Development of farmed fish: a nutritionally necessary alternative to meat

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The projected stagnation in the catch from global fisheries and the continuing expansion of aquaculture is considered against the background that fishmeal and fish oil are major feed stocks for farmed salmon and trout, and also for marine fish. The dietary requirement of these farmed fish for high-quality protein, rich in essential amino acids, can be met by sources other than fishmeal. However, the highly-polyunsaturated fatty acids eicosapentaenoic acid (20:5*n*-3) and docosahexaenoic acid (22:6*n*-3) present in high concentrations in fish oil are essential dietary constituents for marine fish and highly-desirable dietary constituents for salmonids. Currently, there is no feasible alternative source to fish oil for these nutrients in fish feeds. Vegetable oils rich in linoleic acid (18:2*n*-6) can partially substitute for 20:5*n*-3 and 22:6*n*-3 in salmonid and marine-fish feeds. However, this is nutritionally undesirable for human nutrition because the health-promoting effects of fish-derived 20:5*n*-3 and 22:6*n*-3 reflect a very high intake of 18:2*n*-6 relative to linolenic acid (18:3*n*-3) in Western diets. If partial replacement of fish oils in fish feeds with vegetable oils becomes necessary in future, it is argued that 18:3*n*-3-rich oils, such as linseed oil, are the oils of choice because they are much more acceptable from a human nutritional perspective, especially given the innate ability of freshwater fish, including salmonids, to convert dietary 18:3*n*-3 to 20:5*n*-3 and 22:6*n*-3. In the meantime, a more judicious use of increasingly-expensive fish oil in aquaculture is recommended. High priorities in the future development of aquaculture are considered to be genetic improvement of farmed fish stocks with enhanced abilities to convert C_{18} to C_{20} and C_{22} *n*-3 polyunsaturated fatty acids, enhanced development of primary production of 20:5*n*-3 and 22:6*n*-3 by single-cell marine organisms, and continuing development of new species.

Polyunsaturated fatty acids: Eicosapentaenoic acid: Docosahexaenoic acid: Fishmeal: Fish oil

Stagnating fisheries production: expanding aquaculture

Global capture fisheries, i.e. catches of wild fish as distinct from farmed fish, are valuable and finite resources which, although renewable, are highly vulnerable. They have grown since 1984 at an average rate of only 1·8 %/year and now yield somewhat less than 100×10^6 t/year (James, 1994; Tacon, 1999). Moreover, over-fishing has caused the collapse or near collapse of some valuable fisheries. Over-exploiting one fish species, whether for direct human consumption or for reduction to fishmeal and fish oil, can affect other species, not least birds and mammals, in the marine ecosystem. This situation has generated understandable and justifiable pressure from environmentalists to further reduce fishing effort and catches by introducing tighter regulatory measures. The possibility of global warming and the realization that natural climatic events, such as 'El Nino', can profoundly affect major fisheries (especially the anchovy fishery) highlights the inherent vulnerability of global fisheries. Few authorities would now predict other than a stagnating or even declining yield from global fisheries, so that future demand for fisheries products will inevitably outstrip supply, leading to price increases. The cost of fish oil increased substantially from 1997 to 1998 to exceed that of soyabean oil (Tacon, 1999). Against this background fish production from aquaculture has increased substantially over the last decade or more (11·6 % compound growth/year since 1984; Tacon, 1999). Aquaculture has been the world's fastest growing food production sector for over a decade, and it is projected to at least double over the next decade or more (Hempel, 1993). The present article considers the projected increase in aquaculture,

Abbreviations: HUFA, highly-unsaturated fatty acids; PUFA, polyunsaturated fatty acids.

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particularly from the points of view of the nutritional value of fish as a human food and fish farming in western Europe.

According to Food and Agriculture Organization statistics (Tacon, 1999), the global production of aquaculture in 1996 was approximately 34×10^6 t compared with total world capture fisheries landings of approximately 96×10^6 t. These 34×10^6 t farmed 'fish' consisted of 48·8 % fin fish, 24·9 % molluscs, 22·7 % aquatic plants, 3·4 % crustaceans and 0·2 % other species (Tacon, 1999; see also De Silva & Anderson, 1995). In 1996, aquatic meat production of $16{\cdot}3\times10^6$ t accounted for approximately 7 % of global meat production, fourth behind chicken meat ($49{\cdot}5\times10^6$ t, 21·2 % total meat production), beef and veal meat ($53{\cdot}9\times10^6$ t, 23·1 % total meat production) and pig meat ($87{\cdot}2\times10^6$ t, 38·3 % total meat production), and the fastest growing of all these sectors (Tacon, 1999). Whereas aquatic meat accounted for only 1·6 % total meat production in developed countries, it accounted for 11·2 % total meat production in developing countries (Tacon, 1999). Thus, 91·1 % of world aquaculture production occurred in Asia (particularly in China which produced $23{\cdot}1\times10^6$ t), 4·7 % in Europe, 1·8 % in North America, 1·6 % in South America and 0·4 % in Africa. Carp was by far the major species farmed in Asia, especially in China where aquaculture is growing particularly fast, and global production in 1996 was $9{\cdot}4\times10^6$ t. In contrast, salmon and trout farming, which is concentrated largely in Europe and North and South America, produced less than 0·6 and $0{\cdot}4\times10^6$ t respectively in 1996. Specifically, production of Atlantic salmon (*Salmo salar*), which occurs mainly in Norway, Chile, Scotland, Ireland and Canada, was approximately 480 000 t in 1996 (International Fishmeal and Oil Manufacturers Association, 1996). The production in Europe of farmed marine fish, i.e. fish whose life cycle is wholly in sea water in contrast to the salmon which starts its life in freshwater before migrating to sea water, was approximately $0{\cdot}06\times10^6$ t in 1997. This was composed principally of three species: sea bream (*Sparus aurata*), sea bass (*Dicentrarchus labrax*) and turbot (*Scophthalmus maximus*). These tonnages have increased steadily throughout the 1990s, so that salmon and trout, together with an increasing range of marine flat fish and round fish (chiefly sea bream, sea bass, turbot and halibut (*Hippoglossus hippoglossus*)) will be increasingly on offer to the UK consumer as traditionally-caught fish becomes less available and more expensive. What are the constraints to these developments and what are the nutritional consequences to the consumer?

Fishmeal and fish oil: are they essential for fish feeds?

The intensive production of salmonids and marine fish in western Europe and North and South America is heavily dependent on continuing supplies of high-quality fishmeal and fish oil generated by global capture fisheries. Currently, about one-third of the total global catch of marine fish, i.e. approximately 30×10^6 t, is converted to fishmeal and fish oil (Barlow & Pike, 1994). The global production of fishmeal and fish oil from capture fisheries, i.e. from wild fish, in 1996 was $6{\cdot}8\times10^6$ t and $1{\cdot}4\times10^6$ t respectively (Tacon, 1998). In 1990, more than 90 % of the fishmeal produced was used for animal feeds (58, 20 and 14 % for poultry, pigs and fish respectively). Of the global production of fishmeal in 1996, $2{\cdot}0\times10^6$ t was used for feeds used in fish farming, with shrimp farming accounting for 20·3 % of that tonnage, salmon farming 18·8 %, carp farming 18·3 %, marine-fish farming 13·9 %, trout farming 10·9 %, eel farming 10·7 %, milk-fish farming 1·6 % and catfish farming 1·3 % (Tacon, 1999). Of the global production of fish oil in 1996, 576 000 t was used for feeds used in fish farming, with salmon farming accounting for 36·3 % of that total, trout farming 21·6 %, marine-fish farming 14·8 %, carp farming 8·0 %, eel farming 7·5 %, marine-shrimp farming 7·1 %, milk-fish farming 1·9 % and catfish farming 1·8 % (Tacon, 1999). Thus, the bulk of global fishmeal and fish oil used in aquaculture is currently being invested in salmon, trout and marine-fish farming, largely in Western countries, although freshwater-fish farming, largely of carp, also consumes a substantial proportion. Given the current very rapid increase in freshwater-fish farming in Asia, and particularly in China, there is likely to be intense future pressure on, and resulting competition for, limited global supplies of fishmeal and fish oil.

The dependence of salmonid and marine-fish farming on fishmeal and fish oil has a solid scientific basis for two reasons. First, salmon, trout and virtually all marine fish are strict carnivores that have naturally evolved to have a high dietary requirement (400–500 g/kg dietary DM) for protein rich in essential amino acids. This is very conveniently met by fishmeal, which has the additional advantage of being highly acceptable to fish because of its taste and texture. Indeed, the amino acid composition of the flesh of farmed salmonids and marine fish, like that of all fish, is essentially the same as that of fishmeal (Wilson, 1989; Sikorski *et al.* 1990). Second, fish have a high dietary requirement for n-3 polyunsaturated fatty acids (PUFA), reflecting the natural abundance of these nutrients in the phospholipids of their cellular membranes and their body triacylglycerol oils, and in their natural prey in freshwater and marine environments. Freshwater fish, which includes trout and also formally salmon, which are initially grown as parr in freshwater before being on grown as smolts in sea water, are capable of converting linolenic acid (18 : 3n-3) to its higher biologically-active homologues, eicosapentaenoic acid (20 : 5n-3) and docosahexaenoic acid (22 : 6n-3; Sargent *et al.* 1993, 1995). Likewise, freshwater fish can convert linoleic acid (18 : 2n-6) to its higher, biologically-active homologue arachidonic acid (20 : 4n-6) although n-6 PUFA are required by fish to a much smaller extent (about one order of magnitude less for marine fish and salmonids) than n-3 PUFA (Sargent *et al.* 1993, 1995). In contrast, no marine fish so far studied can carry out these conversions (Sargent *et al.* 1993, 1995). Thus, 20 : 5n-3 and 22 : 6n-3 are dietary essential fatty acids for marine fish. Equally, although the main dietary essential fatty acid for freshwater fish is formally 18 : 3n-3, freshwater fish including trout and salmon have a higher growth performance when fed on the endproducts 20 : 5n-3 and 22 : 6n-3 directly than when fed on 18 : 3n-3. Thus, fish oil, which is the only readily-available commercial source of 20:5n-3 and 22:6n-3, is mandatory for farming marine fish, and highly desirable for farming trout and especially salmon. Thus, the farming of salmonids and marine fish as practised in western Europe and North and South America is essentially a means of converting relatively-low-value fishmeal and fish oil from industrial fisheries to high-value food products for the human market. Indeed, 'crude' fishmeal, which routinely contains approximately 100 g residual fish oil/kg DM, is a highly-satisfactory feed for salmonids and marine fish in general, although the oil content of fish feeds can be as high as 300 g/kg dietary DM, particularly in the 'high-energy' diets now routinely used in Norway and Scotland for accelerated salmon production (Bell *et al.* 1998).

Despite the foregoing, the current dependence of fish farming on fishmeal as its dominant protein source is not absolute, because any high-quality protein which meets the essential amino acid requirements of fish, and is readily acceptable and digestible by the fish, can substitute for fishmeal. Soyabean protein is already being used increasingly to substitute partially for fishmeal in salmonid feeds, and this trend is likely to accelerate in future as plant proteins of high nutritional value become increasingly available. In contrast, the current dependence of salmonid and marine-fish farming on fish oil is more fundamental, and real difficulties and issues emerge when considering substitutes for fish oil.

Although the body tissues of all fish in their natural environment have 20 : 5*n*-3 and 22 : 6*n*-3 as their major PUFA, both in the phospholipids of their cellular membranes and the triacylglycerols of their adipose tissues, the fatty acid compositions of fish, especially their body oils (triacylglycerols), can very easily be altered by altering their dietary fatty acid intake. Thus, the fatty acid compositions of fish body oils (triacylglycerols) closely parallel their dietary fatty acid compositions (Table 1). Moreover, although fish have a high dietary requirement for *n*-3 PUFA, the requirement is most critical for the larval and early post-larval stages of the life cycle. Juvenile fish can be grown readily on a range of dietary fats and oils, including the abundantly-available vegetable-seed oils rich in oleic acid (18 : 1*n*-9) and 18 : 2*n*-6. This is particularly the case for freshwater fish which, as noted previously, are capable of converting C_{18} PUFA to their higher C_{20} and C_{22} homologues, and additionally have higher levels of *n*-6 PUFA in their body tissues than marine fish in their natural environments. Thus, channel catfish (*Ictalurus punctatus*) are routinely grown in the Mississippi delta of the USA on diets containing readily-available vegetable oils rich in 18 : 2*n*-6 and 18 : 1*n*-9, e.g. maize or soyabean oils (Table 2). More revealing, the very large tonnage of carps, barbs and tilapias produced in the fresh waters of the far east and southeast Asia (predominantly under extensive conditions) is achieved using a wide variety of feeds. These feeds are usually those most readily available locally, containing a range of dietary fats and oils, but seldom until recently including fish oil. Consequently, channel catfish farmed in the USA are invariably rich in 18:2*n*-6, especially in their body oils (triacylglycerols), and this can also be the case for many freshwater fish produced in the far east and southeast Asia. However, this apparent flexibility should not obscure the fundamental fact that all known fish, even those from freshwater, have a higher dietary requirement for *n*-3 PUFA than for *n*-6 PUFA, particularly in their early life stages (Sargent *et al.* 1999). Thus, in the absence of a dietary input of 20 : 5*n*-3 and 22 : 6*n*-3 from fish oil in administered diets, or from natural aquatic prey items in the fish ponds, there must be an adequate dietary input of 18 : 3*n*-3 for the early stages of development for freshwater fish. For the early stages of development in herbivorous or even omnivorous fish, which include many freshwater fish such as carp, aquatic plants can provide 18 : 3*n*-3 present in their chloroplast lipids. For carnivorous fish the 18 : 3*n*-3 must be provided either by natural prey items or in oils present in administered diets.

Table 1. Fatty acid composition (g/100 g fatty acids) of fish body oils (triacylglycerols)

Fatty acid	Farmed trout*	Trout fed on copepods*	Farmed salmon†	Wild salmon†	Herring (*Clupea harengus*)*	Anchovy*
14:0	2	3	5	4	7	7
16:0	21	13	15	13	13	17
16:1*n*-7	5	7	7	4	7	9
18:0	5	3	3	3	1	4
18:1*n*-9	26	16	17	23	10	12
18:2*n*-6	18	8	3	1	1	1
18:3*n*-3	2	2	2	1	1	1
18:4*n*-3	1	4	2	1	3	0
20:1*n*-9	4	11	8	12	13	2
20:4*n*-6	1	1	1	1	1	1
20:5*n*-3	2	6	7	7	6	17
22:1*n*-11	3	8	9	11	23	2
22:6*n*-3	11	19	12	10	6	9
SFA	28	19	24	20	21	28
MUFA	38	42	42	52	53	23
n-3 PUFA	16	31	28	24	16	31
n-6 PUFA	19	9	4	2	2	2

SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids.

* Data from Sargent & Henderson (1995) and references therein. The farmed trout had been fed on diets containing fish oil supplemented with vegetable oil, as evidenced by the substantial level of 18 : 2*n*-6 in the fish. Feeding these trout copepods rich in 22 : 6*n*-3, 20 : 5*n*-3, 20 : 1*n*-9 and 22 : 1*n*-11 enhanced the levels of these fatty acids in the fish and simultaneously reduced the level of 18 : 2*n*-6.

† Data from Bell *et al.* (1998). Farmed salmon are currently fed on diets containing 'northern hemisphere' fish oils characteristically rich in 20 : 1*n*-9 and 22 : 1*n*-11, as exemplified by herring oil. Herring obtain their 22 : 6*n*-3, 20 : 5*n*-3, 20 : 1*n*-9 and 22 : 1*n*-11 fatty acids from copepods. The fatty acids of the farmed salmon reflect the fatty acids in their herring-oil diet, being rich in 20 : 1*n*-9 and 22 : 1*n*-11 as well as 22 : 6*n*-3 and 20 : 5*n*-3. 'Southern hemisphere' fish oils, exemplified by anchovy, lack 20 : 1*n*-9 and 22 : 1*n*-11 and are correspondingly richer in 22 : 6*n*-3 and especially 20 : 5*n*-3 than 'northern hemisphere' fish oils.

Table 2. Fatty acid composition (g/100 g fatty acids) of commercially-available oils (triacylglycerols)

	Rape*	Soyabean*	Safflower*	Olive*	Linseed†	*Echium*‡	Martek™§
18:1	56	25	68	62	18	19	14
18:2*n*-6	26	51	21	19	15	16	0
18:3*n*-6	0	0	0	0	0	28	0
18:3*n*-3	8	6	1	2	56	12	0
18:4*n*-3	0	0	0	0	0	14	0
20:5*n*-3	0	0	0	0	0	0	0
22:6*n*-3	0	0	0	0	0	0	30

* Data from Okuyama *et al.* (1997).
† Data from Bell *et al.* (1993).
‡ An oil from the plant *Echium* spp.; data from K Coupland (Croda Chemicals Ltd, Hull, Humberside, UK; personal communication).
§ The Martek™ oil (Martek Bioscience Corp., Columbia, MD, USA) is a commercial product from the heterotrophic dinoflagellate *Crypthecodinium cohnii*; data from Sargent & Henderson (1995).

Thus, abundantly-available vegetable-seed oils (including soyabean oil) that are rich in 18:2*n*-6 can substitute substantially but not completely for fish oils in fish feeds for on-growing post-larval fish, encompassing freshwater fish generally, trout and salmon, and probably also marine fish. Indeed, very recently it has been stated authoritatively that vegetable oils rich in 18:1*n*-9 and 18:2*n*-6, as well as beef tallow, can generally substitute for up to 50 % of the fish oils currently used in marine- and freshwater-fish feeds (Watanabe & Cho, 1999). Given the likely decreasing supplies and resultant increasing future costs of fish oils, there is obviously increasing economic pressure to partially replace fish oils in fish feeds with vegetable oils, most notably soyabean, palm and rapeseed oils. This occurs against a background where current (1996–7) world production of fish oils (1 387 000 t) is now less than 2 % of the total world production of fats and oils (93 082 000 t). The major world oils are now soyabean oil (20 799 000 t), palm oil (17 077 000 t) and rapeseed oil (11 410 000 t; O'Mara, 1998). The economic case for developing aquaculture on the broad and growing base of plant protein and 18:2*n*-6-rich oil production is obvious and strong. However, in our opinion, the case against it from a human nutritional perspective is stronger.

Fish as human food: a unique nutritional role

The uniqueness of fish in human nutrition lies not in their high-quality protein, for which there are many competing alternatives, but in their high content of *n*-3 highly-unsaturated fatty acids (HUFA), i.e. 20:5*n*-3 and 22:6*n*-3, for which there are currently no real competing alternatives. The health-promoting effects of 20:5*n*-3 and 22:6*n*-3 in human subjects have been extensively reviewed in recent years (British Nutrition Foundation Task Force, 1992; British Nutrition Foundation, 1993; International Society for the Study of Fatty Acids and Lipids, 1994*a*,*b*) and need only briefly be summarized here. Understanding their roles depends very substantially on the definitive work of Lands *et al.* (1992) who showed using rats that serum levels of the *n*-6 C_{20} PUFA precursors of the eicosanoids, i.e. 20:4*n*-6 and 20:3*n*-6, were directly related to the dietary intake of 18:2*n*-6. At dietary intakes of 18:2*n*-6 greater than approximately 5 % total energy intake, which is below current Western intakes of 18:2*n*-6, serum levels of 20:4*n*-6 and 20:3*n*-6 approached their maxima, i.e. eicosanoid production was maximal. Excess eicosanoid production is undesirable as illustrated, for example, by the extensive use of steroidal and non-steroidal anti-inflammatory agents to block eicosanoid production in many human disorders, including cardiovascular and inflammatory disorders and cancers. Thus, an excessively high dietary intake of 18:2*n*-6, which elevates body levels of C_{20} *n*-6 PUFA and thereby promotes eicosanoid production, is undesirable. However, to depress eicosanoid production substantially from 20:4*n*-6 and 20:3*n*-6 requires a dietary intake of 18:2*n*-6 of less than 2 % total energy intake, well below current dietary intake in Western societies which is in excess of 6 % total energy intake. Fortunately, the desired effect can be achieved by even modest dietary intakes of 18:3*n*-3 of approximately 1 % total energy intake. This is because 18:3*n*-3 competes very effectively with 18:2*n*-6 for the common fatty acid desaturases and elongases that convert the C_{18} PUFA to their C_{20} and C_{22} homologues. Furthermore, 20:5*n*-3 is even more effective than 18:3*n*-3 in this respect and, additionally, competes directly with 20:4*n*-6 and 20:3*n*-6 in eicosanoid production and in eicosanoid actions. Hence, administration of fish oils or consuming oily fish rich in 20:5*n*-3 can be beneficial in a wide range of human disorders by damping down eicosanoid production from *n*-6 PUFA (for example, see British Nutrition Foundation Task Force, 1992). Thus, numerous authoritative bodies including the British Nutrition Foundation (British Nutrition Foundation Task Force, 1992), the Department of Health (1994) and the International Society for the Study of Fatty Acids and Lipids (1994*a*) have recommended an increased consumption of oily fish rich in *n*-3 HUFA in Western diets. These recommendations rest on the fact that, with a continually increasing dietary intake of 18:2*n*-6 over the last few decades, driven by increasing world supplies of vegetable-seed oils rich in 18:2*n*-6 (O'Mara, 1998), the dietary 18:2*n*-6:18:3*n*-3 value in Western diets has steadily increased far above what is now perceived as the desirable value of about 5 : 1. The seriousness of the issue is illustrated in a recent review by Okuyama *et al.* (1997) which notes that the incidences of 'Western-type' disorders have increased progressively in Japan in parallel with increasing dietary intake of 18:2*n*-6, even given the traditionally high consumption of *n*-3 HUFA-rich fish in Japan. Okuyama *et al.* (1997) present the striking case of the

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Okinawa prefecture, which traditionally led longevity tables in Japan if not worldwide. This prefecture was the first in Japan to be subjected to increased dietary intake of 18 : 2*n*-6, following American occupation in 1945. Incidences of Western-type disorders in Japan as a whole have increased most rapidly in Okinawa since 1945, especially in younger individuals. The Okinawa prefecture now stands well below the mean longevity for Japan overall (data cited by Okuyama *et al.* 1997).

In addition, 22 : 6*n*-3 has a special role in human nutrition because of the high concentrations of this fatty acid in neural and visual tissues. Human subjects can undoubtedly convert 18 : 3*n*-3 to 20 : 5*n*-3 and thence to 22 : 6*n*-3, but there are concerns, prompted mainly by studies on premature infants, that the rate of production of 22 : 6*n*-3 from 18 : 3*n*-3 may not be sufficiently fast at all times and under all conditions, especially under the conditions of high demand which occur during the early stages of development, i.e. *in utero* and immediately post-natally (Carlson *et al.* 1993; Uauy *et al.* 1994). This concern is, of course, greatest with a high dietary 18 : 2*n*-6 : 18 : 3*n*-3 value for the mother. Thus, formula feeds for premature and, on occasions, full-term infants are now supplemented with 22 : 6*n*-3, and it is considered prudent to increase the intake of oily fish during pregnancy (British Nutrition Foundation Task Force, 1992; International Society for the Study of Fatty acids and Lipids, 1994*b*). Evidence is also emerging for a role for 20 : 5*n*-3 and 22 : 6*n*-3 in various mental disorders, including schizophrenia (Peet, 1997), and in aggressive behaviour (Okuyama *et al.* 1997).

Although replete with contentions and uncertainties, the evidence that an excessively high dietary *n*-6 : *n*-3 PUFA value is undesirable and related to a whole range of human disorders is, at the very least, compelling. Given the enhanced efficacy of 22 : 6*n*-3 and 20 : 5*n*-3 relative to 18 : 3*n*-3 in the biochemical processes whereby *n*-3 PUFA modulate the undesirable effects of excess *n*-6 PUFA, the case for giving particular prominence to 22 : 6*n*-3 and 20 : 5*n*-3 in human nutrition is now very strong. While fish are not the only source of these nutrients in human nutrition, fish contain by far the highest concentrations of 20 : 5*n*-3 and 22 : 6*n*-3 of any of the foods commonly available to man. It is only prudent, to say the least, to continue to make available *n*-3 HUFA-rich fish in the human diet. There is no nutritional case, to say the least, for exploiting fish as vehicles for delivering yet more 18 : 2*n*-6 in the human diet.

Farmed fish as human food: future opportunities

Given the projected decrease in supplies and increasing costs of traditional wild-caught fish for human consumption, together with the special role of fish as major providers of 20 : 5*n*-3 and 22 : 6*n*-3 for human nutrition, aquaculture has a very important role to play in ensuring future supplies of fish. The development of aquaculture in Western Europe and the UK has been impressive over the last two decades. Problems remain, but these are not insurmountable and are accompanied by opportunities for further, possibly faster, development.

The ready availability of economically-competitive feedstuffs has featured prominently in the present paper, particularly the special role of *n*-3 HUFA in fish feeds. However, the problem of the likely future imbalance between supply and demand for fish oil remains and could well become a serious threat to future aquaculture development, especially the development of salmonid and marine-fish farming. Indeed, fish-feed manufacturers are already promoting the replacement of fish oils in fish feeds with vegetable oils, particularly soyabean oil, coincident with fish oils becoming marginally more expensive than soyabean oil, and with seemingly little or no consideration for human nutritional consequences. However, we caution strongly that, should replacement of fish oil with vegetable oil in aquaculture become inevitable, this should be done as sparingly as possible and in full realization of the nutritional consequences for the consumer. Should high-energy, i.e. oil-rich, diets for salmonids be really essential, then consideration should be given to partially replacing fish oils with oils rich in energy-generating monounsaturated fatty acids such as 18 : 1*n*-9, e.g. high-oleic acid sunflower oils, which are readily available. Should it become necessary to use PUFA-rich vegetable oils for salmonid production, there is a very strong case for using vegetable oils with as high a 18 : 3*n*-3 : 18 : 2*n*-6 value as possible. Such oils exist and have always existed, e.g. linseed oil, but they have yet to receive the development investment accorded to vegetable-seed oils rich in 18 : 2*n*-6, specifically in terms of simultaneously maximizing their contents of 18 : 3*n*-3 and minimizing their contents of 18 : 2*n*-6. This is in stark contrast to the major efforts invested in recent decades to eliminate the already very low levels of 18 : 3*n*-3 in 18 : 2*n*-6-rich vegetable oils such as maize oil. Moreover, there are vegetable oils with *n*-3 PUFA ‘metabolically closer’ to 20 : 5*n*-3 than 18 : 3*n*-3 and these are currently being developed commercially as human ‘nutriceuticals’, e.g. the oil from the plant *Echium* spp. which contains substantial amounts of 18 : 4*n*-3 (Table 2). Modern plant-breeding and genetic-engineering technologies are capable of substantially developing such oils. However, the development of plant oils rich in 20 : 5*n*-3, far less 22 : 6*n*-3, is not (at least in our opinion) a feasible proposition for the foreseeable future. Nonetheless, single-cell oils containing high levels of 22 : 6*n*-3 as the only PUFA have been developed as human nutritional supplements from heterotrophic marine dinoflagellates such as *Crypthecodinium cohnii* and are available commercially (Martek^{TM}; Table 2). It is very doubtful, however, whether such oils can make other than a very small contribution as replacements for commercial fish oils for the foreseeable future.

It is axiomatic that in the future fish oils should be used more selectively in fish feeds than is now the case. Freshwater fish, especially the carps and tilapias, have a proven ability to convert 18 : 3*n*-3 to 20 : 5*n*-3 and thence to 22 : 6*n*-3. Such fish have no strict requirement for dietary *n*-3 HUFA, and thus there is no nutritional case for using fish oils in their diets. Even marine fish have a very slight ability to carry out these conversions, indicating that they, like their freshwater counterparts, possess the necessary genetic information for the required conversions. Thus, fish already possess a system for producing *n*-3 HUFA from 18 : 3*n*-3, and efforts to enhance this production, whether by nutritional or genetic manipulation, deserve immediate and high priority. Such a development may well have implications for the taste of the final product, since 18 : 3*n*-3 and *n*-3 HUFA taste quite different, and it is highly likely that fish farmed on 18 : 3*n*-3-rich oils will deposit a substantial portion of the ingested 18 : 3*n*-3 in their body triacylglycerols. However, this need not necessarily be a disadvantage. A product with a high 18 : 3*n*-3 : *n*-3 HUFA value is certainly better nutritionally for man than a product with a high 18 : 2*n*-6 : *n*-3 HUFA value. Moreover, new taste characteristics resulting from the partial replacement of *n*-3 HUFA in farmed fish with 18 : 3*n*-3 will emerge. This is not necessarily undesirable or disadvantageous, since many individuals are averse to fish in their present form. In short, aquaculture itself may hold the long-term solution to fish oil shortage.

The production of viable larvae remains a bottleneck in many areas of marine fish production. This stems at least partly from the current heavy dependence of marine fish larval production on live microcrustacean feeds, most notably rotifers and brine shrimp nauplii. These live feeds are naturally deficient in *n*-3 HUFA and require supplementing with suitable *n*-3 HUFA-rich oils to meet the nutritional requirements of the larvae (Sargent *et al.* 1998). There is a very real requirement in this field for phospholipids rich in *n*-3 HUFA, together with developments in feed technology to deliver these nutrients efficiently to the larval fish. This problem is linked to an even more fundamental limitation in fish farming in sea water, i.e. that the development of primary (algal) and secondary (microcrustacean) production has lagged far behind tertiary (fish) production in sea water. The problem may be more economic than scientific, since advanced primary production technologies for the mass culture of algae and related organisms already exist. Nonetheless, more emphasis on primary production is needed in aquaculture in sea water, i.e. mariculture, and especially on exploiting modern biotechnological expertise with single-cell organisms to generate speciality high-value materials. Such materials include 22 : 6*n*-3 and 20 : 5*n*-3 themselves, together with other valuable fatty acids that have direct applications in human nutrition as 'nutriceuticals', as well as feed stocks for mariculture.

Finally, aquaculture is still in its infancy in terms of stock improvement. Modern genetics, above all molecular genetics whether including genetic engineering or not, has a very prominent role to play here. Maximizing the ability of fish to convert 18 : 3*n*-3 to 20 : 5*n*-3 and 22 : 6*n*-3 has been referred to already. This is but one aspect of maximizing feed conversion efficiencies using a widened range of feed stocks. Enhancing disease resistance and product quality, not least to tailor oil levels and *n*-3 HUFA compositions and contents to suit particular consumer needs, are other priorities in stock enhancement that can bring major rewards. There is in addition a very wide range of fish and invertebrate species, including filter-feeding herbivores, that are candidates for aquacultural development, many of which hold potential for introducing new products, including speciality products, onto the very large and still growing global market for sea foods.

Aquaculture is now growing at over 11 %/year on a global scale (Tacon, 1999). There is every reason to believe that, given continuing development, it may make up for future shortfalls in global capture fisheries.

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