an essential dietary component that cannot be synthesized by the predator [e.g. an essential fatty acid (Anderson and Pond, 2000)]. These problems variously affect ingestion (I), assimilation efficiency (AE), net growth efficiency (NGE), and thus GGE . For zooplankton such problems may include—

1. presence of less X in a given mass of captured particles, hence I_X may decline or extra energy is expended in capturing sufficient of it,
2. excess C (especially indigestible C) in the ingested food package may result in AE_X declining due to decreased enzyme efficiency for the utilization of X,
3. ingestion may decline due to physical obstruction (e.g. mucus) or rejection of prey due to physiological/behavioural responses allied to the presence of toxins etc. These typically result from the poor nutrient status of phytoplanktonic food.

Point 1 may be countered by increasing the particle capture rate (increasing throughput), but this compounds point 2. Point 3 in turn may exacerbate 1 and 2. To complicate things further, consumption of the prey may be hindered by the presence of other organisms, whose growth is stimulated by the same nutrient regeneration processes [i.e. by the presence of so-called secondary prey (Nejstgaard *et al.*, 1995; Genkai-Kato, 2004)].

When food is N and/or P deplete, GGE_C of the predator will inevitably fall because excess C must be voided consistent with stoichiometric requirements. Low food availability, as may typically affect zooplankton in oligotrophic areas (Huntley and Boyd, 1984), will also result in low efficiency (Anderson and Hessen, 1995) as a higher proportion of ingested C is respired. On the other hand, the presence of a large quantity of food may also result in lowered GGE due to a shortened gut passage time and thence a decrease in AE (Acharya *et al.*, 2004). Behavioural responses may enhance ingestion at high prey densities [e.g. 'superfluous feeding' (Marshall, 1973)], with poor efficiency, consuming more prey with no greater predator production. The relative quantities of large and small prey types also affect GE via sloppy feeding (Møller, 2005). GGE may therefore vary significantly just with changes in food quantity in addition to any stoichiometric impacts with food quality. This has clear ecological implications as predator growth is limited by these responses, affecting zooplankton population size (Irigoién *et al.*, 2005). However, these behavioural responses can only be represented in ecosystem models containing grazing functions relating AE to food ingestion rates. Such functions are not included typically in models of zooplankton.

Supply of a high X:C diet at a given concentration (as $gC L^{-1}$) would, all else being equal and assuming that the maximum food X:C is similar to that of the predator, support a higher zooplankton yield than would the supply of the same prey at a lower X:C. In the latter instance, there will be less X ingested, and therefore lower zooplankton production would result. The immediate impression is that X is limiting; this may be suggested by a constant or elevated GGE_X when the prey is of lower X:C (e.g. Caron and Goldman, 1988). Simple stoichiometric models predict this result (e.g. Anderson, 1992). However, stoichiometric modulation of the predator-prey interactions has potential to alter such predictions significantly.

STOICHIOMETRIC MODULATION OF THE PREDATOR-PREY INTERACTION

Stoichiometric modulation is most significant when it occurs with a relatively small shift in the stoichiometric relationship between predator and prey, resulting in a disproportionate

impact on predator-prey interactions. This may typically be associated with changes in prey physiology, with environmental events such as nutrient depletion.

When exposed to prey with low X:C, throughput of material could be altered by the predator in order to optimise ingestion of the limiting nutrients. There are two contrasting mechanisms. The predator could decrease throughput ($I \downarrow$), allowing more time for the extraction of X from the food as it passes through the gut (mesozooplankton) or resides in the feeding vacuole (microzooplankton). Alternatively, throughput could be increased ($I \uparrow$), increasing the amount of X flowing through the gut/vacuole, rather akin to increasing the volume swept clear for prey capture. Consumption of poor food may thus promote an enhanced ingestion rate [positive modulation, e.g. (Darchambeau and Thys, 2005)]. The increased value of I_X could possibly be balanced with a less efficient handling of the ingested elements resulting in a decreased AE_X , but nonetheless there may be an overall enhancement of growth. At the other extreme, consumption of a nutritionally unbalanced diet can result in continued prey consumption but with little or no growth (Jones *et al.*, 2002; Jones and Flynn, 2005).

The emphasis in discussions on stoichiometric impacts on predator-prey interactions is primarily associated with the absence of X in the prey, perhaps aggravated by the concurrent absence of readily assimilated C. However, rather than the absence of X causing a problem it may be the *presence* of secondary metabolite toxins produced by the prey during nutrient stress that promotes rejection [point 3 above; (Nejstgaard *et al.*, 1995; Flynn *et al.*, 1996; Granéli *et al.*, 1998; Calbet *et al.*, 2002)]. Other changes in the physiology of nutrient-deprived prey may be of similar importance; for example zooplankton digestion of nutrient-deprived phytoplankton is adversely affected by excess phytoplankton mucus production (Malej and Harris, 1993) and thickening of their cell walls (Van Donk *et al.*, 1997). At extreme negative modulation, one could have a situation where a formerly useful food item could be present at a high numeric density but in consequence of its poor quality (low X:C) is either not ingested at all (Flynn and Davidson, 1993) or if ingested cannot be assimilated (Van Donk *et al.*, 1997). With low X:C feed, GGE_X may well not increase or stay constant (as typically projected by stoichiometric models—see below), but may in fact decrease [as seen for GGE_N ; (Jones *et al.*, 2002)]. Such events will impact on food web stability.

STOICHIOMETRIC MODULATION AND MODELS

Nutrient limitation of zooplankton production has been explored through the behaviour of stoichiometric models

(Anderson and Hessen, 1995; Sterner, 1997; Touratier *et al.*, 1999; Anderson and Pond, 2000). The structure of stoichiometric models, and their supporting arguments, typically disregard any association between low food X:C and poor quality of food for reasons other than simply possession of a low X:C. These models consider only the fate of ingested material, with no inclusion of the impact of food quality on the processes of prey selection, ingestion and digestion. It is pertinent to ask whether such a simplification is justified.

Mitra *et al.* (Mitra *et al.*, 2003) showed the potential power of negative, neutral and positive modulations on the predator–prey interaction. Davidson *et al.* (Davidson *et al.*, 1995b) found that it was essential to involve, what we term, negative modulation (through avoiding ingestion of low N:C prey) in the modelling of microflagellate predator–prey interactions (Flynn and Davidson, 1993). This experimental study was of *Isochrysis galbana* consumption by *Oxyrrhis marina* in two systems with different initial prey concentrations; Flasks S and T (Flynn and Davidson, 1993). Flask T showed a classic predator–prey interaction. However, in Flask S the *Isochrysis* prey became N-deplete resulting in rejection by *Oxyrrhis* in a display of negative modulation. Using a new model, designed to specifically enable a consideration of stoichiometric modulation

(A. Mitra, submitted for publication), we show in Fig. 1 fits to the data of Flasks S and T. During tuning (optimisation) of the model, to obtain a fit to the experimental data, constants describing ingestion and assimilation were allowed to vary in response to changes in *Isochrysis* quality (i.e. prey N:C). The tuning resulted in negative modulation for ingestion, and neutral modulation for assimilation, in response to low *Isochrysis* N:C. Thus poor prey were not ingested at a high rate while assimilation of prey that were captured was not affected. Figure 2 shows the model output for Flask S when the negative stoichiometric modulation obtained during the tuning process was replaced with neutral or positive modulation. To implement neutral modulation, ingestion was not linked to prey quality. For positive modulation, the kinetics (rate) of prey ingestion was increased *pro rata* with the decrease in prey N:C, thus retaining a constant ingestion rate of prey-N for a given prey C biomass concentration. Both neutral and positive modulations gave very poor fits (Fig. 2).

In the *Isochrysis*–*Oxyrrhis* interaction described above, only negative modulation of prey capture was required, however this may be insufficient in other instances. For example, in order to simulate the data of Jones *et al.* (Jones *et al.*, 2002) for GGE_C , GGE_N and growth rate in

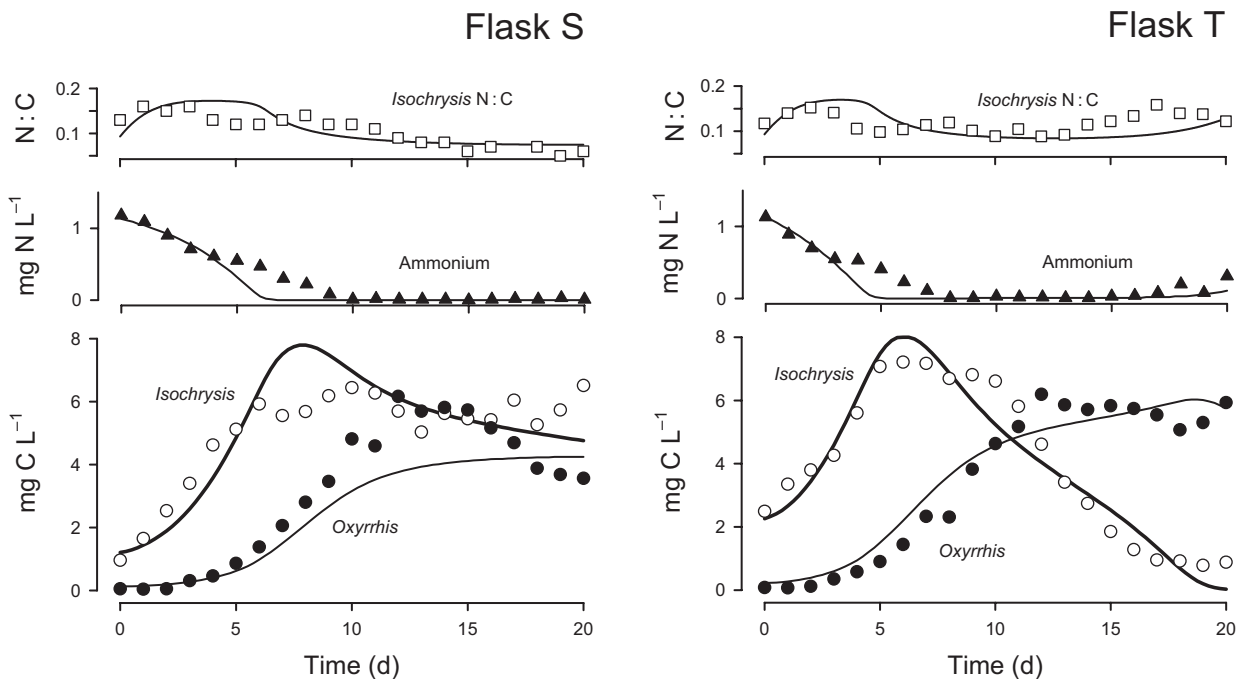


Fig. 1. The data of Flynn and Davidson (Flynn and Davidson, 1993), shown as symbols, for interaction between the prey *Isochrysis galbana* (open circles) and the predator *Oxyrrhis marina* (closed circles), together with model output (lines). The model was tuned simultaneously to data from Flasks S and T and to an *Isochrysis*-only control flask (not shown) for C biomass and ammonium, with common constant values for phytoplankton and zooplankton physiology. *Isochrysis* N:C data are calculated indirectly [see (Davidson *et al.*, 1995a) for discussion]. This particular model did not enable an enhancement of cannibalism to counter rejection of *Isochrysis*, an event that occurs in reality.

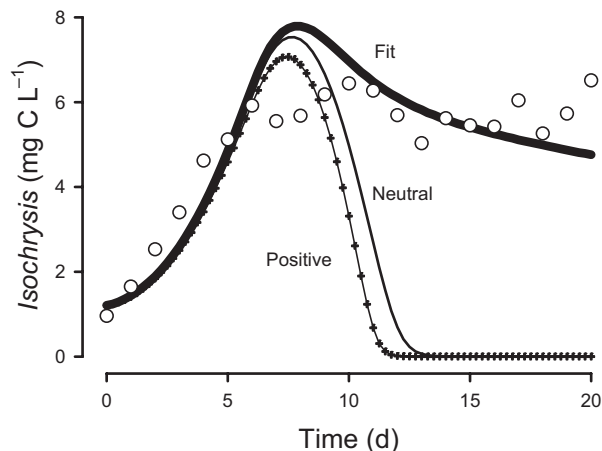


Fig. 2. Model output ('Fit') tuned to *Isochrysis galbana* biomass data of Flask S (open circles; see also Fig. 1) compared to model outputs when neutral or positive stoichiometric modulation of predation is induced.

the copepod *Acartia tonsa*, a negative modulation for assimilation (i.e. AE) is required to reproduce the decrease in GGE_N seen with declining prey N:C (not shown). One may question whether only mesozooplankton, with a relatively short gut passage time, display such variations in AE . Protists lack a gut and digestion can be protracted; it may be that protists are more likely to display modulation at the level of capture and ingestion rather than at digestion.

We (A. Mitra and K. J. Flynn, submitted for publication) have also considered the positive stoichiometric modulation that is implicit in the operation of traditional NPZ-type models (e.g. Evans and Garçon, 1997). In such models, predation is usually a function solely of prey N-biomass while in reality prey ingestion is a function of prey availability reflected as numeric abundance or C biomass. Phytoplankton growth during periods of low N-nutrient availability results in lowered N:C, which would result in N-specific predation being depressed if the zooplankton exhibited neutral stoichiometric modulation (i.e. the default option). Hence, within classic NPZ (single nutrient) models, *de facto* there is a positive modulation as equivalent C biomass ingestion is enhanced. However, inclusion of this feature is not intentional but is simply a consequence of the model being N based. It is possible that the fits of the NPZ model using positive modulation are being obtained by misrepresenting some other processes in compensation. A rebalance of this situation to neutral modulation, by making grazing C-specific rather than N-specific has a significant impact on model output (A. Mitra and K. J. Flynn, submitted for publication). That the model with positive modulation fits the data so well suggests either an inadequacy within the structure of the NPZ model and/or indicates the

importance of stoichiometric modulation of predator-prey interaction.

Application of stoichiometric theory to plankton has raised the question as to which elements limit zooplankton growth (Checkley, 1985; Kiørboe, 1989; Hessen, 1992; Anderson and Hessen, 1995; Steiner, 2004). There are parallels in the model-supported arguments for elemental limitation of zooplankton growth with discussions in the literature concerning N versus P limitation of phytoplankton growth that were based around manipulations of the quota model of phytoplankton growth (e.g. Rhee and Gotham, 1980; Turpin, 1986). Flynn (Flynn, 2002a) criticised this approach, arguing that the kinetics of nutrient transport could easily outweigh those of assimilation, pointing out that traditional phytoplankton quota models contain no link between variable transport kinetics and phytoplankton nutrient status with which to explore such interactions. Noting the analogy between nutrient transport for phytoplankton and food ingestion for zooplankton, nutrient limitation at the point of assimilation may be unimportant if food quality affects prey ingestion into zooplankton significantly (as indeed it appears to be well able to do). The range of responses of a predator to a stoichiometric disparity using neutral modulation alone is far more limited than the response range possible for ingestion and/or digestion kinetics. It follows that consideration should be given in zooplankton models to inclusion of grazing functions related to prey quality as well as to prey type and quantity.

STOICHIOMETRIC MODULATION AND TROPHIC STABILITY

On the face of it, stoichiometric interactions can lead to a stabilising effect where growth of the prey is limited by nutrient regeneration by the predator; the growth of the predator is in turn affected by the prey density and its stoichiometric value (Anderson and Hessen, 1995). Thus the interaction is neither bottom-up (agricultural model) nor top-down (predator-prey model) but somewhere in between (Flynn, 1989). Stoichiometric modulation of the predator-prey interactions, however, has the potential to destabilise or otherwise alter the outcome.

Negative stoichiometric modulation of predation enhances the impact of nutrient deprivation on the prey more than simple stoichiometric calculations would predict. This is due to the decreased level of nutrient regeneration. The resultant positive feedback caused by negative modulation gives rise to a situation where X-limitation of the algal prey may lead to C-limitation of the predator due to prey rejection.

Predators may select against low quality prey, resorting to alternatives, to cannibalism or even to starvation (Goldman and Caron, 1985; Bonnet *et al.*, 2004). This type of event could be important for the formation of blooms (Irigoien *et al.*, 2005).

Rates of nutrient cycling vary greatly between aquatic ecosystems, especially where a physical transport of material occurs (such as sinking of faecal pellets out of the photic zone into deep waters). Stoichiometric modulation of trophic interactions could have a significant effect either by enhanced prey rejection or when changes in predator *AE* and/or *NGE* affect the form of voided material (i.e. dissolved versus particulate). Some of these trophic shifts could be associated with subtle changes in nutrient physiology. For example it has been suggested that colony formation in *Phaeocystis*, resulting from nitrate rather than ammonium-based growth, may subsequently adversely affect predation on this organism (Riegman and van Boekel, 1996). There is then a knock-on effect on microbial loop and mesozooplankton activities (Hansen *et al.*, 1993). Multinutrient zooplankton models need to be capable of representing such behavioural responses.

CONCLUSIONS

In the past, little attention has been paid to the nutrient status (e.g. C:N:P) of zooplankton prey. While it is well known that certain organisms are better prey than others, preference and dietary value varying with prey nutritional status are less widely invoked (Jones and Flynn, 2005). The impact on trophic processes of stoichiometric differences between predator and prey is undisputed (Sterner and Elser, 2002). Ecological stoichiometry describes ‘the balance of energy and chemical elements in ecological interactions and especially in trophic relationships’ (Andersen *et al.*, 2004). It is not a new approach *per se*, but it does perhaps have value in drawing attention to the importance of multinutrient trophic processes to those who have ignored even the most basic implications for too long. However, the processes described within ecological stoichiometry are already included within the established term ‘ecosystem ecology’, describing and explaining fluxes of energy and matter through ecosystems (Calow, 1999). There is nothing to be gained by creating yet another division within ecology. Given the significance of the evidence we have, indicating that prey quality is far more than just a simple function of stoichiometry, to only consider the impact of stoichiometric differences (i.e. neutral modulation) may also be considered as potentially dangerous.

Models invariably present a simplification of reality. The application of Occam’s razor (one should not

increase, beyond what is necessary, the number of entities required to explain anything) is a common argument for simplification. The question is, on what basis is the judgement of necessity made? The description and exploration of ecological processes require more than just consideration of energy and/or stoichiometry (Reiners, 1986). Behaviour is one such factor. Modelling the behaviour of organisms is nontrivial but mechanisms by which organisms overcome or circumvent energetic or stoichiometric barriers to their growth are important and deserve consideration for inclusion in models. An example would be descriptions of the physiology of vertical migrating plankton (Flynn, 2002b; Liu *et al.*, 2003), where omission of behaviour traits would be absurd.

We suggest that for zooplankton, models describing feeding behaviour may enable better simulations of the impacts of food quality on production and thence recycling of nutrients in surface waters, or loss of material as sinking phytoplankton and/or zooplankton faecal pellets. The implications of stoichiometric modulation of predator–prey interactions, in which the quality of the food is indexed to factors more powerful than simply C:N:P, needs consideration both within the stoichiometric function itself (affecting *AE* and *NGE*) and also in conjunction with prey selectivity.

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REFERENCES

- Acharya, K., Kyle, M. and Elser, J. J. (2004) Biological stoichiometry of *Daphnia* growth: an ecophysiological test of the growth rate hypothesis. *Limnol. Oceanogr.*, **49**, 656–665.
- Andersen, T., Elser, J. J. and Hessen, D. O. (2004) Stoichiometry and population dynamics. *Ecol. Lett.*, **7**, 884–900.
- Anderson, T. R. (1992) Modelling the influence of food C:N ratio, and respiration on growth and nitrogen excretion in marine zooplankton and bacteria. *J. Plankton Res.*, **14**, 1645–1671.
- Anderson, T. R. and Hessen, D. O. (1995) Carbon or nitrogen limitation in marine copepods. *J. Plankton Res.*, **17**, 317–331.
- Anderson, T. R. and Pond, D. W. (2000) Stoichiometric theory extended to micronutrients: comparison of the roles of essential fatty acids, carbon, and nitrogen in the nutrition of marine copepods. *Limnol. Oceanogr.*, **45**, 1162–1167.
- Bonnet, D., Titelman, J. and Harris, R. (2004) *Calanus* the cannibal. *J. Plankton Res.*, **26**, 937–948.
- Calbet, A., Broglio, E., Saiz, E. *et al.* (2002) Low grazing impact of mesozooplankton on the microbial communities of the Alboran Sea: a possible case of inhibitory effects by the toxic dinoflagellate *Gymnodinium catenatum*. *Aquat. Microb. Ecol.*, **26**, 235–246.

- Calow, P. (ed.) (1999) *Blackwell's Concise Encyclopaedia of Ecology*. Blackwell Science, Oxford, UK.
- Caron, D. A. and Goldman, J. C. (1988) Dynamics of protistan carbon and nutrient cycling. *J. Protozool.*, **35**, 247–249.
- Checkley, D. M. Jr. (1985) Nitrogen limitation of zooplankton production and its effect on the marine nitrogen cycle. *Arch. Hydrobiol.*, **21**, 103–113.
- Darchambeau, F. and Thys, I. (2005) In situ filtration responses of *Daphnia galeata* to changes in food quality. *J. Plankton Res.*, **27**, 227–236.
- Davidson, K., Flynn, K. J. and Cunningham, A. (1995a) Predator–prey interactions between *Isochrysis galbana* and *Oxyrrhis marina* III. Mathematical modelling of predation and nutrient regeneration. *J. Plankton Res.*, **17**, 465–492.
- Davidson, K., Flynn, K. J. and Cunningham, A. (1995b) A first attempt to model factors affecting the ingestion of prey by the dinoflagellate *Oxyrrhis marina*. *Cytology*, **37**, 969–977.
- Evans, G. T. and Garçon, V. C. (1997) *One-Dimensional Models of Water Column Biogeochemistry*. JGOFS report 23/97. JGOFS Bergen, Norway.
- Flynn, K. J. (1989) Interaction between nutrient and predator limitation of production in the marine euphotic zone. *Chem. Ecol.*, **4**, 21–36.
- Flynn, K. J. (2002a) How critical is the critical N:P ratio? *J. Phycol.*, **38**, 961–970.
- Flynn, K. J. (2002b) Toxin production in migrating dinoflagellates: a modelling study of PSP producing *Alexandrium*. *Harmful Algae*, **1**, 147–155.
- Flynn, K. J. and Davidson, K. (1993) Predator–prey interactions between *Isochrysis galbana* and *Oxyrrhis marina*. II. Release of non-protein amines and faeces during predation of *Isochrysis*. *J. Plankton Res.*, **15**, 893–905.
- Flynn, K. J., Davidson, K. and Cunningham, A. (1996) Prey selection and rejection by a microflagellate; implications for the study and operation of microbial food webs. *J. Exp. Mar. Biol. Ecol.*, **196**, 357–372.
- Genkai-Kato, M. (2004) Nutritional value of algae: a critical control on the stability of *Daphnia*-algal systems. *J. Plankton Res.*, **26**, 711–717.
- Goldman, J. C. and Caron, D. A. (1985) Experimental studies on an omnivorous microflagellate: implications for grazing and nutrient regeneration in the marine microbial food chain. *Deep Sea Res. Part A.*, **32**, 899–915.
- Granéli, E., Johansson, N. and Panosso, R. (1998) Cellular toxin contents in relation to nutrient conditions for different groups of phycotoxins. In Reguera, B., Blanco, J., Fernández, M. L. and Wyatt, T. (eds), *Harmful Algae*. Xunta de Galicia & Intergovernmental Oceanographic Commission of UNESCO, Grafisant, Santiago de Compostela, Spain, pp. 321–324.
- Hansen, F. C., Reckermann, M., Breteler, W. C. M. K. *et al.* (1993) *Phaeocystis* blooming enhanced by copepod predation on protozoa—evidence from incubation experiments. *Mar. Ecol. Prog. Ser.*, **102**, 51–57.
- Hessen, D. O. (1992) Nutrient element limitation of zooplankton production. *Am. Nat.*, **140**, 799–814.
- Huntley, M. and Boyd, C. (1984) Food-limited growth of marine zooplankton. *Am. Nat.*, **124**, 455–478.
- Irigoien, X., Flynn, K. J. and Harris, R. P. (2005) Phytoplankton blooms: a 'loophole' in microzooplankton grazing impact? *J. Plankton Res.*, **27**, 313–321.
- Jónasdóttir, S. H. (1994) Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: Laboratory investigations. *Mar. Biol.*, **121**, 67–81.
- Jones, R. H. and Flynn, K. J. (2005) Nutritional status and diet composition affect the value of diatoms as copepod prey. *Science*, **307**, 1457–1459.
- Jones, R. H., Flynn, K. J. and Anderson, T. (2002) The effect of food quality on carbon and nitrogen growth efficiency in *Acartia tonsa*. *Mar. Ecol. Prog. Ser.*, **235**, 147–156.
- Kjørboe, T. (1989) Phytoplankton growth rate and nitrogen content: Implications for feeding and fecundity in a herbivorous copepod. *Mar. Ecol. Prog. Ser.*, **55**, 229–234.
- Liu, S.-H., Sun, S. and Han, B.-P. (2003) Diel vertical migration of zooplankton following optimal food intake under predation. *J. Plankton Res.*, **25**, 1069–1077.
- Malej, A. and Harris, R. P. (1993) Inhibition of copepod grazing by diatom exudates—a factor in the development in the mucus aggregates. *Mar. Ecol. Prog. Ser.*, **96**, 33–42.
- Marshall, S. M. (1973) Respiration and feeding in copepods. *Adv. Mar. Biol.*, **11**, 57–120.
- Mitra, A., Davidson, K. and Flynn, K. J. (2003) The influence of changes in predation rates on marine microbial predator/prey interactions: a modelling study. *Acta Oecol.*, **24** (Suppl. 1), S359–S367.
- Møller, E. F. (2005) Sloppy feeding in marine copepods: prey-size-dependent production of dissolved organic carbon. *J. Plankton Res.*, **27**, 27–35.
- Nejstgaard, J. C., Bamstedt, U., Bagoien, E. *et al.* (1995) Algal constraints on copepod grazing—growth-state, toxicity, cell-size, and season as regulating factors. *ICES. J. Mar. Sci.*, **52**, 347–357.
- Reiners, W. A. (1986) Complementary models for ecosystems. *Am. Nat.*, **127**, 59–73.
- Rhee, G.-Y. and Gotham, I. J. (1980) Optimum N:P ratios and coexistence of planktonic algae. *J. Phycol.*, **16**, 486–489.
- Riegman, R. and van Boekel, W. (1996) The ecophysiology of *Phaeocystis globosa*: a review. *J. Sea Res.*, **35**, 235–242.
- Steiner, C. F. (2004) *Daphnia* dominance and zooplankton community structure in fishless ponds. *J. Plankton Res.*, **26**, 799–810.
- Sterner, R. W. (1997) Modelling interactions of food quality and quantity in homeostatic consumers. *Freshwater Biol.*, **38**, 473–481.
- Sterner, R. W. and Elser, J. J. (2002) *Ecological Stoichiometry: the Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.
- Touratier, F., Legendre, L. and Vezina, A. (1999) Model of copepod growth influenced by the food carbon: nitrogen ratio and concentration, under the hypothesis of strict homeostasis. *J. Plankton Res.*, **21**, 1111–1132.
- Turpin, D. H. (1986) Growth rate dependant optimum ratios in *Selenastrum minutum* (Chlorophyta): implications for competition, co-existence and stability in phytoplankton communities. *J. Phycol.*, **22**, 94–102.
- Van Donk, E., Lüring, M., Hessen, D. O. *et al.* (1997) Altered cell wall morphology in nutrient-deficient phytoplankton and its impact on grazers. *Limnol. Oceanogr.*, **42**, 357–364.

