

C and P in aquatic food chain: A review on C:P stoichiometry and PUFA regulation

S.K. Saikia⁽¹⁾, S. Nandi⁽¹⁾

Received January 20, 2010 / Reçu le 20 janvier 2010

Revised June 26, 2010 / Révisé le 26 juin 2010

Accepted July 18, 2010 / Accepté le 18 juillet 2010

ABSTRACT

Key-words:
aquatic
ecosystem,
grazing
food chain,
microbial loop,
PUFA,
stoichiometry,
homeostasis

Carbon (C) and phosphorous (P) regulation in aquatic food chains are transferred from lower to upper trophic levels primarily as polyunsaturated fatty acids (PUFAs) and C:P stoichiometry. The majority of C is transferred through algal based pathway. Microbial loop, though optionally contributes to C transfer, highly constrained by P limitation and bacterial predator type. Lack of essential PUFAs in bacteria is also responsible for its low trophic transfer of C. The seston size and algal taxonomic variations directly affect herbivore through P-dependent food quality and *de novo* synthesis of PUFAs. Change in algal community over a gradient could therefore determine C transfer. Feeding nature (herbivorous or carnivorous) and predator sizes also regulate transfer efficiency of C and P to upper trophic levels. As trophic levels move up, P-limitation becomes higher compared to autotrophs. For *Daphnia*, as mostly studied aquatic herbivore member, P limitation becomes critical at C:P > 300 indicating excess C is not always invited under P-deficient situations. However, as a part of homeostasis mechanism for trophic upgrading, conversion of algal-zooplankton interface from qualitative to quantitative could minimize such critical C:P regulation at higher trophic levels. Protists, in turn, with high clearance rate by zooplankton predator could also compensate qualitative effect.

RÉSUMÉ

C et P dans les chaînes alimentaires aquatiques : une revue sur la stoechiométrie C:P et la régulation par les PUFA

Mots-clés :
écosystèmes
aquatiques,
chaîne
alimentaire,
boucle
microbienne,
PUFA,
stoechiométrie,
homéostasie

Les régulations par carbone (C) et phosphore (P) dans les chaînes trophiques aquatiques sont transférées des niveaux trophiques inférieurs vers les supérieurs au travers des acides gras polyinsaturés (PUFAs) et du rapport stoechiométrique C:P. La majorité du C est transférée par la voie reposant sur les algues. La boucle microbienne, bien que contribuant au transfert du C, est très contrainte par la limitation en P et la prédation. Un manque de PUFAs essentiels est également responsable de ce faible transfert du C. La taille du seston et les variations taxonomiques des algues affectent directement les herbivores au travers de la qualité nutritionnelle dépendante du P et de la synthèse *de novo* de PUFAs. Le type de nourriture (herbivorie ou carnivorie) et les tailles de prédateurs régulent aussi l'efficacité du transfert de C et P vers les niveaux trophiques supérieurs. La limitation par P devient plus importante dans les niveaux trophiques supérieurs. Pour *Daphnia*, comme pour beaucoup d'organismes herbivores étudiés, la limitation par P devient cruciale quand C:P > 300, indiquant un excès de C pas toujours dû à des situations de déficience en P. Toutefois, comme part du mécanisme d'homéostasie pour le « trophic upgrading », le passage de l'interface algue-zooplancton

(1) Department of Zoology, Visva Bharati University, Santiniketan, West Bengal, PIN-731235, India, sksaikai@yahoo.com

de qualitatif à quantitatif peut atténuer la régulation critique C:P aux niveaux trophiques supérieurs. Les protistes, avec un taux de prédation par le zooplancton élevé, peuvent compenser l'effet qualitatif.

INTRODUCTION

Aquatic food chains mainly focused on autotrophic primary production resulting phytoplankton growth and the grazing of phytoplankton by zooplankton. Here phytoplankton or algae fix light energy through photosynthesis and store it in chemical bonds of organic molecules that determine the energy and nutrient base. From this point, heterotrophs transfer energy and other nutrients throughout the food chain by eating zooplankton or phytoplankton. In this relationship, the basic functional dynamics of ecosystem is regulated through energy circulation or very simply carbon cycle. The question whether energy transfer alone or coupled with nutrient uptake or whether dependent on herbivore type or number of trophic levels is more important in regulating ecosystem dynamic and is still a basic area of research in ecosystem ecology. There is much current research on these questions for a wide variety of natural communities. The current review is an effort to summarize some recent literature to answer these questions. The simplest food chain (phytoplankton → zooplankton → fish) often described by different authors for aquatic ecosystem has been considered here for most of discussions disregarding the fact that most food 'chains' are actually part of more complex (non-linear) food webs.

CARBON (C) REGULATION IN FOOD CHAIN: MONOTONOUS OR COUPLED?

Hutchinson (1959) and Slobodkin (1960) proposed that energy as carbon (C) regulates the number of trophic levels in a food chain. But Post *et al.* (2000), from studies on temperate lakes suggested resource availability also contributes to food chain length. Certainly, available energy as resource must set some upper limit to the number of trophic levels proportionately to the space available on which the successive top trophic levels can forage (Schoener, 1989). On verifying a productivity-space hypothesis, Doi *et al.* (2009) demonstrated longer food chain length at high C level (as productivity) and maximum ecosystem size (space). These coupling factors would have maximum affect on food chain in river or lakes rather than ocean.

However, two basic pathways are involved in transferring such C based energy from seston to upper trophic levels in aquatic system. They are (1) *Algal based pathway* and (2) *Bacteria based pathway*. The transfer of C at the autotrophic-herbivore interface *i.e.* through the first pathway is a crucial parameter in regulating the efficiency of the transfer of energy and material in aquatic food chain. Low C uptake by autotrophs leads to low energy assimilation by herbivorous zooplankton. Inefficient C transfer decouples primary and secondary producers resulting disproportionate trophic growth. In some cases such situations end up with phytoplankton blooms (Moss *et al.*, 1991; Hansson *et al.*, 1998). One of the important factors of C transfer through this pathway is the predator biomass. Studies of Havens and East (1997) on eutrophic lakes demonstrated that the annual biomass of picoplankton (< 2 µm), nanoplankton (2–20 µm) and microplankton (< 20 µm) averaged 60, 389 and 100 µg C·L⁻¹ respectively, while corresponding rates of C uptake averaged 7, 51 and 13 µg C·L⁻¹·h⁻¹. The biomass of microzooplankton (40–200 µm) and macrozooplankton (< 200 µm) averaged 18 and 60 µg C·L⁻¹, while C uptake rates by these herbivore groups averaged 2 and 3 µg C·L⁻¹·h⁻¹ respectively. Alternatively, with a production efficiency of 70–80% to phytoplankton (Forsberg, 1985; Riemann and Søndergaard, 1986), bacterioplankton through second pathway can add an extra trophic level that may increase C input to the food chain from the surrounding. A substantial amount of fixed carbon from phytoplanktonic photosynthesis is excreted to the surrounding water as dissolve organic carbon (DOC) (Cole *et al.*, 1982)

and routed through bacteria → protozoa → metazoan → higher trophic levels. This pathway of C-transfer through heterotrophic bacteria and picoplankton is referred as **microbial loop** (Azam *et al.*, 1983). It can transport large quantities of carbon in freshwater lakes (Weisse and Müller, 1990) and the open ocean (Cole *et al.*, 1988) and is the route whereby allochthonous DOC enters the food web (Jansson *et al.*, 1999). Bacterial consumers, mostly protozoans, and also metazoans, explore the biomass produced by the microbial loop, which can transport large quantities of C in freshwater lakes (Weisse and Müller, 1990). But the C transfer efficiency through microbial loop could still be constrained by some other factors. Two such factors include herbivore type or bacterial predator and nutrient availability in the system. Some groups of herbivores (e.g. cladocerans) apparently consume detritus and bacteria, whereas others (e.g. calanoid copepod) may or may not (De Mott, 1988; Pace *et al.*, 1990; Kankaala *et al.*, 2010). Such inclusion of bacterial predator leads bacteria to face both competition and predation (Thingstad and Pengerud, 1985). This may cause increase in algal density (thereby algal C source) and allow the persistence of algae when they would otherwise have been excluded by bacteria. These predators (e.g. cladocera or calanoid copepod) are prevalent in freshwater aquatic system and therefore variations in numbers of trophic levels are common in these systems. In oceanic environment, Tanaka *et al.* (2005) demonstrated that specialized zooplankton that can directly consume bacterial particles may be more efficient in C transfer through microbial loop. This efficiency is related to reduction in average number of trophic levels. In their chemostat model with algae, bacteria and bacterial predator Thingstad and Pengerud (1985) explained how nutrient can influence microbial loop mediated C dynamic. Their predictions include competitive exclusion of bacteria when C:nutrient ratio is low (rejecting existence of microbial loop) and algae when C:nutrient ratio is high (existence of microbial loop). The first case might be due to stimulation of fast growing opportunistic primary producers which are predation resistant by larger zooplankton and reduce the C transfer to higher trophic levels. This limits assimilable C source for bacteria leading its exclusion. The second case has direct influence on the growth and reproduction of herbivores through providing low food quality. However, this two can coexist and effectively control the food chain dynamic stoichiometrically, if bacteria are C limited and if the C:nutrient ratios between primary producers and bacteria are sufficiently similar. Thus addition of microbes as trophic level, though variably affects food chain, is coupled to nutrients or predator types.

ALGAL POLYUNSATURATED FATTY ACIDS (PUFAs): C-BASED FOOD QUALITY

Studies on the effect of food quality in aquatic food chains have traditionally addressed the role of nutrients and have had a strong focus on the trophic transfer of C-bonded energy and nutrients from phytoplankton to zooplankton. In recent years, there has been growing concern that essential PUFAs are good descriptor for high food quality for pelagic grazers (Brett and Müller-Navarra, 1997; Müller-Navarra *et al.*, 2004). Poor energy transfer efficiencies between phytoplankton and zooplankton may also be related to low long chain PUFA content in the primary producer group and may result in limited secondary production (Müller-Navarra *et al.*, 2000). PUFAs which are mostly discussed in relation to aquatic trophic regulation are: linoleic acid (LIN; C18:2 ω 6), α -linoleic acid (ALA; C18:3 ω 3), arachidonic acid (ARA; C20:4 ω 6), eicosapentaenoic acid (EPA; C20:5 ω 3) and docosahexaenoic acid (DHA, C22:6 ω 3). In freshwater ecosystems these are synthesized mainly by micro-algae depending upon genetic (Cobalás and Lechado, 1989; Gugger *et al.*, 2002) and environmental factors (Pohl and Zurheide, 1982; Roessler, 1990). Though reports are there that few marine zooplankters, particularly crustacean as herbivores able to synthesize essential PUFAs from ALA *via* elongation and desaturation (Desvillettes *et al.*, 1997; Nanton and Castell, 1998), such synthesis is selective and at a very slow rate. Therefore, their dependency on dietary PUFA is very high. For example, Goulden and Place (1990) demonstrated that *de novo* fatty acid synthesis rates of daphnids are generally < 2%. This leads to assume that at least 98% of the accumulated fatty acids in *Daphnia* were dietary in origin. Studies (Jónasdóttir *et al.*, 1995; Müller-Navarra,

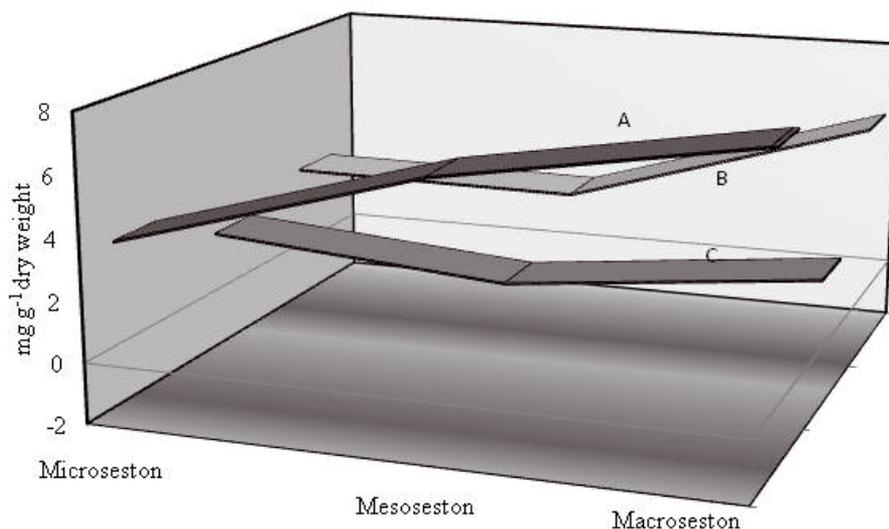


Figure 1

Size dependent sestonic PUFA availability. A: Omega-3:Omega-6 fatty acid; B: DHA and C: EPA (figured with kind permission from the data of Kainz *et al.*, 2009).

Figure 1

Disponibilité des PUFAs dépendant de la taille du seston. A : acides gras Omega-3:Omega-6; B : DHA et C : EPA (figure d'après les données et avec la permission de Kainz *et al.*, 2009).

1995; Müller-Navarra *et al.*, 2000; Brett *et al.*, 2009a, 2009b) revealed that the ARA, EPA and DHA are important biochemical constituents in the natural diet of zooplankton as their prevalence in seston strongly predicts zooplankton growth. The transfer efficiency of PUFAs from seston to higher trophic level is regulated mainly by selective size feeding of herbivorous and carnivorous zooplankton. The DHA is reported to decrease in zooplankters of $> 592 \mu\text{m}$ in size and ALA of $> 774 \mu\text{m}$ in size (Kainz *et al.*, 2004). This is true in case of seston communities too. It is evident that microseston with algal communities as chief source of essential fatty acids (EFA) contributes ALA and ARA in higher concentration (Figure 1). Zooplankters feeding microseston can access maximum of these precursors of EFA (Kainz *et al.*, 2004). Though macroseston contributes higher proportion of essential fatty acids, a large portion of it could be from animal origin. Thus herbivorous or carnivorous nature of zooplankters may further decide the fate of PUFAs transfer to higher trophic positions like fish. Persson and Verde (2006) reported PUFAs contents, as essential fatty acid in general, are much higher in zooplankton (Figure 2) than saturated fatty acids and monounsaturated fatty acids indicating that the later two fatty acids are not efficiently transferred to higher trophic level though they are used as C source. They also added that its content, especially of C20–22 length is higher in carnivorous than herbivorous zooplankters. The C18 PUFAs are though abundant in herbivores, replaced by C20–22 PUFAs in carnivorous predator level as these can be synthesized from C18 PUFAs (Stanley-Samuelson, 1994; Von Elert, 2002) (Figure 3).

However, differences in such conversion capacities and consumers types in trophic level have further implication on C transfer dynamics (Goedkoop *et al.*, 2007). Where *Bosmina leideri* is less dependent on high food quality (Schulz and Sterner, 1999), *Daphnia* shows high dependency on EPA (Weers and Gulati, 1997; Boersma, 2000). The calanoid copepod *Acartia tonsa* shows very low fecundity on a diet deprived of EPA and DHA (Ederington *et al.*, 1995; Kleppel *et al.*, 1998) whereas the harpacticoid copepod *Thisbe holothyria*, a detritus feeder, can complete ontogenesis on C20 PUFA deficient diet due to *de novo* synthesis of EPA and DHA from ALA (Norsker and Støttrup, 1994). Through microbial loop, C transfer as PUFA is not efficient as bacteria are known to lack essential PUFAs (Ederington *et al.*, 1995; Pinkart

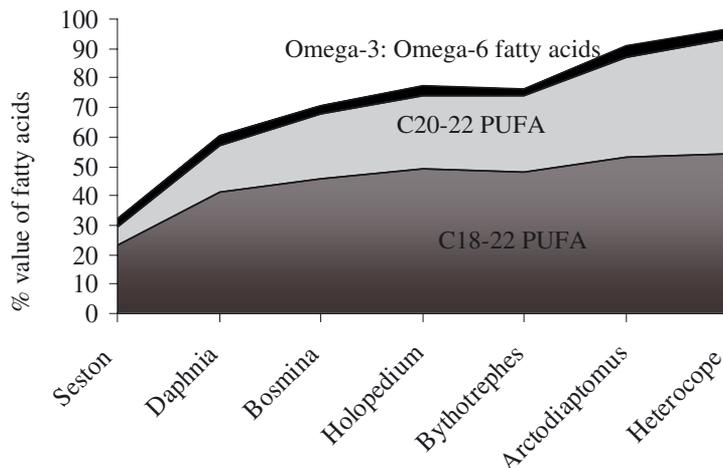


Figure 2

PUFA content in seven major planktonic trophic groups. Autotrophs: seston (1); cladoceran heterotrophs: *Daphnia*, a herbivorous (2), *Bosmina*, large herbivore (3), *Holopedium*, large herbivore (4), *Bythotrephes*, a carnivore (5); and copepoda heterotrophs: *Arctodiaptomus*, a carnivore (6) and *Heterocope*, a carnivore (7). Numbers in parentheses indicates group position on x axis. Except *Omega 3:Omega 6* fatty acid ratio, others are in % of total fatty acid content (figured from the data of Persson and Verde, 2006).

Figure 2

Contenu en PUFAs dans sept principaux groupes trophiques planctoniques. Autotrophes : seston (1); cladocères hétérotrophes : *Daphnia*, un herbivore (2), *Bosmina* (3), *Holopedium*, grands herbivores (4), *Bythotrephes*, un carnivore (5); copépodes hétérotrophes : *Arctodiaptomus*, un carnivore (6) et *Heterocope*, un carnivore (7). Les nombres entre parenthèses indiquent la position des groupes sur l'axe x. Excepté pour le rapport des acides gras Omega 3:Omega 6, tous sont en % du contenu total en acides gras (figure d'après les données de Persson et Verde, 2006).

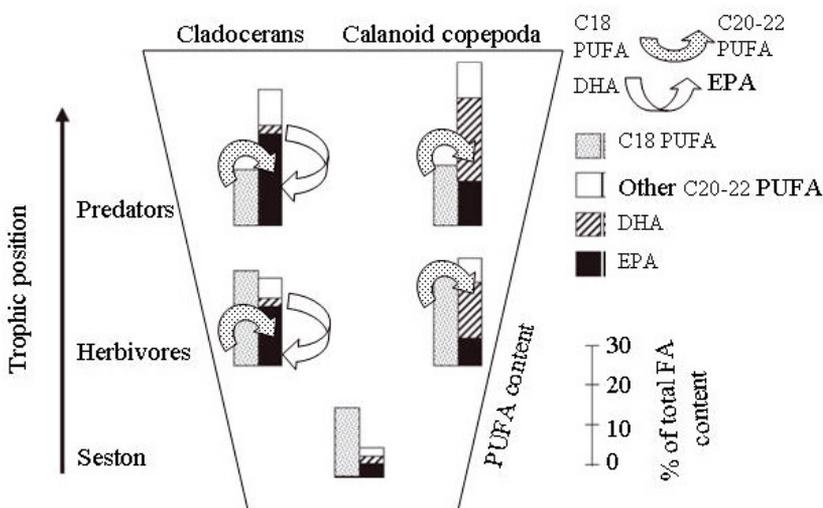


Figure 3

PUFA transfer from seston to herbivorous and carnivorous predators (modified from Persson and Verde, 2006).

Figure 3

Transfert des PUFAs du seston aux herbivores et carnivores prédateurs (modifié d'après Persson et Verde, 2006).

et al., 2002). Thus more essential PUFAs are transferred to top predators like fish through grazing food chain and carnivorous zooplankters.

PUFAs VARIATIONS IN ALGAL TAXA LIMIT HERBIVORES

The C transfer through phytoplankton and herbivorous zooplankton interface in aquatic food chain is influenced by biochemical differences of algal taxa. Such variations of food quality correspond to the predictions of experiments on algal taxa with PUFA (Müller-Navarra *et al.*, 2000). When PUFA emulsions were added to cultures of *Scenedesmus acutus*, a green algae, the *Daphnia* growth rate was observed similar to those observed for high quality cryptophytes (Weers and Gulati, 1997). Demott and Müller-Navarra (1997) found that adding PUFA emulsions to PUFA-poor cyanophytes *Synechococcus* improved the food quality of this mixture to the level observed for *Scenedesmus acutus*. Thus it is plausible that the large differences in food quality noted between the major algal taxa are due to the PUFA content. The algal taxa with high EPA or DHA contents are high food quality and without or very low contents are low food quality for herbivorous zooplankton (Brett *et al.*, 2009a, 2009b). In absence of long chain PUFAs, algal taxa with ALA and LIN could be considered moderate food quality for that these two PUFAs can act as precursor for ARA and EPA respectively (Stanley-Samuelson, 1994; Von Elert, 2002). Earlier evidences on marine algae also suggested that the quantity of long chain PUFAs like DHA and EPA varies significantly between major algal taxonomic groups (Sargent and Whittle, 1981). For example, the EPA percentage value in 17 marine diatoms used in marine aquaculture ranged from 5 to 30% of total fatty acid (Brown *et al.*, 1997). Studies showed that cryptophytes have high proportions of EPA and DHA, while chlorophytes lack or have trace amounts of these fatty acids. Cyanophytes are virtually depleted of EPA and DHA, whereas diatoms are rich in EPA and dinoflagellates have high amounts of DHA (Brett and Müller-Navarra, 1997). Interestingly, the retro-conversion property of DHA to EPA in invertebrate family (Von Elert, 2002) denotes more value to DHA synthesizing plankton groups in aquatic food chain (Figure 3). These results indicate one of the most significant responses of algal assemblages to PUFAs content and therefore shift in phytoplankton community species composition would have direct effect on herbivorous zooplankton. Thus herbivorous trophic level would be strongly limited by the whole PUFA family in terms of food quality of phytoplankton communities whenever these communities are not strongly dominated by diatoms or cryptophytes, or other PUFA/nutrition rich phytoplankters. In addition, recent studies indicate that the absence of non PUFAs like sterols in cyanobacteria may also contribute to their low quality as food for zooplankton (Martin-Creuzberg *et al.*, 2008). Further, absence of sterols reduces carbon transfer efficiency between cyanobacteria and freshwater herbivore (Von Elert *et al.*, 2003). Chlorophytes are generally of intermediate quality in terms of these indicators (Brett *et al.*, 2000).

P DEPENDENT STOICHIOMETRIC REGULATION OF FOOD CHAIN

Alongwith PUFAs, nutrients are a major food quality regulator. In the aquatic ecological studies, nutritional deficiencies, especially P is almost exclusively considered to be a problem of primary consumers (Elser *et al.*, 2000). It is important as a component of phospholipids, in energy storage metabolism (e.g. ATP) and in nucleic acid synthesis, being therefore directly related in growth and reproduction. Studies have suggested that high levels of P in cladocerans are associated with high content of RNA (Hessen, 1990; Main *et al.*, 1997). The link between P-content to maximal growth through RNA and protein synthesis could further be explained through growth rate hypothesis (Elser *et al.*, 1996). This hypothesis suggests that organisms feeding on P-sufficient diets will gather high body P-content and thereby, will have high RNA content as well as high maximal growth rates. At higher trophic level like fish, availability of P is linked to development of bone. It is also known that P limitation can influence lipid content and fatty acid composition of algae (Müller-Navarra, 1995; Kilham *et al.*, 1997;

Lürling and Van Donk, 1997). The contents of PUFAs decrease under P-limitation in algae (Piorreck and Pohl, 1984; Harrison *et al.*, 1990). Thus fast growing predator species in the food chain with high demand of P may be directly or indirectly regulated by algal-P (Main *et al.*, 1997; Sterner and Schulz, 1998). In general, algae with high C:P ratio (low P) can be low quality food for grazers like zooplankton (Boersma and Kreutzer, 2002), snails (Stelzer and Lamberti, 2002) or aquatic insects (Perkins *et al.*, 2004). The degree of nutrient mediated regulation has further been amplified by the variation in the species specific nutrient as between species and within species contents of autotrophs. Autotroph communities with larger variation of stoichiometry have lesser influence than the variation in herbivores and other consumers (Sterner *et al.*, 1998). For example, the C:P ratio of algae ranges from 100–1000 whereas C:P ratio of zooplankton ranges from 70–200 (Boersma *et al.*, 2008). The C:P ratio of *Daphnia*, the mostly studied zooplankton was found to be approximately 80–90 (Sterner and Hessen, 1994). This implies that herbivorous zooplankters are regularly confronted with different quality food, in contrast to zooplanktivorous fish, which only have to deal with a limited range. However, at high C:P ratio, bacteria based pathway can transfer some amount of DOC to higher trophic levels as they are not P-limited. Given that the zooplankton relative P content is much higher than the seston's, one could expect zooplankton production to be strongly limited by P availability (Hessen, 1992; Urabe and Watanabe, 1992) and this limitation increases as the trophic level extends further up in the system (Figure 4). Most researchers have suggested a critical seston C:P ratio of 300 above which *Daphnia* production will be limited by seston P content (Sterner, 1997, 1998; Urabe *et al.*, 1997). Brett *et al.* (2000) also concluded that phytoplankton food quality decreases as the C:P ratio of the algae increases above 300. Of course, at C:P > 1000, PUFAs can still be important and might not be limiting to herbivores (Ferrão-Filho *et al.*, 2003). At high light condition, though the rate of C fixation increases (resulting high C:P), it cannot be efficiently transferred to higher trophic level (Sterner *et al.*, 1998) due to P-deficient food selectivity by herbivores. However, existence of microbial pathway with sufficient P content could solve the problem to some extent. Under low light, reversal of stoichiometry occurs (Sterner *et al.*, 1997; Hall *et al.*, 2004; Dickman *et al.*, 2006) and this increases aquatic herbivore efficiencies (Urabe and Sterner, 1996; Urabe *et al.*, 2002; Malzahn *et al.*, 2007) through improved algal food quality which in turn increases carnivore efficiencies at higher trophic level. This is evident that when algal cells have high concentration of P and PUFAs, zooplankton also will receive high concentration of these resources and represents high quality food for fish. The fixing of C under light environment must couple with P to have direct effect on increasing the food chain efficiency of primary producer to carnivore through herbivore. This indicates increase in C input, as usually practiced, might not necessarily increase the yield in P-limiting aquatic ecosystem.

AUTOTROPHIC TAXONOMY AND C:P REGULATION

Similar to PUFAs, variation of autotrophic taxa could also play significant role to maintain wider C:P range. This has already been discussed that diatoms and cryptophytes are recorded with higher food quality than green algae which are in turn are higher food quality than cyanophytes and therefore, it is evident that herbivorous zooplankton feeding on different phytoplankton taxa experience quite different growth rate due to food quality differences (in terms of availability of PUFAs or nutrients or both) among algal taxa (Ahlgren *et al.*, 1990; Lundtstedt and Brett, 1991). The P-limited algae shows low food quality which might be due to morphological changes that cause some phytoplankton to become less digestible under nutrient stress condition (Lürling and Van Donk, 1997; Van Donk *et al.*, 1997). For example, several types of green algae have been shown to exhibit morphological changes like increased cell wall thickness (Lürling and Van Donk, 1997; Van Donk *et al.*, 1997) or ability to pass through zooplankton gut without digestive action (Ravet and Brett, 2006) when grown in P-limited medium. Such indigestibility is also adopted through changes in phytoplankton cell physical properties and/or biochemical composition (Brett, 1993). To this point, Dickman *et al.* (2008) showed that such phytoplankton compositional food quality had the strongest effects

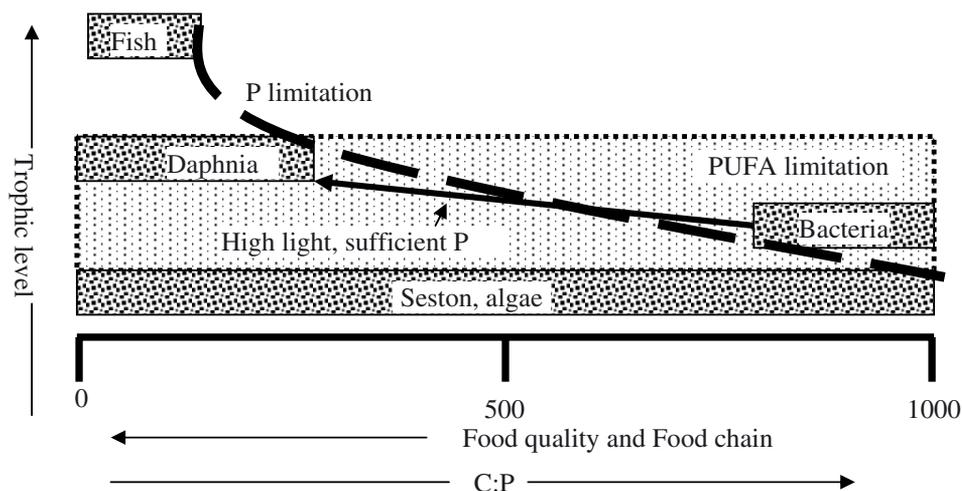


Figure 4

C:P and PUFA regulation on different trophic levels (thick dotted rectangular zone) of a grazing food chain (redrawn from Sterner *et al.*, 1998). The thick dotted bar represent C:P ratio. Under high light environment, bacteria also contribute C transfer in spite of high C:P (bold arrow). At C:P > 500, PUFA is not a limiting factor for herbivorous zooplankton (light dotted rectangular zone). Information on further effect of PUFA on higher trophic level at C:P > 500 is not available.

Figure 4

Régulation C:P et PUFAs sur les différents niveaux trophiques (zone rectangulaire en pointillés gras) dans une chaîne trophique (redessiné d'après Sterner *et al.*, 1998). La ligne grasse en tirets représente le rapport C:P. Dans un environnement lumineux, les bactéries contribuent également au transfert de C en dépit d'un C:P élevé (flèche grasse). À C:P > 500, PUFA n'est pas un facteur limitant pour le zooplancton herbivore (zone rectangulaire en pointillés légers). On ne dispose pas de données sur l'effet des PUFAs sur les niveaux trophiques supérieurs quand C:P > 500.

on food chain efficiency (FCE). Thus considering herbivore efficiency alone, stoichiometric quality had much stronger effects. In 3-level food chain (phytoplankton → zooplankton → fish) high FCE was associated with a relative abundance of cryptomonads and diatoms. Cryptomonads are found dominated under low-light/high-nutrient (low C:P) conditions. As discussed earlier, this taxa corresponding to such favorable condition to synthesize high concentrations of essential fatty acids (Brett *et al.*, 2006) and thereby adds high-quality food for zooplankton. In contrast, cyanobacteria, which are most abundant with high light and low nutrients (high C:P), have low fatty acid concentrations and represent the lowest food quality of any algal taxonomic group.

TROPHIC UPGRADING THROUGH HETEROTROPHIC PROTISTS AND HOMEOSTASIS

Planktonic heterotrophic protists are a diverse group of organisms ranging in size from 2–200 μm (Stoecker and Capuzzo, 1990). They feed on bacteria, detritus, micro, pico and nano-plankton, and are in turn consumed by metazoans (Capriulo *et al.*, 1991). They also play as important intermediaries in the transfer of energy from the 'microbial loop' to higher trophic levels. In coastal waters, heterotrophic protists can be the major grazers of phytoplankton, consuming 20–70% of the primary production (Capriulo, 1990). They also constitute significant component of copepods' diet (Gifford and Dagg, 1991; Atkinson, 1994; Levinson *et al.*, 2000). Experiments have shown that copepods have high clearance rates on heterotrophic protists and may even prefer them over algae (Stoecker and Egloff, 1987; Gifford and Dagg, 1991).

Some studies suggest heterotrophic protists can trophically improve poor algal quality for subsequent use by higher trophic organisms, a phenomenon dubbed “trophic upgrading” (Klein Breteler *et al.*, 1999). Tang *et al.* (2001) reported that *Gyrodinium dominans* increases trophic C transfer efficiency from poor quality phytoplankton to the copepod *Acartia tonsa* by six-fold, resulting in a significantly higher egg production rate in *A. tonsa*. As an intermediate prey, they can improve the quality and quantities of the types of fatty acids obtained from poor quality phytoplankton and efficiently transfer them to mesozooplankton (Kleppel *et al.*, 1998; Klein Breteler *et al.*, 1999). Mayer *et al.* (1997) demonstrated that the zooplankton community possesses strong relationship with bacterial and ciliate source of food than with phytoplankton. But these upgrading of biochemical components in heterotrophic protists appears to be species-specific and affect reproductive parameters of copepods differently (Veloza *et al.*, 2006). Research on this subject still requires some more clarification. Broglio *et al.* (2003) concluded ciliates were not nutritiously superior to algal diets for egg production efficiency and egg viability of *A. tonsa*. Similarly, growth in juvenile copepods was not supported by feeding on the ciliate *Strombidium sulcatum* grown on *Dunaliella tertiolecta* (Klein Breteler *et al.*, 2004). In addition, Tang and Taal (2005) reported differences in egg production efficiencies when copepods were fed on heterotrophic protists grown under different algal treatments.

Another phenomenon to combat poor food quality is homeostasis. Regardless to top down and bottom up control, herbivorous zooplankton showed near-to-perfect homeostasis to C:P limitation. Homeostasis in aquatic food chain means that the food quality effects in terms of nutrient ratios experienced by the primary consumers are buffered in these consumers and not transferred to higher trophic levels (Brett, 1993). Obviously, nutrient stoichiometry as quality factor of algae influences the growth and reproduction of the herbivores dramatically (Boersma, 2000; Elser *et al.*, 2001; Augustin and Boersma, 2006). Thus, a transition of quality effect at the algal-zooplankton interface into quantity effect could induce homeostasis on the zooplankton to higher consumer interface, as explained in case of *Daphnia* (Brett *et al.*, 2000). This means that under such homeostatic situations, secondary consumers such as fish would not be affected by the planktivorous zooplankters feeding on poor food quality algae.

CONCLUSIONS

Under the current preview of environmental disturbances, the nutrient specific food chains bear great significance in understanding aquatic ecosystems. Human interference has either led to fixation of excess nutrients (N and P) to aquatic body (Vitousek *et al.*, 1997; Bennett *et al.*, 2001; Galloway and Cowling, 2002) or turned them nutrient deficient through pollutant replacements. Study reveals that P limitation is more prevalent in freshwater (Hecky and Kilham, 1988) than N limitation which is a characteristic of marine water (Ryther and Dunstan, 1971; Howarth, 1988). A clear understanding on the effects of such nutrient variation on primary producer is the need of present scenario of changing ecological conditions since they are the first component to respond to C and nutrient stoichiometry. In this context, the carbon:silicate may also have some degree of regulatory significance on PUFAs rich diatoms dominated ecosystem and needs further research. On the other hand, for commercially productive practices, the general belief of ‘high energy input for high production’ requires a turn towards sustainable energy management not only in extraneous energy supply rates but also at the level of eligibility of trophic levels for efficient energy transfer. Effects of other ecological factors like light and temperature on food chain too, need extensive research priority under prevalent scenario of climate change and global warming.

REFERENCES

- Ahlgren G., Lundstedt L., Brett M.T. and Forsberg C., 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. *J. Plankton Res.*, 12, 809–818.
- Atkinson A., 1994. Diets and feeding selectivity among the epipelagic copepod community near South Georgia in summer. *Polar. Biol.*, 14, 551–560.

- Augustin C.B. and Boersma M., 2006. Effects on nitrogen stressed algae on different *Acartia* species. *J. Plankton Res.*, 28, 429–436.
- Azam F., Fenchel T., Field J.G., Meyer-Reil L.A. and Thingstad F., 1983. The ecological role of water column microbes in the sea. *Mar. Ecol. Prog. Ser.*, 10, 257–263.
- Bennett E.M., Carpenter S.R. and Caraco N.F., 2001. Human impact on erodable phosphorus and eutrophication: a global perspective. *BioScience*, 51, 227–234.
- Boersma M., 2000. The nutritional quality of p-limited algae for *Daphnia*. *Limnol. Oceanogr.*, 45, 1157–1161.
- Boersma M. and Kreutzer C., 2002. Life at the edge: is food quality really of minor importance at low quantities? *Ecology*, 83, 2552–2561.
- Boersma M., Aberle N., Hantzschke F.M., Schoo K.L., Wiltshire K.H. and Malazahn A.M., 2008. Nutritional limitation travels up food chain. *Internat. Rev. Hydrobiol.*, 93, 479–488.
- Brett M.T., 1993. Comment 'Possibility of N or P limitation for planktonic cladocerans – an experimental test (Urabe and Watanabe) and nutrient element limitation of zooplankton production (Hessen)'. *Limnol. Oceanogr.*, 38, 1333–1337.
- Brett M.T. and Müller-Navarra D.C., 1997. The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshwater Biol.*, 38, 483–499.
- Brett M.T., Müller-Navarra D.C. and Park S., 2000. Empirical analysis of mineral P limitation's impact on algal food quality for freshwater zooplankton. *Limnol. Oceanogr.*, 45, 1564–1575.
- Brett M.T., Müller-Navarra D.C., Ballantyne A.P., Ravet J.L. and Goldman C.R., 2006. *Daphnia* fatty acid composition reflects that of their diet. *Limnol. Oceanogr.*, 51, 2428–2437.
- Brett M.T., Kainz M.J., Taipale S.J. and Seshan H., 2009a. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proc. Natl. Acad. Sci. USA*, 106, 21197–21201.
- Brett M.T., Müller-Navarra D.C. and Persson J., 2009b. Crustacean zooplankton fatty acid composition. In: Arts M.T., Brett M.T. and Kainz M.J. (eds.), *Lipids in aquatic ecosystems*, Springer, New York, 115–146.
- Broglio E., Jónasdóttir S.H., Calbet A., Jakobsen H.H. and Saiz E., 2003. Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. *Aquat. Microb. Ecol.*, 31, 267–278.
- Brown M.R., Jeffrey S.W., Volkman J.K. and Dunstan G.A., 1997. Nutritional properties of microalgae for mariculture. *Aquaculture*, 151, 315–331.
- Capriulo G.M., 1990. *Ecology of marine protozoa*, 1st edn., New York: Oxford University Press.
- Capriulo G.M., Sherr E.B. and Sherr B.F., 1991. Trophic behavior and related community feeding activities of heterotrophic marine protists. In: Reid P.C., Turley C.M. and Burkill P.H. (eds.), *Protozoa and their role in marine processes*, Springer, Berlin, 219–265.
- Cobalás M.A. and Lechado J.Z., 1989. Lipids in microalgae. A review I. *Biochemistry. Grasas y aceites (Esp.)*, 40, 118–145.
- Cole J.J., Likens G.E. and Strayer D.L., 1982. Photosynthetically produced dissolved organic carbon: an important carbon source for planktonic bacteria. *Limnol. Oceanogr.*, 27, 1080–1090.
- Cole J.J., Findlay S. and Pace M.L., 1988. Bacterial production in fresh and saltwater: a cross system overview. *Mar. Ecol. Prog Ser.*, 43, 1–10.
- De Mott W.R., 1988. Discrimination between algae and detritus by freshwater and marine zooplankton. *Bulletin of Marine Science*, 43, 486–499.
- De Mott W.R. and Müller-Navarra D.C., 1997. The importance of highly unsaturated fatty acids in zooplankton nutrition: evidence from experiments with *Daphnia*, a cyanobacterium and lipid emulsions. *Freshwater Biol.*, 38, 649–664.
- Desvillettes C., Bourdier G. and Breton J.C., 1997. On the occurrence of a possible bioconversion of linolenic acid into docosahexanoic acid by copepod *Eucyclops serrulatus* fed on microalgae. *J. Plankton Res.* 19, 273–278.
- Dickman E.M., Vanni M.J. and Horgan M.J., 2006. Interactive effects of light and nutrients on phytoplankton stoichiometry. *Oecologia*, 149, 676–689.
- Dickman E.M., Newell J.M., Gonzalez M.J. and Vanni M.J., 2008. Light, nutrients, and food-chain length constrain planktonic energy transfer efficiency across multiple trophic levels. *PNAS*, 105, 18408–18412.

- Doi H., Chang K.-H., Ando T., Ninomiya I., Imai H. and Nakano S., 2009. Resource availability and ecosystem size predict food-chain length in pond ecosystems. *Oikos*, 118, 138–144.
- Ederington M.C., Mcmanus G.B. and Harvey H.R., 1995. Trophic transfer of fatty acids, sterols, and a triterpenoid alcohol between bacteria, a ciliate, and the copepod *Acartia tonsa*. *Limnol. Oceanogr.*, 40, 860–867.
- Elser J.J., Dohherfuhr D., Mackay N.A. and Schampel J.H., 1996. Organism size, life history, and N:P stoichiometry: towards a unified view of cellular and ecosystem processes. *BioScience*, 46, 674–684.
- Elser J.J., Fagan W.F., Denno R.F., Dobberfuhr D.R., Folarin A., Huberty A., Interlandi S., Kilham S.S., Mccauley E., Schulz K.L., Siemann E.H. and Sterner R.W., 2000. Nutritional constrains in terrestrial and fresh water food webs. *Nature*, 408, 578–580.
- Elser J.J., Hayakawa K. and Urabe J., 2001. Nutrient limitation reduces food quality for zooplankton: *daphnia* response to seston phosphorus enrichment. *Ecology*, 82, 898–903.
- Ferrão-Filho A.S., Fileto C., Lopes N.P. and Arcifa M.S., 2003. Effects of essential fatty acids and N and P-limited algae on the growth rate of tropical cladocerans. *Freshwater Biol.*, 48, 759–767.
- Forsberg B.R.F., 1985. The fate of planktonic primary production. *Limnol. Oceanogr.*, 30, 807–819.
- Galloway J.N. and Cowling E.B., 2002. Nitrogen and the world. *Ambio*, 31, 64–71.
- Gifford D.J. and Dagg M.J., 1991. The microzooplankton-mesozooplankton link: consumption of planktonic protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Murkukawa. *Mar. Microb. Food Webs*, 5, 161–177.
- Goedkoop W., Demandt M. and Ahlgren G., 2007. Interactions between food quantity and quality (long-chain polyunsaturated fatty acid concentrations) effects on growth and development of *Chironomus riparius*. *Can. J. Fish. Aquat. Sci.*, 64, 425–436.
- Goulden C.E. and Place A.R., 1990. Fatty acid synthesis and accumulation rates in daphnids. *J. Exp. Zool.*, 256, 168–178.
- Gugger M., Lyra C., Suominen I., Tsitko I., Humbert J.-F., Salkinoja-Salonen M.S. and Sivonen K., 2002. Cellular fatty acids as chemotaxonomic markers of the genera *Anabaena*, *Aphanizomenon*, *Microcystis*, *Nostoc* and *Planktothrix* (cyanobacteria). *Int. J. Syst. Evol. Microbiol.*, 52, 1007–1015.
- Hall S.R., Leibold M.A., Lytle D.A. and Smith V.H., 2004. Stoichiometry and planktonic grazer composition over gradients of light, nutrients, and predation risk. *Ecology*, 85, 2291–2301.
- Hansson L.A., Annadotter H., Bergman E., Hamrin S.F., Jeppesen E., Kairesalo T., Luokkanen E., Nilsson P.A., Sondergaard M. and Strand J., 1998. Biomanipulation as an application of food chain theory: constrains, synthesis and recommendations for temperate lakes. *Ecosystems*, 1, 558–574.
- Harrison P.J., Thompson P.A. and Calderwood G.S., 1990. Effects of nutrient and light limitation on the biochemical composition of phytoplankton. *J. Appl. Phycol.*, 2, 45–56.
- Havens K.E. and East T.L., 1997. Carbon dynamics in the grazing food chain of a subtropical lake. *J. Plankton Res.*, 19, 1687–1711.
- Hecky R.E. and Kilham P., 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.*, 33, 796–822.
- Hessen D.O., 1990. Carbon, nitrogen and phosphorus status in *Daphnia* at varying conditions. *J. Plankton Res.*, 12, 1239–1249.
- Hessen D.O., 1992. Nutrient element of zooplankton production. *Am. Nat.*, 140, 799–814.
- Howarth R.W., 1988. Nutrient limitation of net primary production in marine ecosystems. *Ann. Rev. Ecol. System.*, 19, 898–910.
- Hutchinson G.E., 1959. Homage to *Santa rosalia*, or why are there so many kinds of animals? *Am. Nat.*, 93, 145–159.
- Jansson M., Bergstrom A.K., Blomqvist P., Isaksson A. and Jonsson A., 1999. Impact of allochthonous organic carbon on microbial food web carbon dynamics and structure in Lake Ortrasket. *Arch. Hydrobiol.*, 144, 409–428.
- Jónasdóttir S.H., Fields D. and Pantoja S., 1995. Copepod egg production in long island sound USA, as a function of the chemical composition of seston. *Mar. Ecol. Prog. Ser.*, 119, 87–98.
- Kainz M., Arts M.T. and Mazumder A., 2004. Essential fatty acids in the planktonic food web and their ecological role for higher trophic levels. *Limnol. Oceanogr.*, 49, 1784–1793.

- Kainz M.J., Perga M.-E., Arts M.T. and Mazumder A., 2009. Essential fatty acids concentrations of different seston sizes and zooplankton: a field study of monomictic coastal lakes. *J. Plankton Res.*, 31, 635–645.
- Kankaala P., Taipale S., Li L. and Jones R.I., 2010. Diets of crustacean zooplankton, inferred from stable carbon and nitrogen isotope analyses, in lakes with varying allochthonous dissolved organic carbon content. *Aquatic Ecol.*, DOI: 10.1007/s10452-010-9316-x.
- Kilham S.S., Kreeger D.A., Goulden C.E. and Lynn S.G., 1997. Effects of algal food quality on fecundity and population growth rates of *Daphnia*. *Freshwater Biol.*, 38, 639–647.
- Klein Breteler W.C.M., Schogt N., Baas M., Schouten S. and Kraay G.W., 1999. Trophic upgrading of food quality by protozoans enhancing copepod growth: role of essential lipids. *Mar. Biol.*, 135, 191–198.
- Klein Breteler W.C.M., Koski M. and Rampen S., 2004. Role of essential lipids in copepod nutrition: no evidence of trophic upgrading of food quality by a marine ciliate. *Mar. Ecol. Prog. Ser.*, 274, 199–208.
- Kleppel G.S., Burkart C.A. and Houchin L., 1998. Nutrition and the regulation of egg production in the calanoid copepod *Acartia tonsa*. *Limnol. Oceanogr.*, 43, 1000–1007.
- Levinson H., Turner J.T., Nielsen T.G. and Hansen B.W., 2000. On the trophic coupling between protists and copepods in arctic marine ecosystems. *Mar. Ecol. Prog. Ser.*, 204, 65–77.
- Lundstedt L. and Brett M.T., 1991. Differential growth rates of 3 cladoceran species in response to mono-algal and mixed-algal cultures. *Limnol. Oceanogr.*, 36, 159–165.
- Lürling M. and Van Donk E., 1997. Life history consequences for *Daphnia pulex* feeding on nutrient-limited phytoplankton. *Freshwater Biol.*, 38, 693–709.
- Main T., Dobberfuhl D.R. and Elser J.J., 1997. N:P stoichiometry and ontogeny in crustacean zooplankton: a test of the growth rate hypothesis. *Limnol. Oceanogr.*, 42, 1474–1478.
- Malzahn A.M., Aberle N., Clemmesen C. and Boersma M., 2007. Nutrient limitation of primary producers affects planktivorous fish condition. *Limnol. Oceanogr.*, 52, 2062–2071.
- Martin-Creuzburg D., Von Elert E. and Hoffman K.H., 2008. Nutritional constraints at the cyanobacteria-*Daphnia magna* interface: the role of stories. *Limnol. Oceanogr.*, 53, 456–468.
- Mayer J., Dokulil M.T., Salbrechter M., Berger M., Posch T., Fister G.P., Kirschner A.K.T., Velimirov B., Steitz A. and Ulbricht T., 1997. Seasonal successions and trophic relations between phytoplankton, zooplankton, ciliate and bacteria in a hypertrophic shallow lake in Vienna, Austria. *Hydrobiologia*, 342/343, 165–174.
- Moss B., Stanfield J. and Irvine K., 1991. Development of daphnid communities in diatom-dominated and cyanophyte-dominated lakes and their relevance to lake restoration by biomanipulation. *J. Appl. Ecol.*, 28, 568–602.
- Müller-Navarra D.C., 1995. Evidence that a highly unsaturated fatty acid limits *Daphnia* growth in nature. *Arch. Hydrobiol.*, 132, 297–307.
- Müller-Navarra D.C., Brett M.T., Liston A.M. and Goldman C.R., 2000. A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature*, 403, 74–77.
- Müller-Navarra D.C., Brett M.T., Park S., Chandra S., Ballantyne A.P., Zorita E. and Goldman C.R., 2004. Unsaturated fatty acid content in seston and trophodynamic coupling in lakes. *Nature*, 427, 69–72.
- Nanton D.A. and Castell J.D., 1998. The effects of dietary fatty acids on the fatty acid composition of the harpacticoid copepod, *Tisbe* sp. for use as a live food for marine fish larvae. *Aquaculture*, 163, 251–261.
- Norsker N.H. and Støttrup J.G., 1994. The importance of dietary HUFAs for fecundity and HUFA content in the harpacticoid *Thisbe holothuriae*. *Aquaculture*, 125, 155–166.
- Pace M.L., Mcmanus G.B. and Findlay S.E.G., 1990. Planktonic community structure determines the fate of bacterial production in a temperature lake. *Limnol. Oceanogr.*, 35, 795–808.
- Perkins M.C., Woods H.A., Harrison J.F. and Elser J.J., 2004. Dietary phosphorus affects the growth of larval *Manduca sexta*. *Arch. Insect. Biochem. Physiol.*, 55, 153–168.
- Persson J. and Verde T., 2006. Polyunsaturated fatty acids in zooplankton: variation due to taxonomy and trophic position. *Freshwater Biol.*, 51, 887–900.
- Pinkart H.C., Ringelberg D.B., Piceno Y.M., Mac Naughton S.J. and White S.J., 2002. Biochemical approaches to biomass measurements and community structure analysis. In: Hurst C.J. and Hendon V.A. (eds.), *Manual of environmental microbiology*, Asm press, Washington, 101–113.

- Piorreck M. and Pohl P., 1984. Formation of biomass, total proteins, chlorophylls, lipids and fatty acids in green and blue-green algae during one growth phase. *Phytochemistry*, 23, 217–223.
- Pohl P. and Zurheide F., 1982. Fat production in freshwater and marine algae. In: Hoppe H.A., Levring T. and Tanaka Y. (eds.), *Marine Algae in Pharmaceutical Science*, Vol. 2, Walter De Gruyter & Co., Berlin-New York, 65–80.
- Post D.M., Pace M.L. and Hairston N.G., 2000. Ecosystem size determines food-chain length in lakes. *Nature*, 405, 1047–1049.
- Ravet J.L. and Brett M.T., 2006. Phytoplankton essential fatty acid and phosphorus content constraints on *Daphnia* somatic growth and reproduction. *Limnol. Oceanogr.*, 51, 2438–2452.
- Riemann B. and Søndergaard M., 1986. Bacteria. In: Riemann B. and Søndergaard M. (eds.), *Carbon dynamics in eutrophic, temperate lakes*, Elsevier, Amsterdam, 127–197.
- Roessler P.G., 1990. Environmental control of glycerolipid metabolism in microalgae: commercial implications and future research directions. *J. Phycol.*, 26, 393–399.
- Ryther J.H. and Dunstan W.M., 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. *Science*, 171, 1008–1013.
- Sargent J.R. and Whittle K.J., 1981. Lipids and hydrocarbons in the marine food web. In: Longhurst A.R. (ed.), *Analysis of marine ecosystems*, Academic press, London, 491–533.
- Schoener T.W., 1989. Food webs from the small to the large. *Ecology*, 70, 1559–1589.
- Schulz K.L. and Sterner R.W., 1999. Phytoplankton phosphorus limitation and food quality for *Bosmina*. *Limnol. Oceanogr.*, 44, 1549–1556.
- Slobodkin L.B., 1960. Ecological energy relationships at the population level. *Am. Nat.*, 94, 213–236.
- Stanley-Samuelson D.W., 1994. Prostaglandins and related eicosanoids in insects. *Adv. Insect Physiol.*, 24, 115–212.
- Stelzer R.S. and Lamberti G.A., 2002. Ecological stoichiometry in running waters: periphyton chemical composition and snail growth. *Ecology*, 83, 1039–1051.
- Sterner R.W., 1997. Modeling interactions of food quality and quantity in homeostatic consumers. *Freshwater Biol.*, 38, 473–481.
- Sterner R.W., 1998. Demography of a natural population of *Daphnia retrocurva* in a lake with low food quality. *J. Plankton Res.*, 20, 471–489.
- Sterner R.W. and Hessen D.O., 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Ann. Rev. Ecol. System.*, 25, 1–29.
- Sterner R.W. and Schulz K.L., 1998. Zooplankton nutrition: recent progress and reality check. *Aquat. Ecol.*, 32, 261–279.
- Sterner R.W., Elser J.J., Fee E.J., Guildford S.J. and Chrzanowski T.H., 1997. The light/nutrient ratio in lakes: the balance of energy and materials affect ecosystem structure and process. *Am. Nat.*, 150, 663–684.
- Sterner R.W., Clasen J., Lampert W. and Weisse T., 1998. Carbon: phosphorus stoichiometry and food chain production. *Ecol. Lett.*, 1, 146–150.
- Stoecker D.K. and Capuzzo J.M., 1990. Predation on protozoa: its importance to zooplankton. *J. Plankton Res.*, 12, 891–908.
- Stoecker D.K. and Egloff D.A., 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. *J. Exp. Mar. Biol. Ecol.*, 110, 53–68.
- Tanaka T., Rassoulzadegan F. and Thingstad T.F., 2005. Analyzing the trophic link between the mesopelagic microbial loop and zooplankton from observed depth profiles of bacteria and protozoa. *Biogeosciences*, 2, 9–13.
- Tang K.W. and Taal M., 2005. Trophic modification of food quality by heterotrophic protists: species-specific effects on copepod egg production and egg hatching. *J. Exp. Mar. Biol. Ecol.*, 318, 85–98.
- Tang K.W., Jakobsen H.H. and Visser A.W., 2001. *Phaeocystis globosa* (prymnesiophyceae) and the planktonic food web: feeding, growth and trophic interactions among grazers. *Limnol. Oceanogr.*, 46, 1860–1870.
- Thingstad T.F. and Pengerud B., 1985. Fate and effect of allochthonous organic material in aquatic microbial ecosystems: An analysis based on chemostat theory. *Mar. Ecol. Prog. Ser.*, 21, 47–62.
- Urabe J. and Sterner R.W., 1996. Regulation of herbivore growth by the balance of light and nutrients. *Proc. Natl. Acad. Sci. USA*, 93, 8465–8469.

- Urabe J. and Watanabe Y., 1992. Possibility of N-limitation or P-limitation for planktonic cladocerans: an experimental test. *Limnol. Oceanogr.*, *37*, 244–251.
- Urabe J., Clasen J. and Sterner R.W., 1997. Phosphorus limitation of *Daphnia* growth: is it real? *Limnol. Oceanogr.*, *42*, 1436–1443.
- Urabe J., Kyle M., Makino W., Yoshida T., Andersen T. and Elser J.J., 2002. Reduced light increases herbivore production due to stoichiometric effects of light/nutrient balance. *Ecology*, *83*, 619–627.
- Van Donk E., Lürling M., Hessen D.O. and Lokhorst G.M., 1997. Altered cell wall morphology in nutrient-deficient phytoplankton and its impact on grazers. *Limnol. Oceanogr.*, *42*, 357–364.
- Veloza A.J., Chu F.-L.E. and Tang K.W., 2006. Trophic modification of essential fatty acids by heterotrophic protists and its effects on the fatty acid composition of the copepod *Acartia tonsa*. *Mar. Biol.*, *148*, 779–788.
- Vitousek P.M., Aber J.D., Howarth R.W., Likens G.E., Matson P.A., Schindler D.W., Schlesinger W.H. and Tilman D.G., 1997. Human alterations of the global cycle: sources and consequences. *Ecol. Appl.*, *7*, 737–750.
- Von Elert E., 2002. Determination of limiting polyunsaturated fatty acids in *Daphnia galeata* using a new method to enrich food algae with single fatty acids. *Limnol. Oceanogr.*, *47*, 1764–1773.
- Von Elert E., Martin-Creuzburg D. and Le Coz J.R., 2003. Absence of sterols constrains carbon transfer between cyanobacteria and a freshwater herbivore (*Daphnia galeata*). *Proc. R. Soc. Lond.*, *270*, 1209–1214.
- Weers P.M.M. and Gulati R.D., 1997. Effect of the addition of polyunsaturated fatty acids to the diet on the growth and fecundity of *Daphnia galeata*. *Freshwater Biol.*, *38*, 721–729.
- Weisse T. and Müller H., 1990. Significance of heterotrophic nanoflagellates and ciliates in large lakes: evidence from Lake Constance. In: Tilzer M.M. and Serruya C. (eds.), Large Lakes, Springer Verlag, Berlin, 540–553.