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The role of highly unsaturated fatty acids in aquatic foodweb processes

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SUMMARY

1. Polyunsaturated fatty acids (PUFA) are almost exclusively synthesized by plants. Animals can convert from one form of PUFA to another through elongation and desaturation, but very few can synthesize PUFA *de novo*. PUFA play an important role in regulating cell membrane properties, serve as precursors for important animal hormones and are essential for animals.
2. In aquaculture studies, highly unsaturated fatty acids (HUFA), a subset of PUFA, have been found to be critical for maintaining high growth, survival and reproductive rates and high food conversion efficiencies for a wide variety of marine and freshwater organisms.
3. The plankton literature suggests high food-quality algae species are rich in HUFA and low food-quality algae are poor in HUFA. Adding semi-pure emulsions of HUFA to algae monocultures can markedly increase the growth rates of zooplankton feeding on these mixtures.
4. A study measuring zooplankton biomass accrual when feeding on natural phytoplankton found a strong correlation between phytoplankton HUFA (specifically eicosapentaenoic acid) content and herbivorous zooplankton production.
5. The aquatic ecology literature suggests that planktonic foodwebs with high HUFA content phytoplankton have high zooplankton to phytoplankton biomass ratios, while systems with low HUFA phytoplankton have low zooplankton biomass. Also, the seasonal succession of plankton in many temperate lakes follows patterns tied to phytoplankton HUFA content, with intense zooplankton grazing and 'clear-water-phases' characteristic of periods when the phytoplankton is dominated by HUFA-rich species.
6. Herbivorous zooplankton production is constrained by the zooplankton's ability to ingest and digest phytoplankton. It is becoming increasingly clear, however, that much of the phytoplankton which is assimilated may be nutritionally inadequate. HUFA may be key nutritional constituents of zooplankton diets, and may determine energetic efficiency across the plant–animal interface, secondary production and the strength of trophic coupling in aquatic pelagic foodwebs.

Introduction

Understanding the processes which regulate the efficiency of energy transfer and thus food-quality is a critical challenge confronting the study of aquatic foodwebs. These processes strongly influence fisheries production and biogeochemical cycling in freshwater and marine ecosystems (Sterner & Hessen, 1994). The basic process in foodweb dynamics is the transfer of energy from one trophic level to another (Lindeman, 1942). In its most simple form this can be envisioned as the assimilation of solar energy into primary production, and energy flow from plants to herbivores and ultimately to predators. It is generally understood that in freshwater and marine foodwebs, phytoplankton production is limited by the availability of inorganic nutrients, mainly phosphorus, nitrogen, silica and iron (in open oceans), and in some cases light (in hypertrophic lakes) (Tilman, 1982; Vollenweider & Kerekes, 1982; Horne & Goldman, 1994; Martin *et al.*, 1994). The production of predators is generally thought to be limited by the availability of prey, and the abilities of predators to capture and process these prey (Ivlev, 1961).

Whereas primary production can be predicted from nutrient concentrations and predator production can be predicted from prey availability, the flow of energy across the plant–animal interface is highly variable and the factors controlling the efficiency at which plant material is converted to herbivore biomass are poorly understood. Furthermore, the plant–animal interface represents the greatest disparity in biochemical and elemental composition of any interface in a typical foodweb (Hastings & Conrad, 1979; Brett, 1993a; Sterner & Hessen, 1994). Some aquatic foodwebs, such as many hypereutrophic lakes, have very high primary producer biomass but relatively little zooplankton and fish production, as demonstrated by Eltonian biomass pyramids (Fig. 1). In contrast, other systems, such as some marine upwelling zones, do not have particularly high phytoplankton biomass, but they nevertheless have very high zooplankton biomass and fisheries production (Fig. 1) (Dortch & Packard, 1989; Minas & Minas, 1992). Comparing these systems shows that a given biomass of phytoplankton in efficient systems like marine upwelling zones can support twenty-five times as much zooplankton biomass and fifty times as much fish biomass compared to inefficient systems like many hypereutrophic lakes.

In planktonic foodwebs, phytoplankton colony architecture, cell morphology and the presence or absence of secondary metabolites affect the rate at which plant material is ingested and digested by herbivores (Porter, 1973; Lampert, 1981, 1987). There are also large disparities in the nutritional quality of the most common phytoplankton taxa, with some groups, such as diatoms and cryptophytes, promoting high zooplankton growth rates and others, such as cyanophytes, promoting very low growth rates. Although zooplankton ecologists would agree that there are vast differences in phytoplankton food-quality for herbivorous zooplankton, there is no uniform understanding of the specific nutritional characteristics which determine these differences.

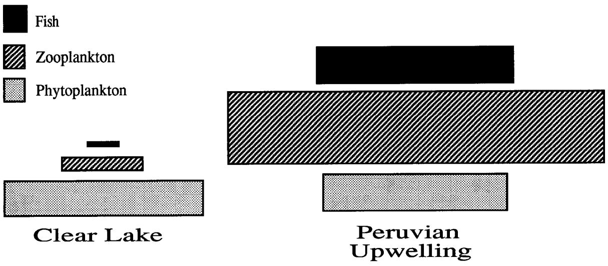

Fig. 1 Eltonian biomass pyramids for the hypereutrophic Clear Lake and the Peruvian upwelling zone. The size of the boxes is proportional to their relative biomass. The Clear Lake foodweb pyramid was generated by Carney and Goldman using extensive data from that lake (H.J. Carney and C.R. Goldman, unpublished data). The Peruvian Upwelling Zone foodweb pyramid was generated using the data of Dortch & Packard (1989). This was achieved by comparing the chlorophyll *a* (Chl *a*)/protein-N ratios of marine diatom monocultures to the corresponding ratios for the 140 plankton samples collected from the Peruvian upwelling zone and assuming diatoms are 26% and copepods are 32% protein by dry weight, respectively (various sources). Fish biomass was assumed to be 30% of zooplankton biomass in the Peruvian upwelling zone.

Because the study of foodwebs was conceptualized as a dynamic of energy flow, and most energy is contained in carbon bonds (Morowitz, 1968), early research on zooplankton feeding ecology focused on carbon as a measure of food availability (Lampert, 1977). However, it has been clear for many years that variation in the rate at which primary production is converted to zooplankton biomass is quite large. This variation in carbon transfer efficiency can be attributed to variation in food-quality, but there is no generally accepted view on what determines planktonic herbivore food-quality. Both nitrogen and phosphorus have been suggested to be determinants of algal food-quality for herbivorous zooplankton. Data to support these hypotheses have primarily been supplied by laboratory experiments using cultured algae (for N limitation see Checkley, 1980; Kiørboe, 1985; for P limitation see Sommer, 1992; Urabe & Watanabe, 1992; Sterner, 1993; Sterner *et al.*, 1993; Sterner & Hessen, 1994). However, nitrogen and phosphorus limitation does not explain the large variation in energy transfer efficiency across the plant–animal interface in natural planktonic ecosystems (Cahoon, 1981; Ambler, 1986; Müller-Navarra, 1995b).

This paper will summarize a substantial body of information which shows highly unsaturated fatty acids (HUFA) are critical biological compounds with key regulatory roles for animal cell membrane physiology and are precursors to many animal hormones. Extensive research in aquaculture demonstrates HUFA are essential for the nutritional physiology of many marine and freshwater organisms. There is a strong correlation between HUFA content of various phytoplankton species and their food-quality for zooplankton. Evidence will also be detailed which suggests seston HUFA content may be associated with the efficiency at which phytoplankton is converted to zooplankton biomass and influences foodweb architecture in freshwater and marine ecosystems.

Zooplankton growth and growth efficiency

The relationship between zooplankton growth and food consumption can be described as:

$$\text{Growth} = \text{Consumption}^*\text{Efficiency}, \qquad (1)$$

where growth equals biomass accrual in carbon units, consumption equals food consumption in carbon units and efficiency equals the proportion of food consumed converted to zooplankton biomass, otherwise known as gross growth efficiency (Hessen, 1992; Urabe & Watanabe, 1992; Brett, 1993a). Essentially this equation states:

$$\text{Growth} = \text{Quantity}^*\text{Quality}, \qquad (2)$$

where consumption is a measure of food quantity and efficiency is a measure of food-quality. This relationship is somewhat more complex than implied in eqn 2 because at low food concentrations an increasing proportion of food consumed is utilized for basal metabolism and is therefore unavailable for growth (Peters, 1987). A closely related equation states zooplankton growth can be predicted from lake seston quantity and quality:

$$\begin{gathered}\text{Growth rate} = m^*\text{Seston C}^* \\ (\text{Limiting Resource/Seston C}),\end{gathered} \qquad (3)$$

where growth rate is the instantaneous accrual of zooplankton biomass, m is a slope relating lake seston characteristics to zooplankton growth, seston C is a measure of seston biomass in carbon units, and limiting resource/seston C equals the ratio of some limiting resource to seston biomass. Since seston C is in the numerator of seston biomass and in the denominator of seston quality, this equation simplifies to:

$$\text{Growth rate} = m^*\text{Limiting Resource}, \qquad (4)$$

which states that zooplankton biomass accrual will be a function of the total availability of the resource (or resources) which determines food-quality.

Müller-Navarra (1995b) compared *Daphnia* biomass accrual rates to seston (< 30 μm) carbon (C), nitrogen (N), phosphorus (P) and fatty acid (FA) content in Schöhsee, Germany, and found a moderate correlation between seston C content and *Daphnia* growth ($r^2 = 0.62$) (Fig. 2). Seston N and P content were only weakly correlated with *Daphnia* growth ($r^2 = 0.42$ and 0.08, respectively), which suggests seston nitrogen and phosphorus were not correlated with seston quality in these experiments. However, a very strong ($r^2 = 0.93$) correlation was observed between seston eicosapentaenoic acid (a HUFA) content and *Daphnia*. A weaker correlation ($r^2 = 0.78$) was observed between *Daphnia* growth and seston total FA content. This strongly suggests eicosapentaenoic acid determined seston food-quality and, in turn, zooplankton growth in these experiments (see eqn 2 above)(Fig. 2).

The results of Müller-Navarra (1995b) suggest that experiments designed to measure zooplankton biomass accrual when feeding on natural seston are a strong general approach to measuring the quality of lake seston for secondary production. Once similar experiments have been conducted in a variety of lake types a general understanding of the factors that determine zooplankton food-quality will be obtained. Müller-Navarra's experiments strongly suggested seston eicosapentaenoic acid content was the most limiting resource in Schöhsee, Germany. New experiments in *other lake types* may identify alternative limiting resources; for example, mineral P in lakes with low seston P/C ratios (*sensu* Hessen, 1992; Urabe & Watanabe, 1992; Sterner & Hessen, 1994). Multivariate regression techniques can be used to identify combinations of limiting resources when one resource alone is not strongly predictive of zooplankton growth rates. Eventually the statistical approach of meta-analysis (Gurevitch & Hedges, 1993; Hasselblad, 1994) could be used to quantify general relationships between seston elemental and biochemical composition and

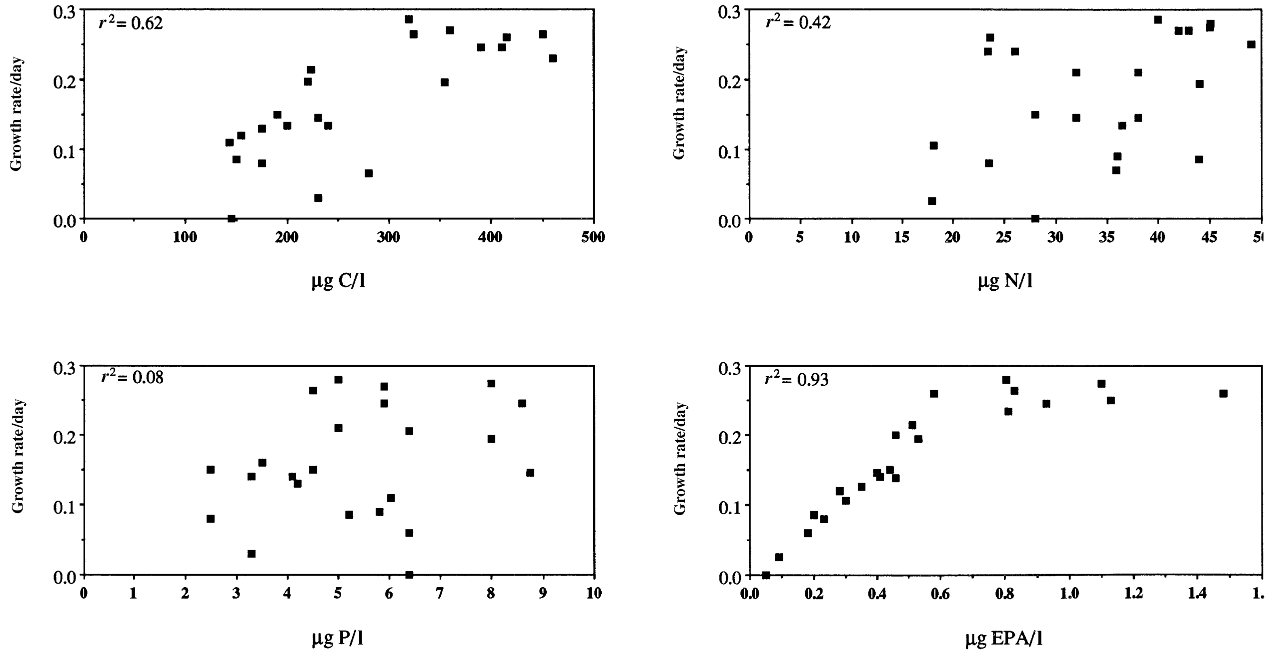

Fig. 2 The relationship between seston C, N, P and highly unsaturated fatty acids (HUFA) content and *Daphnia* growth in Schöhsee, Germany (from Müller-Navarra, 1995b). All seston was passed through a 30-µm screen prior to adding to the flow-through system. Each observation represents one experiment lasting 6 days.

seston nutritional quality, as measured by zooplankton biomass accrual rates.

The HUFA hypothesis

A suite of evidence from disparate systems suggests phytoplanktonic content of HUFA is predictive of trophic transfer efficiency, secondary production and foodweb architecture in aquatic planktonic foodwebs. We pose several hypotheses concerning HUFA's role in aquatic foodwebs.

Working hypotheses

Hypothesis 1. Seston HUFA content strongly influences the efficiency of energy transfer between phytoplankton 1- to 30-µm diameter and new zooplankton biomass, and herbivore production in planktonic foodwebs.

Hypothesis 2. Seston HUFA content strongly influences the strength of the trophic cascade at the plant–animal interface with intense zooplankton grazing impacts at high phytoplankton HUFA content (positive feedbacks) and weak grazing impacts at low HUFA content (negative feedbacks).

Alternative hypotheses

Alternative hypothesis 3. Seston HUFA content merely correlates with a suite of seston elemental and biochemical constituents which act in concert to determine seston nutritional quality; for example, seston HUFA may simply act as a marker for those phytoplankton taxa (diatoms and cryptophytes) that are, themselves, high food-quality and for some unknown reason result in high energetic efficiency, high secondary production and strong positive feedbacks.

Alternative hypothesis 4. Some other measure of food-quality, such as seston protein, phosphorus or total lipid content, is a stronger predictor of seston nutritional quality, energy transfer efficiency, secondary production and the strength of trophic coupling.

HUFA biochemistry, synthesis and metabolism

The morphology of FA can be designated $X:Y\omega Z$, where X equals the number of carbon atoms, Y equals the number of double bonds, and Z equals the position of the first double bond counting from the methyl end, the ω3 and ω6 designations. Fatty acids are characterized by having a carbonyl group at one end of their aliphatic chain, and a methyl group on the opposite end. Fatty acids can be either saturated (without double bonds in the chain) or unsaturated (with double bonds) (Vance & Vance, 1985). In general, double bonds are introduced in FA with sixteen or eighteen carbon atoms. Thus, an unsaturated FA (UFA) is synthesized from a saturated FA (SAFA), introducing double bonds by enzymes called desaturases. The position is determined by the type of desaturases, which are distributed differently between animals and lower and higher plants (Vance & Vance, 1985); for example, Δ9 desaturases are only found in animals, Δ6 desaturases are found in animals and lower plants, and Δ15 desaturases are only found in algae and plants with chlorophyll. Fatty acids with no double bonds are called SAFA, and FA with one double bond are called monounsaturated FA (MUFA). Fatty acids with more than one double bond are called polyunsaturated FA (PUFA) and HUFA, however, the use of these terms is not always strictly defined. We will use PUFA to designate all FA with more than one double bond, and HUFA to designate a subsample of PUFA with twenty or more C atoms. Our use of the acronym HUFA is consistent with general usage in the aquaculture literature. We are particularly interested in eicosapentaenoic acid (20 : 5ω3 or EPA) and docosahexaenoic acid (22 : 6ω3 or DHA), for example HUFA. Linolenic acid (18 : 3ω3) may also be important because all herbivores, and probably all omnivores, can convert this FA to EPA and DHA.

Linoleic (18 : 2ω6) and linolenic acid are essential for almost all animals because organisms without chlorophyll lack the Δ15 desaturase. Consistent with this, Moreno, Moreno & Brenner (1979) found the marine copepod *Paracalanus parvus* and Kanazawa *et al.* (Kanazawa, Teshima & Endo 1979a; Kanazawa *et al.* 1979b) and Shenker *et al.* (1993) found four species of the prawn *Penaeus* could synthesize SAFA and MUFA *de novo*, but could not synthesize PUFA *de novo*. Blomquist, Borgeson & Vundla (1991), however, showed that some terrestrial omnivorous insects are unique in possessing the Δ12 desaturase and are thus able to convert the monounsaturate oleic acid (18 : 1ω9) to linoleic acid (18 : 2ω6), thereby eliminating a strict need for plant-derived PUFA in their diets (Blomquist *et al.*, 1991). However, all herbivorous insects studied require PUFA of plant origin (Blomquist *et al.*, 1991).

It is generally thought that marine fish are unable to convert linolenic acid to EPA and DHA, while freshwater fish can (Watanabe, 1982). Most terrestrial vertebrates are also thought to be able to synthesize EPA and DHA from linolenic acid (Lehninger, Nelson & Cox, 1993). Although many organisms can convert linolenic acid to EPA and DHA, this conversion seems to be inefficient and there is reason to suspect that most organisms, whether aquatic or terrestrial, invertebrate or vertebrate, will grow better when provided with direct sources of EPA and DHA; for example, this conversion is probably too inefficient to maintain optimal growth rates for several aquatic invertebrates (Jones, Kanazawa & Ono, 1979; Kanazawa *et al.*, 1979a for *Penaeus* spp.; Waldock & Holland, 1984 for *Crassostrea gigas* juveniles). Goulden & Place (1990, 1993) found daphnid carbohydrate to lipid conversion capacities were quite low and almost all lipid accumulated was derived from the diet, which again suggests FA synthesis may be too low to support optimal growth. This is consistent with the results of Müller-Navarra (1995b), who found EPA as a single FA, and not ω3 FA as a family, was most strongly related to *Daphnia* growth. Therefore, high zooplankton growth rates may only be attainable when direct dietary sources of HUFA are available for these fast-growing zooplankters.

Considerable research in aquaculture has demonstrated strong dietary demands for HUFA-rich diets by larval stages of a very wide variety of marine and freshwater organisms (see later). Larval organisms may be more dependent on dietary HUFA than adults because their high somatic growth rates cannot be satisfied by their FA conversion capacities, which probably vary considerably during their life cycle. Because animals vary in their dependence on dietary EPA and DHA and their abilities to synthesize these compounds from related precursors, the specific PUFA content of available food may strongly influence competitive interactions in herbivore communities.

There is some disagreement amongst authors working with FA nutrition as to what constitutes an 'essential fatty acid' and whether one can say PUFA, as a class, are plant derived. Clearly linoleic and linolenic acid are essential because very few animals can produce them. In addition, all EPA and DHA is either obtained directly from plants or by converting from linolenic acid, and most animals grow best when provided with direct sources of EPA and DHA. Thus, it should be clear that almost all PUFA are obtained, either directly or indirectly, from plants, and HUFA are at the very least 'semi-essential'.

HUFA impacts on animal physiology

The role of FA in animal physiology is varied. Saturated fatty acids with their high caloric content are primarily used as a source or storage form of energy. However, it must be emphasized that unlike the majority of FA, PUFA are not primarily used for energy storage. It is commonly suggested that certain PUFA affect animal physiology through their impacts on cell membrane fluidity and the production of eicosanoids, a class of biochemicals associated with a wide range of physiological processes.

One of the most characteristic responses of poikilotherm cell membranes to reductions in ambient temperatures is an increase in the ratio of PUFA to SAFA in the lipid bilayer (Singer & Nicholson, 1972; Pruitt, 1990; Hazel, 1995). PUFA affect cell membrane fluidity because they have very low melting points compared to other biolipids. It is thought that increasing the proportion of PUFA in membrane lipids acts to reduce solidification of the total membrane lipid pool (Singer & Nicholson, 1972; Farkas, 1979; Farkas, Nemez & Csengeri, 1984; Pruitt, 1990). In effect, PUFA act as membrane lipid anti-freeze. The capacity to adjust cell membrane fluidity is an advantageous characteristic of organisms which remain active at low temperatures (Pruitt, 1990). This has been well established for many aquatic poikilotherms, in particular fish, as well as freshwater cladocerans and marine and freshwater copepods (Farkas, 1979; Farkas, Kariko & Csengeri, 1981; Farkas *et al.*, 1984; Farkas, Storebakken & Bhosle, 1988). Aquatic insects have higher HUFA content than do related terrestrial organisms (Hanson *et al.*, 1985). This correlates with the fact that most temperate aquatic insects remain physiologically active for prolonged periods at low water temperatures, while terrestrial insects generally undergo diapause during the winter. Similarly, the HUFA content of aquatic insects decreases as they metamorphose from aquatic larvae and pupae to terrestrial adults (Hanson *et al.*, 1985).

As stated previously, PUFA and, in particular, arachidonic acid and EPA serve as precursors to eicosanoids (Smith & Borgeat, 1985; Weber, 1989; Blomquist *et al.*, 1991). Eicosanoids, which include prostaglandins, thromboxanes, leukotrienes, hydroxy FA and lipoxines, are critical in a very wide range of physiological processes in invertebrates. These include regulating egg-production, egg-laying, spawning and hatching, mediating immunological responses to infections, and regulating epithelial ion and water flux, temperature set points, and neurophysiology (Stanley-Samuelson, 1994a, b). DHA is also important for the development and normal physiological activities of brain and eye tissues.

HUFA and aquatic organism nutrition

There is a vast body of information in the aquaculture literature which unequivocally shows HUFA-rich diets are essential for a wide range of marine and freshwater fishes, molluscs and crustaceans. The literature for crustaceans documents strong impacts of dietary HUFA on cladocerans, copepods, brine shrimp, mysids, prawns, crabs and lobsters (Levine & Sulkin, 1984; Støttrup & Jensen, 1990; Kreeger *et al.*, 1991; Jónasdóttir, 1994; Kanazawa & Koshio, 1994; Norsker & Støttrup, 1994; Müller-Navarra, 1995b). The prawns *Penaeus* and *Macrobrachium* have the most thoroughly studied nutritional physiology of any crustaceans because of their economic importance as food for humans. Studies show the HUFA content of artificial and natural diets impacts survival, growth, feed conversion, fecundity, egg hatchability, molting and osmotic stress tolerance for these genera (Kanazawa *et al.*, 1978; Kanazawa *et al.*, 1979a, b; Kanazawa, Teshima & Tokiwa, 1979c; Millamena *et al.*, 1988; D'Abramo & Sheen, 1993; Xu *et al.*, 1993, 1994a, b; Rees *et al.*, 1994).

While prawns are interesting because their nutritional physiology has been studied in great detail, they differ from the herbivorous zooplankton because they are primarily carnivores. The most well studied herbivores in the aquaculture literature are bivalve molluscs, which, similar to mainly freshwater zooplankton, primarily consume phytoplankton. The nutritional physiology literature for bivalves, clams, mussels and oysters, also documents a strong dietary demand for HUFA-rich phytoplankton (Enright *et al.*, 1986a, b, Coutteau *et al.*, 1996). A recent paper (Vanderploeg, Liebig & Gluck, 1996) goes so far as to suggest that phytoplankton HUFA content determines the recruitment success of zebra mussels in the Great Lakes.

Many studies have also noted that the FA composition of crustaceans and bivalves closely matches that of their diets (Kanazawa *et al.*, 1978; Frolov & Pankov, 1992; D'Abramo & Sheen, 1993; Albentosa *et al.*, 1994; Cahu *et al.*, 1994; Xu *et al.*, 1994a, b). Aquaculture studies have used HUFA-enriched zooplankton to demonstrate that many fish require HUFA-rich diets to obtain high growth and survival rates (Verreth *et al.*, 1994). Therefore, the relation between dietary and somatic FA composition suggests zooplankton feeding on high HUFA content diets will both grow faster and also be of higher nutritional quality for fish that may consume them.

Aquatic foodweb sources of FA

It is important to emphasize that linoleic and linolenic acid are only produced by plants, and that all EPA and DHA is either obtained directly from plants or by converting from linolenic acid. Therefore, the hypothesis that seston HUFA content determines foodweb efficiency and secondary production can also be viewed as a biochemical bottom-up process. Phytoplankton FA content varies dramatically between major taxonomic groupings and mirrors the distribution of the desaturase enzymes. Similar to the more familiar systematic differences in pigment distribution among alga groups, algal FA composition can be used to categorize taxa (Wood, 1974; Pohl & Zurheide, 1979; Cobelas & Lechado, 1989; Harwood & Jones, 1989; Mourente, Lubi & Odriozola, 1990; Ahlgren, Gustafsson & Boberg, 1992). These patterns are seen in Fig. 3, which summarizes recent quantitative phytoplankton FA data for non-nutrient stressed cultures (Ahlgren *et al.*, 1992; Müller-Navarra, 1995a and unpublished data; De Lange & Van Donk, 1997; Lürling, De Lange & Van Donk, 1997). These data show diatoms have very high proportions of EPA and DHA and very low linolenic and linoleic acid content. Cryptophytes have very high proportions of EPA and DHA as well as linolenic acid. Chlorophytes lack or only have traces of EPA and DHA but have high linolenic acid content. Cyanophytes have virtually no DHA and EPA, and often very little linolenic and linoleic acid. In addition, many cyanophytes have a much lower total FA content than do other phytoplankton taxa.

Generally speaking, phytoplankton FA content varies much more between taxa than within taxa, however, within taxa alga FA content is influenced by environmental conditions (Kattner, Gercken & Eberlein, 1983; Cobelas, 1989; Harwood & Jones, 1989; Roessler, 1990; Hama, 1991; Ahlgren *et al.*, 1992). Nutrient limitation tends to increase the amount of SAFA and decrease the amount of UFA (for N-limitation see Paschke & Wheeler, 1954; Morris, 1981; Baasch, Kohlhase & Pohl, 1984; Piorreck & Pohl, 1984; El-Fouley *et al.*, 1985; for P-limitation see Reitan, Rainuzzo & Olsen, 1994; Ahlgren, Zeipel & Gustafsson, 1997); for example, Müller-Navarra (1995a; D.C. Müller-Navarra and U. Sommer, unpublished data) found N- and P-saturated *Scenedesmus acutus* had significant quantities of EPA and DHA, whereas N- and P-starved *S. acutus* had no HUFA. In addition to nutrient stress, temperature (Baasch *et al.*, 1984; Harwood & Jones, 1989), light (Thompson, Harrison & Whyte, 1990; Sicko-Goad & Andresen, 1991) and oxygen (Harwood & Jones, 1989) can have profound impacts on the FA content and composition of algae. When interpreting FA data from the literature, one should keep in mind that most FA data have been published as a proportion of total

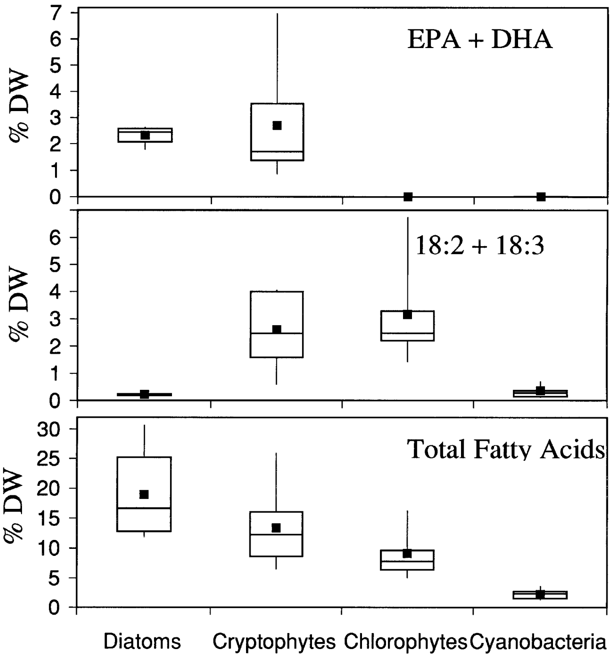

Fig. 3 Measured HUFA, 18 : 2ω6 and 18 : 3ω3, and total FA content for a variety of freshwater phytoplankton taxa. Data were taken from Ahlgren *et al.* (1992), Müller-Navarra (1995a and unpublished data), De Lange & Van Donk (1997), Lürling *et al.* (1997). The sample sizes for the summarized taxa are diatoms (n = 4), cryptophytes (n = 5), chlorophytes (n = 13) and cyanophytes (n = 13). The line through the middle of the box shows the median and the dot shows the mean of the distribution. The outer edges of the box correspond to the 25th and 75th percentiles, and the 'whiskers' to the 10th and 90th percentiles.

FA content. The absolute quantity of single FA (e.g. % DW) have only recently been reported (Ahlgren *et al.*, 1992; Müller-Navarra, 1993). This is important because the absolute, and not the relative, quantity of EPA has the strongest association with zooplankton growth (Fig. 2).

Phytoplankton HUFA content and zooplankton food-quality

Recent research has noted that highly nutritious algae have high HUFA content (Ahlgren *et al.*, 1990; Støttrup & Jensen, 1990; Jónasdóttir, 1994; Norsker & Støttrup, 1994). D'Abramo (1979) was the first to suggest that the FA content of phytoplankton may determine its food-quality zooplankton. Figure 4 compares phytoplankton food-quality, as determined in zooplankton growth bioassays, to an index of the phytoplankton's linolenic acid and EPA and DHA content. This relationship shows there is generally a good fit between phytoplankton food-quality and linolenic acid and EPA and DHA content. Figure 4 also suggests that variation in the food-quality of the phytoplankton may also be related to digestibility, as *Chlamydomonas*, which is easily digestible, was higher food-quality than predicted and *Scenedesmus quadricauda*, which is difficult to digest, was lower food-quality than predicted.

In addition, many studies comparing zooplankton growth and reproductive rates for different phytoplankton food types have demonstrated a clear hierarchy in phytoplankton food-quality. In general, cryptophytes and diatoms have been found to be very high food-quality, green algae have been found to be high quality in some cases and poor food-quality in others, and cyanobacteria and bacteria are generally poor quality food (Arnold, 1971; Porter & Orcutt, 1980; Schwartz & Ballinger, 1980; de Bernardi, Giussani & Pedretti, 1981; Stemberger, 1981; Pace, Porter & Feig, 1983; Infante & Litt, 1985; May, 1987; Skogstad, Granskog & Klaveness, 1987; Ahlgren *et al.*, 1990; Breteler, Schogt & Gonzalez, 1990; DeBiase, Sanders & Porter, 1990; Giani, 1991; Lundstedt & Brett, 1991; Xu & Burns, 1991; Vanni & Lampert, 1992; Brett, 1993b; Chen & Folt, 1993; Santer, 1994; Stutzman, 1995). Thus there is a strong fit between those phytoplankton taxa which are known to have high HUFA content and those which are known to promote high zooplankton growth and reproduction. Recent experiments have shown that adding semi-pure emulsions of EPA and DHA to low (DeMott & Müller-Navarra, 1997) or moderate (Weers & Gulati, 1997) food-quality phytoplankton or natural lake seston (Brett *et al.*, unpublished data) substantially increases its food-quality for *Daphnia*. Weers & Gulati (1997) suggested their results indicate HUFA are growth enhancing but not essential

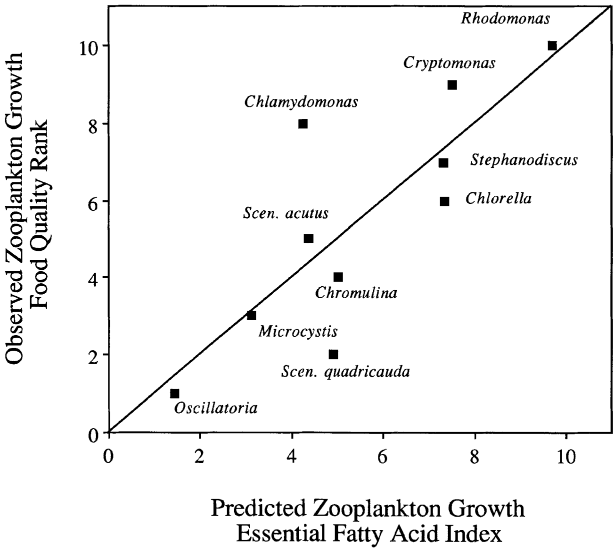

Fig. 4 A model predicting zooplankton growth (x-axis) from phytoplankton essential fatty acid data vs. observed zooplankton growth (y-axis), calculated using the data of Lundstedt & Brett (1991) and Ahlgren *et al.* (1990, 1992). The diagonal line is the theoretical one-to-one relation between the ranks of observed and predicted zooplankton growth. This relation shows zooplankton growth can be predicted by the HUFA and 18 : 2ω6 + 18 : 3ω3 content of the phytoplankton. Phytoplankton food-quality was determined as the observed change in individual zooplankter abundance in growth bioassays using *Daphnia*, *Bosmina* and *Chydorus* as test organisms. The food-quality rank was the average for the three cladocerans. A model predicting zooplankton growth using phytoplankton essential fatty acid data (the essential fatty acid index) was derived by regressing the rank of these phytoplankters' HUFA and 18 : 2ω6 + 18 : 3ω3 content against the food-quality rank. This resulted in a model which explained 64% of the variation in the food-quality rank, with the phytoplankton's HUFA content explaining 34% and phytoplankton's 18 : 2ω6 + 18 : 3ω3 content explaining 30% of the variation ($P = 0.08$). Phytoplankters above the diagonal line were higher food-quality than expected based on their essential fatty acid content, while phytoplankters below this line were lower food-quality than expected. Notably, *Chlamydomonas* was substantially higher food-quality than expected based on its fatty acid content and is probably easy to digest, while *Scenedesmus quadricuada* was substantially lower food-quality than expected and is probably difficult to digest.

per se, while 18 : 3ω3 is essential because very few animals can produce it *de novo*.

Recent research has shown green algae, such as *Scenedesmus* and *Chlamydomonas*, are poor food-quality for *Daphnia* when P-starved and high food-quality when P-saturated (Mitchell *et al.*, 1992; Sommer, 1992; Urabe & Watanabe, 1992; Sterner, 1993; Sterner *et al.*, 1993; Sterner & Hessen, 1994; Müller-Navarra, 1995a). Brett (1993a) suggested this result was due to changes in the biochemical composition of nutrient-stressed algae, while Urabe & Watanabe (1992) and Sterner & Hessen (1994) have suggested this is evidence for direct mineral P limitation of zooplankton growth. The results of Van Donk & Hessen (1993, 1995) strongly suggest the low food-quality of P- and N-starved green algae is, at least partially, due to greatly increased cell wall thickness, which makes nutrient-stressed green algae digestion-resistant. Van Donk *et al.* (1997) also found that a mutant strain of *Chlamydomonas* which lacked cell walls was not ingested and digested less efficiently when nutrient-stressed. Van Donk suggests the increased thickness of green algae cell walls when nutrient-stressed is a defensive mechanism against herbivore grazing when algal growth rates are low. Müller-Navarra (1995a), when comparing *Daphnia* growth on P-stressed diatoms (*Cyclotella*) and green algae (*Scenedesmus*), found *Daphnia* grew better when fed P-stressed (but HUFA-rich) diatoms than when fed P-saturated (but HUFA-poor) green algae. She also suggested that reduced daphnid growth in P-stressed green algae may be partially caused by reductions in the HUFA content of green algae with nutrient stress. It has also been shown that *Daphnia* grow poorly on N-stressed green algae (Groeger, Schram & Marzolf, 1991; Mitchell *et al.*, 1992; Kilham *et al.*, 1997; Van Donk *et al.*, 1997), which suggests that poor daphnid growth on nutrient-stressed green algae may be a general phenomenon which is not exclusively caused by direct mineral P limitation.

It is a general rule in aquaculture that most organisms grow better on combinations of food sources than they do on any one food source, independent of any measurable components of food-quality. These results are consistent with Lundstedt & Brett's (1991) observation that the cladoceran *Bosmina longirostris* grew substantially better on a combination of the diatom *Stephanodiscus* and the cryptophyte *Rhodomonas* than on either of these HUFA-rich algae singly. DeMott (W.R. DeMott, unpublished data) has also found that combinations of the green algae *Scenedesmus* and the cyanophyte *Synechococcus* resulted in better growth than for either of these algae alone.

Hypertrophy, marine upwelling and foodweb architecture

It is well established that hypereutrophic aquatic ecosystems are characterized by very high phytoplankton biomass and, relatively speaking, low zooplankton biomass (Fig. 1); for example, extensive data from hypereutrophic Clear Lake (CA U.S.A.), shows zooplankton biomass averages 15% of phytoplankton biomass (H.J. Carney and C.R. Goldman, unpublished data). In contrast, marine upwelling zones can have inverted food pyramids with more zooplankton biomass than phytoplankton biomass (Dortch & Packard, 1989, and references therein). We used the data of Dortch & Packard to calculate a foodweb pyramid for the diatom-dominated Peruvian upwelling zone, which is perhaps the world's most productive fishery. This shows that zooplankton biomass is, on average, 3.7 times greater than phytoplankton biomass in this planktonic foodweb. Comparing Clear Lake to the Peruvian upwelling zone shows that a given biomass of phytoplankton supports approximately twenty-five times as much zooplankton biomass in the Peruvian upwelling zone.

There are several explanations for this tremendous disparity. The diatoms of upwelling zones have quite high production to biomass ratios and they are easier to graze than cyanobacteria. The vast differences in diatom and cyanobacteria HUFA content may also be responsible for the tremendous disparity in the ability of these systems to support zooplankton production. The Peruvian upwelling zone has an extremely productive fishery, probably because diatoms are converted to zooplankton biomass very efficiently. Because the zooplankton in the upwelling zone are, due to their diatom diet, richer in HUFA, the efficiency of zooplankton conversion to fish biomass is also likely to be higher. Therefore a given biomass of phytoplankton is likely to support fifty times as much fish production in the Peruvian upwelling zone. The Peruvian upwelling zone is evidence of both high zooplankton growth efficiency and strong grazer impacts with HUFA-rich seston; that is, zooplankton grow well and graze the phytoplankton to relatively low levels.

In a study very similar to the above discussion, Hecky (1984) compared biomass partitioning and estimated trophic level efficiency for five tropical lakes. Hecky found that, although primary producer biomass varied tremendously between these lakes, fish production was similar, and, in fact, the two lakes with the lowest primary producer biomass (Lakes Tanganyika and Malawi) had the highest fish biomass. Hecky noted that in the lakes with very low zooplankton to phytoplankton biomass ratios (Lakes George and Chad), the phytoplankton was strongly dominated by cyanobacteria. In the lakes with high zooplankton to phytoplankton biomass ratios and high fish production (Lakes Lanao, Tanganyika and Malawi), the phytoplankton was dominated by diatoms, chlorophytes and, to a lesser extent, by cyanobacteria. These results again suggest that high food-quality (and HUFA-rich) phytoplankton assemblages support relatively higher zooplankton biomass and fish production.

In a study of two adjacent and connected hypereutrophic lakes, Moss, Stansfield & Irvine (1991) found one lake was strongly dominated by diatoms because of its rapid flushing rate and the other was dominated by cyanobacteria. Moss and colleagues conducted mesocosm experiments with enclosures constructed of 1-mm mesh. This allowed phytoplankton to flow freely through the enclosures but protected the zooplankton from vertebrate predators. This essentially allowed for measurement of the impact of different algal assemblages on daphnid population size, unconfounded by predation. These authors observed somewhat similar phytoplankton biomasses in the diatom- (105 Chl *a* l^{-1}) and cyanobacteria- (196 μg Chl *a* l^{-1}) dominated lakes. However, they reported far greater daphnid abundances in the diatom-dominated lake; for example, 1043 and 117 individuals l^{-1}, respectively. If the zooplankton data of Moss and colleagues is converted to biomass using the species abundance and length data reported in their study and the length to biomass regressions of McCauley (1984), one finds that a given amount of chlorophyll (it was not possible to convert their chlorophyll values to phytoplankton biomass because the authors did not correct for phaeophytin fluorescence) supported 100 times more zooplankton biomass in the enclosures in the diatom-dominated lake. This also emphasizes the ability of high-quality phytoplankton assemblages to support greater zooplankton production. However, this result is not directly analogous to the comparison between the Peruvian upwelling zone and Clear Lake because the zooplankton in the study of Moss and colleagues were protected from vertebrate predators and were unable completely to control the phytoplankton community (or cause it to crash) because the experiment was conducted in a flow-through system.

The trophic cascade, feedback loops, and the spring clear-water-phase

Brett & Goldman (1996) found, in a meta-analysis of fifty-four mesocosm experiments, that the response of phytoplankton community biomass to zooplanktivorous fish treatments is highly variable, with weak responses (mean 40% increase in biomass) in about two-thirds of the experiments and very strong responses (700% increase) in one-third of the experiments. These authors also found that nutrient additions to mesocosms often resulted in large increases in phytoplankton biomass, but only small increases in zooplankton biomass (Brett & Goldman, 1997). We expect that much of the variation in the phytoplankton's response to the trophic cascade may be caused by the fact that some species of phytoplankton are more susceptible to zooplankton grazing than others, and some zooplankters are more efficient grazers than others. However, some of this variation may also be related to the previously mentioned feedback between phytoplankton HUFA content and zooplankton growth. In cases where seston HUFA content is low, zooplankton will have poor growth and recruitment and will exert only weak control over the phytoplankton. In cases where phytoplankton HUFA content is high, the zooplankton will have high growth and recruitment rates and will exert strong control over the phytoplankton. This feedback process between food-quality and zooplankton grazing impacts has been suggested previously by Kerfoot, Levitan & DeMott (1988).

In the intensively studied clear-water-phase of many temperate lakes, the phytoplankton species composition and biomass and zooplankton growth rates and egg production follow predictable patterns (Fig. 5) (Lampert *et al*., 1986; Sommer *et al*., 1986; Vanni & Temte, 1990; Sarnelle, 1993). The seasonal pattern is initiated by a spring bloom of HUFA-rich diatoms and cryptomonad flagellates, which, in turn, fuels a rapid population increase of large zooplankton grazers like

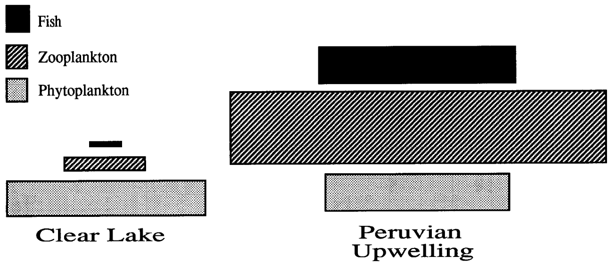

Fig. 5 The hypothetical seasonal dynamics of the phytoplankton and zooplankton communities in a typical temperate lake according to the Plankton Ecology Group-model (Sommer *et al.*, 1986). This figure shows strong coupling between phytoplankton and zooplankton community growth dynamics during the spring when the phytoplankton is dominated by HUFA-rich flagellates and diatoms and weak coupling during the summer when the phytoplankton is dominated by HUFA-poor cyanophytes and nutrient-stressed green algae.

Daphnia. Daphnia often 'overshoot' their food supply and produce the clear-water-phase characterized by very low phytoplankton biomass, and then undergo a crash. A new phytoplankton community then develops which is dominated by low-HUFA cyanobacteria and green algae. This phytoplankton community is low food-quality and does not support good zooplankton growth or egg production (Müller-Navarra & Lampert, 1996), and is resistant to grazing.

HUFA trophic transfer in aquatic foodwebs

Several studies have examined FA trophic transfer in marine planktonic systems by comparing the relative FA composition of different trophic levels. Fraser *et al.* (1989) examined FA trophic transfer in a mesocosm study with natural phytoplankton, copepods and herring larvae. Of the FA studied, EPA and DHA were the most concentrated in the copepods and herring larvae relative to the phytoplankton. Ederington, McManus & Harvey (1995) measured FA in the copepod *Acartia tonsa* feeding on the diatom *Thalassiosira weissflogii* and the bacterivorous ciliate *Pleuronema* sp. *Acartia* had a tenfold greater egg production rate when feeding on diatoms compared to the ciliate diet; that is, forty-eight and five eggs per individual per day, respectively. Of the twenty-four FA examined, EPA stood out by being abundant in the diatom diet, abundant in diatom-fed copepods and their eggs, rare in ciliates, rare in ciliate-fed copepods and their eggs, and rare in starved copepods. Thus, of all the FA measured, EPA had the strongest association with the high egg production rates seen in the diatom diet. Jónasdóttir, Fields & Pantoja (1995) suggested that marine copepod egg production was related to the HUFA content of natural phytoplankton assemblages in Long Island Sound, U.S.A.

Potential implications of the role of HUFA in aquatic foodwebs

It could be argued that understanding the processes which regulate the rate at which plant production is converted to herbivore production is the most important challenge confronting foodweb ecology today. These processes are also critical to understanding the factors that control fisheries production. It may also be possible to use this information to restore lakes biologically; for example, one might increase the zooplankton community's ability to control phytoplankton biomass (and water clarity) by selectively stimulating the growth of HUFA-rich diatoms and cryptophytes. The seston HUFA content and zooplankton food-quality hypothesis may provide important insights into stoichiometric studies of phytoplankton nutrient limitation and biogeochemical cycling in planktonic foodwebs (Elser *et al.*, 1988; Sterner, Elser & Hessen, 1992; Elser & Hassett, 1994; Urabe, Nakanishi & Kawabata, 1995). If HUFA regulates the efficiency at which phytoplankton carbon is converted to zooplankton biomass, it should also have a very large impact on the rate at which phytoplankton N and P are converted to zooplankton biomass. Our HUFA hypothesis may also be applicable to freshwater benthic insect and crustacean biology. As previously mentioned, aquatic insects have high HUFA content (Hanson *et al.*, 1985), and several studies have shown benthic diatoms are a particularly high-quality food source for aquatic invertebrates (Fuller & Mackay, 1981; Sweeney & Vannote, 1984; Rosillon, 1988; Johnson & Wiederholm, 1992; Pinder, 1992; Delong, Summers & Thorp, 1993). A recent paper (Napolitano *et al.*, 1996) compared the FA composition of herbivorous minnows and their periphyton food and found that, although diatoms comprised a small proportion of periphyton biomass in one stream, diatom FA (EPA) comprised a surprisingly large portion of the minnow FA.

Analyses of seston FA content may be as useful to studies of secondary production as analyses of seston nutrient and chlorophyll content have proven to be for studies of primary production. Seston HUFA content may be a 'rough and ready' index of potential secondary production in aquatic foodwebs. We believe future research on the role of HUFA in aquatic ecosystems will make an important contribution to foodweb ecology. The key to gaining future insights into the nature of foodweb dynamics may come from drawing ideas from biochemistry, nutritional physiology and molecular biology.

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