Comment on "Possibility of N or P Limitation for Planktonic Cladocerans: An Experimental Test" (Urabe and Watanabe) and "Nutrient Element Limitation of Zooplankton Production" (Hessen)

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Comment on "Possibility of N or P limitation for planktonic cladocerans: An experimental test" (Urabe and Watanabe) and "Nutrient element limitation of zooplankton production" (Hessen)[1]

The literature has provided a surge in studies claiming that zooplankton may be limited by elemental N or P (Hessen 1992; Sommer 1992; Urabe and Watanabe 1992). The stoichiometric approach of these studies is appealing because it explains a portion of zooplankton dynamics in terms of the basic elemental composition of lake seston, which can be easily measured, and because it presents parallels between plant (Tilman 1982) and animal nutritional physiology. I would like to make three general points regarding the modeling approach and results of Urabe and Watanabe (1992) and Hessen (1992). First, I present in simple terms the model on which their results are based and make several original predictions that can be logically derived from this model. Second, I discuss the true meaning of ratios of food nitrogen to carbon (N : C) and phosphorus to carbon (P : C) in relation to the nutritional physiology of animals and the problem of correlation vs. causation. Third, I discuss practical details of real planktonic ecosystems which question the validity of conclusions drawn by Urabe and Watanabe and Hessen.

Consider a *Daphnia* which initially had a carbon mass of 1.0 μg and which doubled its C mass during a 5-d interval to 2.0 μg C. If the N : C ratio of this animal ($N:C_Z$) was 0.20 and this ratio was in homeostasis during the sampling interval, then the N mass of the animal would have changed from 0.2 to 0.4 μg during the interval. If this animal had a C gross growth efficiency (K_C) of 0.25, it had to consume 4.0 μg C food to double its weight. If the N : C ratio ($N:C_F$) of the food was 0.16, the food would have contained 0.64 μg N. Thus, the animal would have incorporated 0.20 μg of N into biomass for 0.64 μg N consumed, giving a N gross growth efficiency (K_E) of 0.31. K_E can be expressed as

$$K_E = \mu_{Z\text{-}E}/I_E. \qquad (1)$$

Here $\mu_{Z\text{-}E}$ is the net production rate in terms of N, and I_E is the N ingestion rate. It follows that

$$\mu_{Z\text{-}E} = \mu_{Z\text{-}C}(N:C_Z). \qquad (2)$$

$\mu_{Z\text{-}C}$ is the net production rate in terms of C. It also follows that

$$I_E = I_C(N:C_F). \qquad (3)$$

I_C is the C ingestion rate. As for Eq. 1, K_C can be expressed as

$$K_C = \mu_{Z\text{-}C}/I_C. \qquad (4)$$

By rearranging Eq. 1–4 we find

$$K_E/K_C = (N:C_Z)/(N:C_F). \qquad (5)$$

Both Urabe and Watanabe and Hessen calculated the critical food nutrient ratio ($Q^*_{C\text{-}E}$) —the ratio of food N or P to C below which zooplankton production would be partially N or P limited—by assuming the maximum possible N or P gross growth efficiency, $K_E = 1$, and solving for $N:C_F$ accordingly:

$$Q^*_{C\text{-}E} = N:C_F = K_C(N:C_Z). \qquad (6)$$

Equation 5 predicts that as the food N : C ratio deviates from the zooplankton N : C ratio, the K_E and K_C values will diverge. In other words, as the N or P ratio of the food decreases below that of the animal, the animal will have to balance N or P gross growth efficiency against carbon gross growth efficiency by either increasing N or P gross growth efficiency or, after reaching the maximum possible N or P gross growth efficiency, by reducing C gross growth efficiency. At the point at which C gross growth efficiency is reduced, the animal becomes at least partially N or P limited. Since carnivores consume food which is relatively similar to

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their own elemental ratio, they would not be constrained by the problem of balancing K_E against K_C. However, depending on the N : C or P : C ratios of the available food, herbivores could be expected to be constrained by food quality as well as quantity. Herbivores could balance K_E against K_C by preferentially selecting food with high N : C or P : C ratios, by developing very efficient means of digesting and assimilating N and P, or by consuming more food to compensate for the low C gross growth efficiency.

These arguments lead to the following predictions: first, carnivores will be limited by food quantity, not quality; second, herbivores will be limited both by food quantity and quality; third, herbivores will preferentially select food with high N : C and P : C ratios; fourth, herbivores will have efficient or elaborate means of digesting their food in order to optimize N and P gross growth efficiency; fifth, animals feeding on food of low quality will need to consume more of it; sixth, herbivores will husband their N and P efficiently at low food N : C and P : C ratios; seventh, animals will be limited by the quality of their food at low food N : C or P : C ratios. The first five predictions have tremendous support in the literature of animal nutritional physiology and behavior. The sixth is supported by two studies (Lehman and Naumoski 1985; Olsen et al. 1986) showing greater P turnover times when animals consume food with low P : C ratios. The first six of these predictions are presented for the first time. Urabe and Watanabe and Hessen presented only the seventh prediction in their papers.

The seventh prediction, the main conclusion of Urabe and Watanabe and Hessen, is certainly true at the correlation level, but I argue it is clearly false for at least N at the causation level as is shown by a large body of literature on animal nutritional physiology. Hessen clearly states that animals may be *directly* limited by the ratios of P or N to C of their food, which clearly assumes food elemental ratios determine (or cause) food quality. Urabe and Watanabe do not explicitly make this point, but a careful reading of their paper shows they make it implicitly. The problem of correlation vs. causation for N metabolism is not semantic wrangling: there is a very clear distinction between arguing food quality is correlated with food N : C (as has been assumed in many previous studies of plant–herbivore interactions) and arguing that food quality is caused by food N : C.

At no point do Hessen or Urabe and Watanabe indicate that their N : C ratio was merely an index of food protein to carbohydrate content. N cannot be used by animals in elemental or inorganic forms and must be metabolized as proteins and amino and nucleic acids (Claybrook 1983; Harrison 1990). Animals, including crustaceans (Harrison 1990), are unable to synthesize ten of the essential amino acids and must obtain them from their diets. Thus, a specific food can have a high N : C ratio, but if it lacks any one of the essential amino acids it will be insufficient for sustaining growth. In fact, specific amino acids, nucleic acids, sterols, fatty acids, and vitamins have been shown to limit the production of the cladoceran *Moina macrocopa* (Conklin and Provasoli 1977). Crustaceans may also be unable to synthesize at least two important fatty acids (Harrison 1990). Although lipids and fatty acids are poor in N, their "essential" nature further emphasizes the reliance on complex organic molecules in the diets of crustaceans and other animals. It should be noted that plants are said to be limited by elemental N because they use N as NH_4 or N_2 and C as CO_2, while animals use N mainly as amino acids and C as carbohydrates and fatty acids which are then broken down to glucose before being assimilated.

The metabolism of P is quite different from that of N because P is a mineral like Ca or Mg. Direct P limitation of vertebrates, or rickets, is a well-known deficiency. Rickets is, however, not a major constraint to the production of many animals and is closely related to the metabolism of Ca and in some cases vitamin D. In general the literature on crustacean nutritional physiology indicates a clear hierarchy in the major constraints to the growth and production of crustaceans (Dall and Moriaty 1983; Harrison 1990). This hierarchy is obtaining energy (in the form of carbon bonds), obtaining sufficient protein and associated essential amino acids, obtaining critical or essential lipids or fatty acids, and finally, obtaining sufficient vitamins and minerals. In all likelihood mineral deficiencies (such as P) can occur, but they are probably rare compared to limitation due to lack of calories, protein, essential amino acids, lipids, etc.

In terms of applying their model to real planktonic ecosystems, the greatest weakness of the papers of Urabe and Watanabe and Hessen is their assumption that lake seston elemental ratios are representative of the food actually consumed by zooplankton. If one were to similarly define the quality of food available to deer in a forest as the average elemental ratio of all plant matter in the forest, one would surely conclude that deer could never survive there given the constraint of balancing P against C gross growth efficiency. We know however that deer, as well as almost all zooplankton species, are highly selective when choosing food. That is, most zooplankton solve the problem of balancing P gross growth efficiency against C gross growth efficiency by the third prediction (i.e. being selective) instead of being limited by the seventh prediction (i.e. having their growth rates reduced due to low available food quality).

Copepods, rotifers, and most cladocerans will be constrained by the elemental ratios of diatoms, cryptophytes, chlorophytes, and other preferred algae. The ratios of these algae will certainly be higher than the elemental ratios of lake seston which often contains refractory detritus, bacteria, cyanobacteria, and other low quality particles. For example, Urabe and Watanabe determined that the green algae *Chlamydomonas* and *Scenedesmus* had N:C ratios of 0.164 and 0.158 and P:C ratios of 0.019 and 0.024, which are much higher ratios than those normally found for lake seston. Even zooplankton like *Daphnia,* which selects food particles more or less randomly within a specific particle size range (i.e. 1–30 μm), will be unable to consume much of the lake seston which is either too large to handle (colonial or chain-forming algae) or too difficult to digest (refractory detritus). Furthermore, *Daphnia* can preferentially select high quality algae by locating and staying in vertically oriented patches of algae (Johnsen and Jakobsen 1987; Leibold 1990). In other words, lake seston elemental ratios are probably a poor measure of the quality of the food actually consumed by the zooplankton, and thus one cannot, based on lake seston elemental ratios, conclude that zooplankton will be limited by the quality of their food.

When calculating the critical food ratio for *Daphnia,* Hessen assumed a C gross growth efficiency of 0.6 and concluded that *Daphnia* would be P limited at a P:C ratio of 0.018 when assuming a P gross growth efficiency of 1.0 and a zooplankton P:C ratio of 0.030. However, it is obvious from Eq. 5 that a high C gross growth efficiency can be realized only when the food is of extremely high quality. If one were to use a C gross growth efficiency of 0.32 as Urabe and Watanabe determined for *Daphnia* grown on the high quality green algae *Chlamydomonas* and *Scenedesmus,* one would find a critical food P:C ratio of 0.0096. By using a very high, and I believe unrealistic, C gross growth efficiency, Hessen exaggerated the theoretical potential for mineral P limitation of crustacean zooplankton. Adjusting the C gross growth efficiency used in Hessen's model to 0.32 cuts his critical food P:C ratio nearly in half. Of the 32 lakes shown in figure 6 of his paper, 23 fell below his critical food P:C ratio of 0.018, while only nine of these lakes fall below the recalculated critical food ratio of 0.0096. Of these nine lakes, eight had P:C ratios of ~0.008 which represents only a 17% loss of potential production; in the remaining lake, the potential lost production was 58%. If one assumes that *Daphnia* do not use any selective feeding mechanisms and if these values are averaged for all 32 lakes, then P limitation may have theoretically accounted for a 6% loss of production across all lakes.

The critical food N:C ratios calculated for *Daphnia* and *Bosmina* at Urabe and Watanabe's low food concentrations are the most relevant critical food elemental ratios, because at high concentrations of food, animals can compensate for low quality by simply eating more food (*see the fifth prediction*). If the critical N:C ratios above are compared with the range of N:C ratios observed in various lakes (*see* table 3 of Urabe and Watanabe), it is apparent that lake N:C ratios were below the critical ratios only in Lake Biwa. This comparison of predicted critical food ratios vs. observed lake seston ratios shows that, given the constraints of their own model, there is almost no support for their conclusion that zooplankton can be expected to be limited by lake seston N:C ratios.

Hessen presented a correlation between particulate phosphorus (PP) and zooplankton biomass to support his claim that zooplankton are P limited. He discounted the possibility that the strong relationship between PP and zooplankton biomass was merely an autocorrelation by arguing that (Hessen 1992, p. 802) "zooplankton P made up nearly 8% of TP [total P] and 16% of PP (medians). Autocorrelation would thus not be expected to contribute significantly to the zooplankton-PP (or -TP) correlations." Obviously if zooplankton P comprised 16% of PP in all samples, the autocorrelation between zooplankton biomass and PP would be equal to nearly 1.0, while little variance about 16% would produce a strong autocorrelation. The only way for him to test the true relationship between zooplankton biomass and PP, in reference to his hypothesis of P limitation of zooplankton, would be to correlate zooplankton biomass with nonzooplankton PP.

Regardless of whether elemental N or P limitation is theoretically possible, it has not actually been tested. Four experimental studies (Hessen 1990; Watanabe 1990; Sommer 1992; Sterner et al. 1993) have been cited as possible evidence for N or P limitation of zooplankton because *Daphnia* growth was lower in P- or N-stressed *Scenedesmus* than in nonnutrient-stressed *Scenedesmus*. However, the reduced *Daphnia* growth noted in each of these experiments could be due to changes in the biochemical status of *Scenedesmus* (Sterner et al. 1993). When algae are starved of N or P, the cell biochemical composition changes; specifically the ratio of protein to carbohydrate may decrease and the algae may totally cease synthesis of specific amino and fatty acids (Piorreck et al. 1984; Harrison et al. 1990). It is known that many common algae are of only marginal food quality for zooplankton when grown with saturating nutrients (Lundstedt and Brett 1991), so it is highly probable that nutrient stress can change the biochemical composition of *Scenedesmus* sufficiently to reduce its nutritional quality.

In conclusion, I do not believe that the stoichiometric approach can be applied to N metabolism because N metabolism is much more complex than models based on simple N : C ratios would suggest. One cannot conclude that highly selective zooplankters, which include almost all nondaphnid zooplankton, will be limited by the quality of measured lake seston, because lake seston P : C ratios do not reflect the quality of the food they actually consume. If one assumes that *Daphnia* uses no mechanisms to preferentially select high quality food, then a recalculated critical food P : C ratio suggests P limitation may account for a 6% loss of production when averaged across the 32 lakes given by Hessen. Any selective strategies by *Daphnia*, such as optimally feeding in vertically oriented patches of high quality algae, could partially or wholly ameliorate this 6% loss. Thus, for purely theoretical reasons zooplankton are highly unlikely to be limited by elemental N and P. Extensive experimental evidence (Conklin and Provasoli 1971; Claybrook 1983; Harrison 1990) suggests mineral deficiencies (such as P) can occur, but are probably rare compared to limitation due to lack of energy, protein, essential amino acids, lipids, etc. Any direct effects of mineral P on zooplankton nutrition are likely to be trivial compared to indirect effects of P on zooplankton nutrition mediated through phytoplankton biomass and biochemical composition.

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Implications of sestonic elemental ratio in zooplankton ecology: Reply to the comment by Brett

Elemental or *mineral limitation* represents a limit to the rate of production due to a deficiency of an element in a resource relative to the demand of a consumer. In our study (Urabe and Watanabe 1992), we emphasized that an elemental imbalance between food and consumers has important implications in terms of production and community structure. An analysis based on bioelements is advantageous for investigating interaction and feedback processes over a trophic level, because such bioelements are the ultimate and common substance necessary for both autotrophs and heterotrophs. However, we do not believe that the quality of food for zooplankton is determined by the relative contents of these elements alone. In his comment on our study and that of Hessen (1992), Brett (1993) argues that elemental limitation for zooplankton is unlikely for two reasons. First, zooplankton cannot use N in inorganic form but only in organic form. The N : C ratio of food is, therefore, an index, but not a determinant, of food quality. We agree with this point. The N : C ratio of organic matter largely reflects the protein : lipid ratio (Omori and Ikeda 1984). In zooplankton, therefore, protein limitation may be a more accurate term than N limitation. However, there is no reason for rejecting the possibility of P limitation in zooplankton, because they can obtain P in an inorganic form from food. Second, Brett asserts that zooplankton avoid elemental shortage through their physiological and behavioral flexibility. Here, we comment on this point and argue that available evidence indicates that zooplankton are, in fact, frequently affected by food quality.

In our study, we suggested that zooplankton showing selective feeding suffer less from elemental imbalance between food and consumer. *Bosmina* may have an advantage over *Daphnia* if variance in the elemental ratio between edible particles is large (Urabe and Watanabe 1992). Brett repeats this possibility emphatically. Growth of selective feeders is, however, not always free from the problem of elemental shortage in the possible food. First, phytoplankton are not always rich in N and P. Studies have revealed that the elemental ratios of algae are not constant, but change according to nutrient supply rate and growth rate even within the same species (e.g. Goldman et al. 1979). In fact, Sommer (1991) showed that there was a period in Plußsee when the N : C weight ratio of several algal species decreased to 0.07, which is the same level as the threshold elemental ratio (TER) for N we calculated for cladocerans. In this context, it should also be noted that the calculated TER was estimated

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on the basis of an unlikely assumption (gross growth efficiency = 100%). Realistically, as we stated previously, the TER is probably higher than we calculated, making elemental limitation more likely than we proposed originally.

Second, let us consider a situation where the total abundance of possible foods is insufficient for maximal growth of a zooplankton species, and the mean N : C or P : C ratios are below the level of the TER due to a low elemental ratio of the dominant food item. If the animals ingest the dominant food item, they will suffer from a shortage of mineral (in the case of P) or protein (in the case of N). On the other hand, if the zooplankton do not ingest that food, they will suffer from severe food shortage because of the limitation of high quality food items. In any event, the production rate of the zooplankton is lower than that expected under food conditions where total C abundance is the same, but the elemental content is higher. Thus, the resulting production rate can be said to be limited by the shortage of the mineral or protein in the possible food pool. Zooplankton with selective feeding will enjoy an increasing advantage with increasing abundance of high quality food.

We used lake seston to estimate the food pool for zooplankton in our study. Unlike "wood for deer," sestonic particles are a possible food source for at least some zooplankton species (Kerfoot and Kirk 1991). There is evidence that some zooplankton use detritus as food (e.g. Hessen et al. 1990). Indeed, daphnids, one of the target animals in our study, ingest particles of <30 μm with little or no discrimination (Burns 1968; DeMott 1990). The weakness of our study is, therefore, not the use of lake seston as the food pool, but lack of consideration of the seston size range ingestible by the zooplankton species. Unfortunately, less is known about the elemental ratio of lake seston within the edible size range. In our experience with the Ogochi Reservoir and Lake Biwa (Watanabe 1990; Nakanishi et al. unpubl.), however, it is not uncommon to encounter a P : C ratio of seston passing through a 30-μm mesh that is the same as or below the calculated TER for *Daphnia galeata,* which is again probably lower than the actual TER.

Brett argues that at high concentrations of food animals can compensate for low quality by eating more. However, Sterner et al. (1993) showed that the feeding rate of *Daphnia obtusa* is lower on algae with lower P content. It should be noted that the increase in ingestion rate may decrease retention time of food in the gut and thus absorption efficiency for the element in question. Such a relationship implies that animals cannot necessarily compensate for low quality food by increasing feeding rate even at high concentrations of food. Theoretical studies indicate that when food quality is low, it is more advantageous for animals to increase the absorption efficiency by reducing their ingestion rate (e.g. Taghon 1981).

Zooplankton may avoid elemental imbalance by staying or moving to a depth where food of high nutritional quality has accumulated. At the population level, however, this situation implies a limit to the areal production rate, because habitat space and the size of the available food pool are restricted overall. In addition, this depth may not be suitable for zooplankton because of predators. If zooplankton locate or stay at a specific depth due to deficiency of a certain element within the potential food at another depth, such a phenomenon per se would be definite evidence that the production rate of zooplankton is affected by the quality of potential food.

With regard to P, one might suspect that zooplankton solve a shortage in the food pool by taking P directly from the lake water. However, this possibility is unlikely. Rigler (1961) suggested that direct uptake of free phosphate from water is negligibly small in daphnids. It should be noted that a low P : C ratio in algae occurs when the concentration of dissolved P is very low (Goldman et al. 1979), and a low P : C ratio in lake seston occurs when dissolved P is lower than the limit of detection by the usual methods of chemical analysis (~1 ppb: Tezuka 1986). Assuming a volume : carbon ratio of 20 as a conversion factor, we calculate the volume-specific P content of phytoplankton at a low P : C ratio to be ~0.0002. This rough estimate indicates that, when lake seston has a low P : C ratio, zooplankton must take up a volume of lake water at least five orders higher than that of the phytoplankton cell to obtain the same amount of P. The direct uptake of P from lake water is, thus, much less efficient than taking it from the food pool. In addition, if zooplankton can take in P directly from lake water more efficiently than algae, they will lose other important nutrient sources like protein, because algal abundance will be reduced due to competition with zooplankton for dissolved P in the lake water.

The stoichiometric model makes several predictions about the physiological and behavioral flexibility of zooplankton, as Brett points out. However, these predictions do not imply that zooplankton can always solve the problem of elemental imbalance because there are behavioral and physiological constraints. Predictions of behavioral and physiological flexibility (predictions 3–6 of Brett) and of elemental limitation (prediction 7) do not contradict each other. Rather, prediction 7 and the others are like different sides of the same coin. Zooplankton may be limited at times by the quality of their food when food elemental ratios are low and thus may maintain such behavioral or physiological flexibility to optimize their fitness *by expending some costs.*

The TER should be interpreted as a "fundamental" limiting point, where zooplankton cannot compensate for elemental imbalance. Brett's comment implies a kind of "realized" limitation concerning food quality. In nature, food quality for zooplankton is probably determined by factors that may not be immediately identified by investigators. If the elemental ratio of possible foods for a zooplankton is not higher than the TER, one should suspect that the animal is affected by food quality. Needless to say, however, algae with a higher elemental ratio are not always food of nutritionally high quality, because they may be deficient in some essential organic compounds (essential amino acids, essential fatty acids, etc.) or resistant to digestion by zooplankton. In other words, production and community structure of zooplankton are affected by the chemical composition of food, perhaps even more often than we illustrated from the elemental imbalance.

Ahlgren et al. (1990) indicated that the fatty acid composition of algal species can affect the population growth rate of some cladocerans, whereas Sterner et al. (1992*b*, unpubl.) demonstrated that growth rate of *D. obtusa* is more tightly related to the specific P content of algae than to that of fatty acids and proteins. We need to learn much more about the nature of food quality. On the other hand, the elemental imbalance between consumer and food pools is also an important aspect of community and ecosystem ecology, because it provides an opportunity to find a new aspect of trophic interaction (Sommer 1992), to clarify the role of heterotrophs in elemental cycling (Urabe in press), and to blend the differing views within these disciplines (Sterner et al. 1992*a*). We hope that scientists pay more attention to and challenge the food quality–elemental imbalance issues before hastily rejecting all the possibilities of elemental or mineral limitation for zooplankton. Integration of such efforts will accelerate the progress of our understanding of zooplankton behavioral and physiological flexibility, trophic interaction, and dynamics of elemental cycling in aquatic ecosystems.

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The role of mineral nutrients for zooplankton nutrition: Reply to the comment by Brett

Several recent studies have suggested that a "stoichiometric approach" may be a fruitful supplement to conventional food-web theory (e.g. DeAngelis 1990; Sterner et al. 1992). One part of this theory deals mainly with regeneration and elemental cycling. The amount and proportion of released nutrients depend on elemental proportions both in the food and the grazer, and this will create feedbacks affecting the entire food web (Lehman 1984; Elser et al. 1988; Sterner et al. 1992). The other part is related to the possible element constraints on heterotrophic production. For a grazer, a too low proportion of mineral nutrients in the diet could lead to limitation by that element. For common freshwater crustacean zooplankters like *Daphnia,* with nearly stoichiometric homeostasis (Andersen and Hessen 1991) and high phosphorus demands, a *relative* P limitation can be predicted when there is an imbalance between assimilated P : C and the somatic demands for P relative to C (Olsen et al. 1986; Hessen 1992).

Brett (1993) argues against this view and suggests that other nutritional factors such as energy, fatty acids, proteins, or amino acids are the proper units when discussing food quality. Before examining the arguments more thoroughly, let me first state that I certainly do not disagree with the role these and other biochemical constituents play in zooplankton (or animals in general) nutrition. Naturally, nutrient deficiency in zooplankton can be ascribed to several reasons—as has been repeatedly demonstrated for any number of herbivores. There is a vast literature on this, and I think it should be fairly obvious that the stoichiometric approach never intended to replace past evidence. I specifically made this point in the introduction of my paper (Hessen 1992, p. 800), stating that ". . . factors such as shape and digestibility, vitamins, proteins, and fatty acid composition may be of great importance." In fact, in a more recent paper (Van Donk and Hessen 1993), we emphasized this and also demonstrated reduced assimilation of nutrient-deficient green algae. Thus, my point is certainly not to pinpoint strict P limitation as *the* ultimate reason for reduced growth in zooplankton feeding on nutrient-deficient algae; rather, I propose an additional hypothesis to accompany the well-known factors listed by Brett. This point is important, because his comment could be interpreted as if these factors are incompatible. Indeed, they are not. There are other assumptions in his comment that need clarification.

I will restrict my discussion largely to the possibility of P limitation, since that was my theme in the paper that Brett criticizes. I have, however, a few comments concerning N limitation. I do not specifically comment that the N : C ratio largely reflects the protein : lipid ratio, simply because it is fairly obvious and there is no reason to repeat it. Correspondingly, the P : C ratio might reflect the relative share of macromolecules like phospholipids, DNA, RNA, other nucleotides, or mineral P in the carapace (for zooplankton). I do agree that one should be aware that the unit of N generally assimilated is in the form of organic molecules and not inorganic or elemental N; semantically, it would be most appropriate to use a term like protein limitation rather than elemental N limitation. The same argument can be applied to C limitation. In aquatic ecology there is a long tradition of judging production and food limitation of zooplankton in units of C, although C, like N, is not assimilated in elemental form, but is bound in various macromolecules. The same arguments can be applied in speaking about elemental limitation among other heterotrophs like bacteria, where conventionally we speak about C, N, or P limitation. To what extent is this merely a question of definitions and semantics or of real inconsistencies?

When it comes to P, which is largely assimilated in inorganic form by the gut, one can speak of P limitation for zooplankton as an analog to P limitation in primary producers. There is no theoretical evidence against this possibility, as Brett also acknowledges (p. 1336): "Extensive experimental evidence . . . suggests mineral deficiencies (such as P) can occur. . . ." This is a major point, and the question is thus not whether strict P limitation *may* occur, but rather its ecological relevance, and thus whether it is ". . . probably rare compared to limitation due to lack of energy, protein, essential amino acids, lipids, etc." It should be stated, however, that this discussion also concerns laboratory studies evaluating growth parameters in zooplankton and food quality of various algae (Van Donk and Hessen 1993).

It is fairly evident that food quantity (in terms of carbon or energy) most frequently limits zooplankton production. Hessen (1992, p. 800) referred to the general positive relationship between zooplankton and phytoplankton biomass in a number of studies, yet stated that "pronounced scatter in such field correlations is due to variations in environmental factors and interlake variability in biotic interactions such as vertebrate and invertebrate predation that suppress the herbivores. Composition and quality of food could contribute to this scatter." This variability may be seen as analogous to the factors causing scatter in phosphorus–phytoplankton relationships—a theme that has attracted tremendous research effort. Yet no one denies P as a main determinant to freshwater phytoplankton production and biomass.

In my earlier paper, I did not assume that lake seston elemental ratios are equal to those of the food actually consumed by zooplankton. Rather I stated that "although element composition in crude seston may not mimic that of ingested food (Q_F), it should approach Q_F for non-selective feeders" (Hessen 1992, p. 811). For selective feeders, there is a good evidence that high quality food (if available) is preferred, and elemental ratios in crude seston certainly would not reflect those in their food. *Daphnia* (and related nonselective herbivores)—which I primarily discussed in my study—approach a nonselective ingestion of seston in the range 1–30 μm and would not distinguish between high and low quality food (Butler et al. 1989). Thus calanoid copepods could be favored relative to *Daphnia*, if some minor proportion of the food is nutritionally adequate. However, even for *Daphnia*, crude seston is only suggestive of the stoichiometry of ingested food, and I also stated that ". . . a high proportion of poorly assimilated, recalcitrant detritus in the diet may, however, obscure the relevance of sestonic P : C-ratios in this context" (Hessen 1992, p. 811). If we know the C : P ratio of the grazer and (more or less) that of its ingested food, then potential P limitation is determined by net assimilation of C vs. that of P.

Brett claims that the maximum growth efficiency for C (∂_C) applied in my model (0.6) is unrealistically high and correctly states that a lowered ∂_C would reduce the likelihood of P limitation. However, in applying a growth efficiency of 0.32 to his recalculations, Brett chooses a value that is very low (cf. Lampert 1987). It should also be recalled that the model itself predicts reduced growth efficiency when P : C (or N : C) is below a critical limit. Thus estimates of growth efficiency based on nutrient-deficient food would ultimately reduce ∂_C. This model also uses a 100% growth efficiency for P (∂_P) to estimate a minimum P : C ratio at which P limitation may occur. Lowering ∂_P, which is reasonable even when feeding P-deficient food, would counteract an eventual overestimate of ∂_C and increase the potential P : C threshold. Thus Brett's calculation of a 6% loss of production across selected lakes, based on a lowered ∂_C and a ∂_P of 1.0, first hinges on some debatable assumptions, but, more importantly, averaging over a number of lakes is not relevant in this context. My main point is that P limitation may be important in some lakes, or at some times, just as the effects of grazing have obvious seasonal and interlake variability, but is still an interesting ecological parameter.

Brett's assumption that ". . . animals can compensate for low quality by simply eating more food" (p. 1335), does not catch the essence of the stoichiometric theory. Certainly zooplankton can speed up their filtering rate when feeding on nutrient-deficient food (Hessen et al. 1989), although contrasting strategies are also proposed (Taghon 1981). The point is that when elements are unbalanced, excess C either is not assimilated (most probably) or is disposed of as respiration, and growth efficiency declines. More carbon simply "goes to waste."

Undoubtly, starvation affects the biochemical composition of cells. If, however, the biochemical constituents are assimilated, the effects of some biochemical deficiency or pure P limitation may not be separated easily. From stoichiometric considerations and simple mass balance equations, we can calculate when P is in short supply relative to C; turned the other way, effects judged as biochemical constraints could be caused by insufficient supply of P. This question is not "either-or." Most likely, both mechanisms operate, but while the first possibility is well recognized, the other is new.

There is no disagreement that a number of nutritional factors can restrict growth. I appreciate Brett's attempt to stress the role of food quality in zooplankton nutrition. The crucial point is that stoichiometry of phytoplankton is, for several reasons, a good indicator of nutritional quality and that low P : C (or protein content expressed as N : C) reduces carbon utilization of the food (i.e. it lowers the amount of ingested C allocated to production). This reduced growth efficiency implies that in nature, zooplankton growth is not a monotonous function of C or energy. No doubt this effect is caused by a set of various mechanisms, depending on zooplankton species, stage, food, etc. I see, however, no theoretical or experimental evidence against the possibility of a direct P limitation of *Daphnia,* although it may be regarded as a reductionist (but more applicable?) approach. In addition to recent experiments supporting this view (Hessen 1990; Watanabe 1990; Sommer 1992; Sterner et al. 1992), Olsen et al. (1986) measured P release from *Daphnia* along a gradient of P : C in the food and proposed the possibility of direct P limitation of *Daphnia.* In parallel, several workers have demonstrated that N limitation of food may reduce growth of marine (Checkley 1986) and freshwater zooplankton (Giani 1991; Mitchell et al. 1992; Urabe and Watanabe 1992), although the limiting unit here may be amino acids or proteins. Anderson (1992) indicated a C : N ratio near 10 (by wt) where heterotrophs might become N limited, which is actually above the subsistence quota of N for many phytoplankton species.

Yet, supported by increasing evidence from laboratory experiments, this hypothesis is largely a theoretical exercise, and I repeat the precautions and conclusions from my paper: "Further field and laboratory studies of this hypothesis are recommended, but so far P-limitation of growth appears to be a probable, but overlooked determinant of structure and production in herbivore zooplankton communities" (Hessen 1992, p. 812).

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