Vol. 1: 187–200, 2011
doi: 10.3354/aei00019

AQUACULTURE ENVIRONMENT INTERACTIONS
Aquacult Environ Interact

Published online March 10

OPEN ACCESS

AS I SEE IT

Resources for fish feed in future mariculture

Yngvar Olsen*

Trondhjem Biological Station, Department of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway

ABSTRACT: There is a growing concern about the ability to produce enough nutritious food to feed the global human population in this century. Environmental conflicts and a limited freshwater supply constrain further developments in agriculture; global fisheries have levelled off, and aquaculture may have to play a more prominent role in supplying human food. Freshwater is important, but it is also a major challenge to cultivate the oceans in an environmentally, economically and energy-friendly way. To support this, a long-term vision must be to derive new sources of feed, primarily taken from outside the human food chain, and to move carnivore production to a lower trophic level. The main aim of this paper is to speculate on how feed supplies can be produced for an expanding aquaculture industry by and beyond 2050 and to establish a roadmap of the actions needed to achieve this. Resources from agriculture, fish meal and fish oil are the major components of pellet fish feeds. All cultured animals take advantage of a certain fraction of fish meal in the feed, and marine carnivores depend on a supply of marine lipids containing highly unsaturated fatty acids (HUFA, with ≥3 double bonds and ≥20 carbon chain length) in the feed. The availability of HUFA is likely the main constraint for developing carnivore aquaculture in the next decades. The availability of fish meal and oil will decrease, and the competition for plant products will increase. New harvested resources are herbivore zooplankton, such as Antarctic krill and red feed, and new produced resources are macroalgae, transgenic higher HUFA-producing plants and bacterial biomass. These products are to a limited extent components of the human food chain, and all these resources will help to move cultured carnivores to lower trophic levels and can thereby increase the production capacity and the sustainability of the production. Mariculture can only become as successful as agriculture in the coming century if carnivores can be produced at around Trophic Level 2, based mainly on plant resources. There is little potential for increasing the traditional fish meal food chain in aquaculture.

KEY WORDS: Global aquaculture · Mariculture · Feed resources · Marine lipids · HUFA · Trophic level

INTRODUCTION

A fundamental question for mankind is if and how agriculture will be able to supply the nutritious food needed by the global human population beyond 2050, when the population is predicted to reach 9.1 billion (Miller 2008, UN 2009). There are signs of sustained, increased food prices in international food markets and the suggested causes are, among others, rising and changing patterns of consumption in large and fast-growing developing countries such as China and India, an increasing trade-off between biofuels and food, and the effects of climate change (Conceicao & Mendoza 2009). There is also a growing concern about the supply of freshwater for agricultural production in the decades to come (Oki & Kanae 2006, CAWMA 2007, Duarte et al. 2009). There are in all events reasonable doubts about the ability to produce the food needed in the decades to come, and this is indeed a major challenge for society.

*Email: ynvar.olsen@bio.ntnu.no

In light of these questions about the future perspectives of agriculture and the fact that harvesting through fisheries has levelled off since about 1990, the Food and Agriculture Organization (FAO 2006) has pointed to aquaculture as the most promising future source for food protein for humans. Freshwater aquaculture is probably the most important form of aquaculture for the time being, but because of the uncertain supply of freshwater, there are indications that future generations will need to develop marine aquaculture in a wider sense. Agriculture, from which some 98% of food energy is produced (FAO 2006), will no doubt be the most important form of human food production for a long time, but the oceans will most likely become more important in the future (Marra 2005, FAO 2006, Duarte et al. 2009). The primary production of terrestrial and aquatic biospheres are of comparable magnitude (Field et al. 1998), and the major difference in their contribution to human food originates mainly in the fact that humans feed some 2 steps higher in the marine food web than in the agricultural food web (Olsen 2002, Duarte et al. 2009). Our major future challenge is to learn to cultivate the oceans in an environmentally and economically sustainable way while moving a major part of the seafood production to lower trophic levels.

Intensive marine aquaculture is technologically quite well developed, but there is a fundamental difference in the developmental stage of agriculture and mariculture. Agricultural technology developed slowly in ancient times but has developed very quickly in the 20th century (Miller 2008). Plant and meat production in agriculture has become gradually more and more predictable and controlled. Through access to cheap fertilizers during the so-called Green Revolution, farmers could more easily produce the surplus plants needed to feed their livestock. The carrying capacity of agriculture increased accordingly, and the food chain for meat production became well controlled.

The food chain of mariculture is, however, not yet controlled. Back in the 1980s, most of the feed resources needed for the cultivation of carnivorous and omnivorous fish and crustaceans originated from pelagic forage fisheries. Thanks to major investments in research, there has been a change in this over the last decade with a tendency towards greater use of agricultural feed resources for both fish and crustacean production (e.g. Gatlin et al. 2007, Naylor et al. 2009). This change has been driven by the limited availability of marine feed resources and the lower production costs obtained with plant resources from agriculture. The strategy of increasing the fraction of plant products in formulated pellet feeds has been successful for aquaculture; it has most likely mitigated a feed resource crisis in global fish and shrimp mariculture and supported a continuous increase in production volumes. It is important that an increased use of plant products as feed ingredients is the main means to move the cultured marine carnivorous species to a lower trophic level, and the trophic level of many cultured species is lower than in nature (Kaushik & Troell 2010, Tacon et al. 2010).

A complete replacement of the marine resources for feed in mariculture is unlikely because most cold-blooded animals suitable for mariculture depend on dietary long-chain highly unsaturated fatty acids (HUFA, with ≥3 double bonds and ≥20 carbon chain length), and most freshwater and diadromous species require generally less HUFA in their diets than carnivore marine fish (Glencross 2009, Tocher 2010). The critical HUFA moieties are mainly found in marine and freshwater food webs and not in oils from terrestrial plants (e.g. Venegas-Calerón et al. 2010). The major marine resource bottleneck for aquaculture is the availability of HUFA found in marine lipids, but the proteins for feed must be increased steadily as well (Opsahl-Ferstad et al. 2003, Gatlin et al. 2007, Naylor et al. 2009).

The availability of feed resources for mariculture will likely become one of the main drivers of the structural development of global mariculture. The use of agricultural resources for aquaculture will strengthen the competition between aquaculture and agriculture for animal production and affect the availability of these agricultural resources for direct human consumption. It should therefore be an ultimate long-term goal to mainly use feed resources taken from outside the human food chain. In a foresight paper, Duarte et al. (2009) concluded that the ocean will become more important for the production of human food in the future. Assuming that the freshwater supply will be a major constraint in global food production, they predicted that agriculture will deliver the majority of plant products for humans in the future, whereas the oceans will deliver the majority of the animal products, which contain marine lipids and are also very important for human health and welfare (Shahidi & Miraliakbari 2005, Venegas-Calerón et al. 2010). There will presumably be a growing long-term evolution towards a reduction in both harvested fish resources and agricultural products in the feed of cultured animals, but this will obviously take time.

The aim of this paper is to evaluate if and how new feed resources can be made available for mariculture over a short- and a long-term perspective and to speculate on how the feed requirements for mariculture can be met by and beyond 2050. The paper aims to draw up a 21st century scenario where food from aquaculture gradually becomes as important for humans as food from agriculture and suggests a possible roadmap for achieving this goal in the decades to come. No efforts are made either to comprehensively review the present situation with respect to the availability of fish meal, fish oils and agricultural products for feed as this has recently been done elsewhere (e.g. Gatlin et al. 2007, Tacon & Metian 2008, Naylor et al. 2009) or to answer comprehensive questions about environmental, ethical and food security issues related to their use (see Kautsky et al. 1997, Alder et al. 2008, Tacon & Metian 2010).

PRESENT CULTURED SPECIES

There are some differences in organisms and their development in freshwater and seawater aquaculture. Fish is by far the dominating product in freshwater aquaculture; only crustaceans have also shown a small increase in production throughout the last decade (Fig. 1A, FAO statistics; www.fao.org/fishery/statistics/global-aquaculture-production/query/en). The pattern of variation in sea- and brackish water is more diverse, with molluscs and marine plants as the dominant and fastest-growing groups in marine and brackish aquaculture, here defined as mariculture (Fig. 1B). Marine plant production has exhibited the fastest growth since ca. 2004. The production of fish and crustaceans has also increased steadily, although at a lower rate. Total production in freshwater and marine-brackish water aquaculture is of the same magnitude (Fig. 1C).

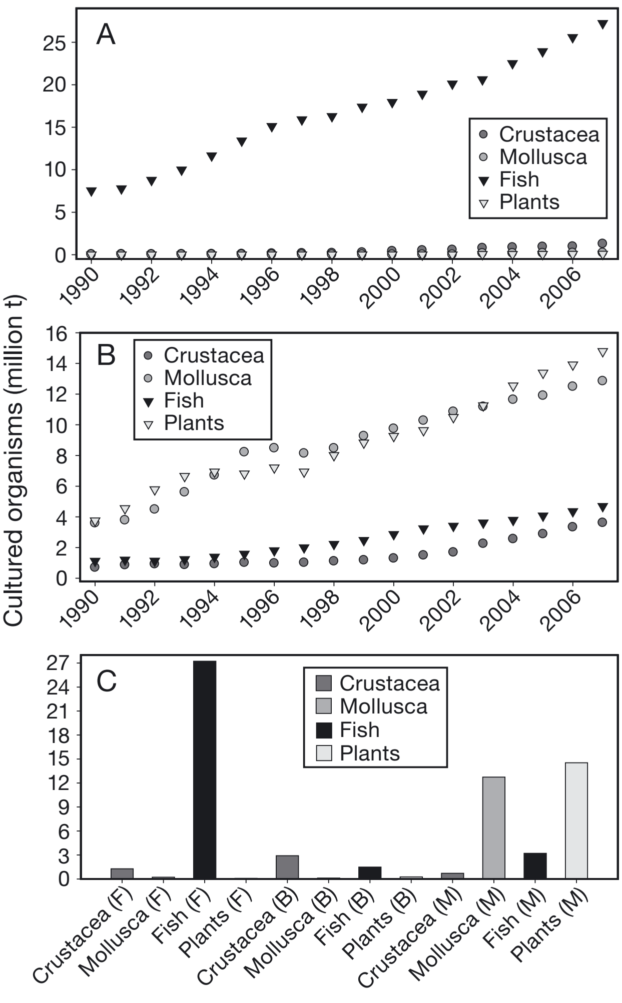

Fig. 1. Developments in the global production of the main groups of cultured organisms in (A) freshwater and (B) marine plus brackish aquaculture over the last 2 decades and (C) distribution among main groups produced in the 3 water types in 2007 (FAO statistics; www.fao.org/fishery/statistics/global-aquaculture-production/query/en). F: freshwater; B: brackish; M: marine

Most of the freshwater finfish production consists of carp species produced mainly in pond cultures in Asia (Fig. 2). Six species of cyprinids and Nile tilapia are annually produced in quantities above 1 million t, and the production yields of these species continue to increase steadily in spite of increasing pressure on freshwater resources in the region (Oki & Kanae 2006, CAWMA 2007), suggesting that the increase is a result of increased intensity during production.

Only diadromous finfish species have exhibited a rapid increase in production in mariculture (Fig. 3D), and Atlantic salmon dominates (1.4 million t in 2007, 30 % of total finfish), being the only finfish produced in quantities >1 million t yr^{-1}. Milkfish production and that of a few more species have increased quite rapidly over the last decade in brackish water, but it is noticeable that most marine species have shown a relatively slow, although steady, increase over the last decade.

The dominating crustacean species in mariculture (Fig. 3C), mostly produced in brackish waters, is white-leg shrimp, which was cultured in quantities of 2.3 million t in 2007 (47 % of total crustaceans, 70 % of total shrimps). Giant tiger prawn was the dominant species up to 2002, but has shown a decreasing trend thereafter (0.59 million t in 2007, 18 % of total shrimps). Three other species (banana prawn, kuruma prawn, and fleshy prawn) are cultured in amounts of more than 50 000 t yr^{-1}.

Molluscs are by far the most important group of marine cultured animals (Fig. 1B), and more than 99 % of the mollusc production is undertaken in marine waters. Pacific cupped oyster was produced in quantities above 4 million t in 2007 and was the dominant species (Fig. 3B). Besides this species, Japanese carpet shell and Yesso scallop were also produced in quantities above 3 and 1 million t yr^{-1}, respectively.

The production yields of marine plants have increased faster than any other group over the past years (Fig. 1B), and Japanese kelp is clearly dominant, exhibiting production yields of around 4.5 million t in 2007 (Fig. 3A). Some other species are produced in quantities around 1 million t yr^{-1}. The increase in production in China has apparently levelled off over the last few years, but other countries have increased their production.

The FAO data accordingly reveal that there are only few a dominant cultured species among all groups in fresh-, brackish-, and seawater. Besides these species, there is a high number of species which are produced in lower quantities (FAO statistics; Duarte et al. 2007), many of these primarily for local markets. These species, and other new emerging species, represent a great potential for future cultivation (Duarte et al. 2007). It is noticeable that the fastest developments in mariculture production are for extractive species of molluscs and marine plants (Chopin et al. 2001, Rie 2004). Freshwater fish species are believed to be less dependent on the nutritional

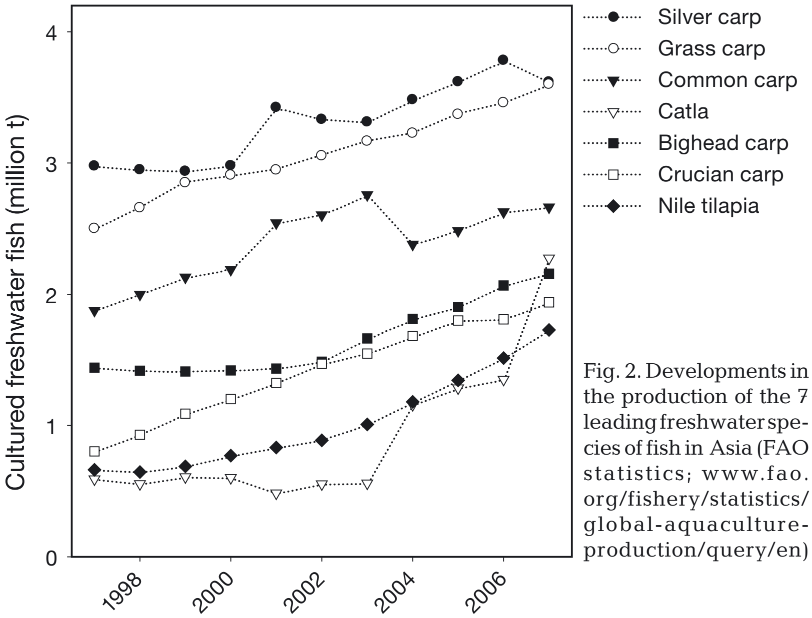

Fig. 2. Developments in the production of the 7 leading freshwater species of fish in Asia (FAO statistics; www.fao.org/fishery/statistics/global-aquaculture-production/query/en)

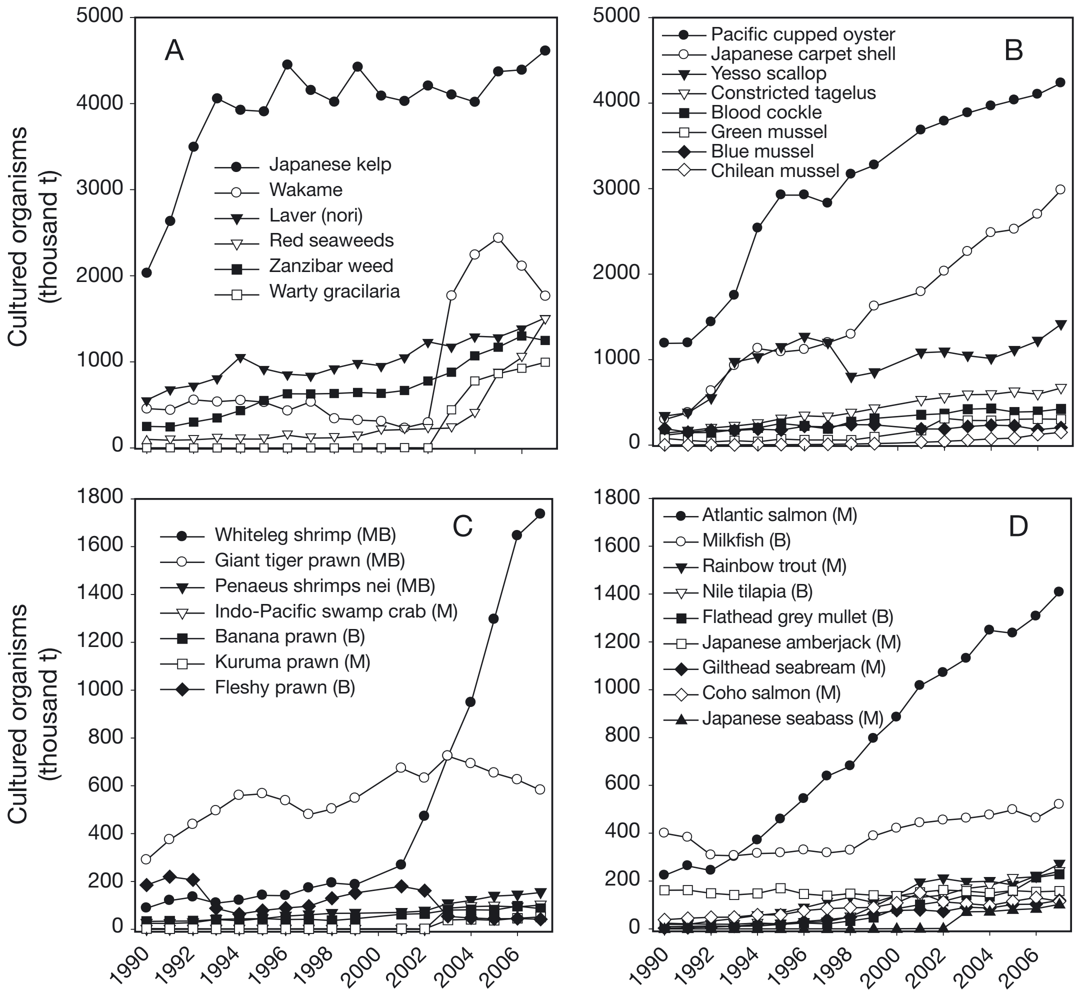

Fig. 3. Developments in the global production of the dominant species of the main groups of organisms in marine (M) and brackish (B) waters. Species of (A) marine plants, (B) molluscs, (C) crustaceans, (D) finfish (FAO statistics; www.fao.org/fishery/statistics/global-aquaculture-production/query/en)

quality of the feed (Tocher 2010), but smaller amounts of fish meal and oil are also used in pellet feeds for intensive rearing of many freshwater species (Tacon & Metian 2008).

TRENDS IN TECHNOLOGY AND TROPHIC LEVEL OF PRODUCTION

The production technologies of freshwater finfish are highly diverse and include production in ponds with pellet feed and in polyculture (land–water interaction) or integrated multi-trophic culture with variable feed input. There is an apparent general trend towards intensified production, and the use of cages has become more common (Table 1, information concerning technology is based on FAO Fact Sheets; www.fao.org/fishery/collection/cultured-species/en). Cultures of low intensity can be fed by freshwater plants and wastes from agriculture, whereas the use of commercial pellet feeds involves low fractions of fish meal and for some species also small amounts of fish oil (Table 1). The estimated trophic positions of cultured cyprinids are in the range of 2.0 to 2.4 (e.g. Duarte et al. 2009, Kaushik & Troell 2010, Tacon et al. 2010). These calculations omit the natural animal live feed consumed by the fish and other animal ingredients in the pellet feed, and values therefore express minimum values. The production technology and trophic positions in culture for milkfish and flathead grey mullet produced in brackish water are similar to those for freshwater carp. They are also herbivore-omnivore, and both are frequently produced using commercial pellet feeds.

The dominant salmonids and marine fish species are produced in sea cages or in land- or coastal-based systems, and they are fed relatively standardised commercial pellet feeds. The fraction of fish meal and fish oil in the pellet feed varies between 36 and 52% (Table 1), meaning that a major fraction of the feed comes from terrestrial resources. The mean trophic positions vary between 2.8 and 3.0, representative of planktivore fish in nature. Other papers report higher trophic positions for cultured salmonids (Kaushik & Troell 2010, Tacon et al. 2010). The values in Table 1 are based on data for salmonids given by Tacon & Metian (2008), and they ignore other animal products in the diet.

The fraction of marine resources in the feed of carnivore fish has been steadily reduced over the last decades. Major European research projects under the Fifth Framework Programme, such as RAFOA (Research on Alternatives to Fish Oil in Aquaculture) and PEPPA (Perspectives of Plant Protein Use in Aquaculture), have demonstrated that significant reductions can be achieved in the levels of fish oils and fish meals in feeds for farmed fish. The ongoing AQUAMAX project (www.aquamaxip.eu) examines the possibilities of reducing both fish oils and fish meals simultaneously. Table 2 (taken from AQUAMAX, www.aquamaxip.eu/content/view/78/118/) reviews the status for 2008 and the AQUAMAX targets for the species studied, suggesting that the fraction of marine resources in diets can be reduced to <25% (Trophic Level 2.5) for marine fish and totally abandoned for carp.

Feed for shrimps contain less fish meal, and in particular less fish oil, than pellet feed for finfish (Table 1). Whiteleg shrimp is produced in ponds at different intensities (Table 1), whereas the nutritional requirements of the more carnivorous giant tiger prawn are comparable to fish. The trophic positions of the 2 species are both based on the global average of fish meal and oil in shrimp feed (Tacon & Metian 2008), and the value is most likely an underestimate for the latter species. Innovations in feeds for fish will likely also affect feeds for shrimps.

All dominant species of molluscs, and all macroalgae, are extractive organisms which are not fed directly. The molluscs are believed to be herbivore-omnivore-detritivore, feeding at a trophic level of 2.2 (10% animal in natural diet, Table 1). Marine plants are primary producers that depend on inorganic resources and energy from light (Trophic Level 1, per definition).

The data compiled in Table 1 suggest that all cultured animal species are provided with some marine resources in their diets, but the quantitative requirements are highest for the marine carnivorous fish species. It is, moreover, likely that low-intensity cultures, like traditional pond polyculture, are less dependent on dietary fish meal and fish oil compared to high-intensity cultures because the availability of naturally occurring live prey per standing stock of cultured animals must be higher there. A further intensification of freshwater aquaculture will then most likely result in an increased dependence on fish meal and fish oils. Another suggestion, apparent from Fig. 1, is that the limited availability of marine products for feeds in the worlds markets already drives the development of species structure in global aquaculture, because primary producers and non-fed herbivore-omnivore animals generally exhibit the fastest growth in production.

ESSENTIAL FATTY ACID REQUIREMENTS

It is likely that proper refinement and adaptation of plant proteins will continue to make mariculture of carnivorous fish and shrimp less dependent on fish meal proteins in the future (AQUAMAX, www.aquamaxip.eu/). The situation is, however, different for lipids, because there are HUFAs such as docosahexaenoic acid

Table 1. Dominant cultured species with a brief review of production technology (FAO Fact Sheets, www.fao.org/fishery/culturedspecies/search/en), fish meal (FM) and fish oil (FO) contents of pellet feeds (% of dry matter, mean, range in parentheses; taken from Tacon & Metian 2008) and estimated trophic position for fish and shrimp fed pellet feeds assuming no other input of animal resources in the feed. Silver carp and molluscs are assumed to have a 10% animal fraction with 10% lipids of dry matter in their natural diets. Trophic position is estimated according to: $\tau_i = 1 + \Sigma_j (D_{ij} \times \tau_j)$, where D_{ij} is the proportion of the prey j, τ_j is the mean trophic level of the prey j (Gascuel & Pauly 2009)

Dominant species	Cultivation systems and feed resources for on-growing in aquaculture	FM in pellet feed (%)	FO in pellet feed (%)	Trophic position in culture	Feeding habit
Freshwater fish					
Silver carp *Hypophthalmichthys molitrix*	Systems: ponds, polyculture Feed: phytoplankton, detritus, conglomerations of bacteria, rotifers and small crustaceans	10[a]	1[b]	2.2	Herbivore, filter feeding
Grass carp *Ctenopharyngodon idellus*	Systems: ponds, polyculture, cage culture Feed: plants, benthic algae, aquatic weeds, terrestrial grasses	1.5 (0–3)	0	2.0 (2.0–2.1)	Herbivore
Common carp *Cyprinus carpio*	Systems: polyculture, integrated culture, ponds Feed: plants, plant wastes, zoobenthos, zooplankton, detritus	5 (3–8)	0	2.1 (2.1–2.2)	Herbivore, omnivore
Bighead carp *Hypophthalmichthys nobilis*	Systems: polyculture, ponds, pens, extensive culture in lakes Feed: plants, phytoplankton, detritus, zooplankton, other invertebrates, blue-green algae	5 (0–20)[c]	0	2.1 (2.0–2.4)	Herbivore, omnivore
Crucian carp *Carassius carassius*	Systems: polyculture, ponds, rice paddies Feed: natural and pellet feeds of byproducts from oil extraction and grain processing, some fish meal	10 (8–12)	0	2.2 (2.2–2.2)	Herbivore, omnivore
Catla *Catla catla*	Systems: polyculture, ponds Feed: natural, aquatic weeds, terrestrial grasses	5 (0–20)[c]	0	2.1 (2.0–2.4)	Herbivore, omnivore
Freshwater/brackish fish					
Nile tilapia *Oreochromis niloticus*	Systems: pond, pen Feed: agricultural byproducts, manures, inorganic fertilizers, and industrial feeds based on e.g. soybean meal or fish meal	6 (0–20)	0.5 (0–10)	2.13 (0–2.6)	Herbivore, omnivore
Brackish/marine fish					
Milkfish *Chanos chanos*	Systems: ponds, pens and cages Feed: phytoplankton and macroalgae, fertilization. Special commercial feeds for milkfish are now almost exclusively used	3 (1–5)	1 (0–2)	2.1 (2.0–2.1)	Herbivore, omnivore
Flathead grey mullet *Mugil cephalus*	System: polyculture in semi-intensive ponds, netted enclosures Feed: natural food, byproducts of grain mills and rice-polishing plants, manufactured extruded pellets	6 (2–10)	2	2.2 (2.1–2.2)	Herbivore, omnivore
Diadromous fish					
Atlantic salmon *Salmo salar*	Systems: cages Feed: industrial pellet feeds prepared from fish meal and oil, with increased fraction of vegetable protein and oil over time	31 (25–40)[d]	21 (15–30)	3.0 (2.8–3.4)	Carnivore, omnivore
Rainbow trout *Oncorhynchus mykiss*	Systems: cages and land-based systems Feed: industrial pellet feeds prepared from fish meal and oil, with increased fraction of vegetable protein and oil over time	30 (15–55)[e]	15 (3–40)	2.9 (2.4–3.9)	Carnivore, omnivore
Marine fish					
Gilthead seabream *Sparus aurata* Linneus	Systems: intensive cage systems, land-based installations, coastal ponds/lagoons Feed: industrial pellet feeds prepared from fish meal and oil, with increased fraction of vegetable protein and oil over time	35 (25–50)[f]	11 (10–12)	2.9 (2.7–3.2)	Carnivore, omnivore
Japanese amberjack *Seriola quinqueradiata*	Systems: cages Feed: formulated pellet feeds (40%) and trash fish/moist pellets	32 (7–70)[g]	8 (1–15)	2.8 (2.2–3.7)	Carnivore, omnivore
European sea bass *Dicentrarchus labrax*	Systems: intensive cage systems, land-based installations, coastal ponds/lagoons Feed: industrial pellet feeds prepared from fish meal and oil, with increased fraction of vegetable protein and oil over time	35 (25–50)[f]	11 (10–12)	2.92 (2.7–3.2)	Carnivore, omnivore
Brackish shrimp					
Whiteleg shrimp *Penaeus vannamei*	Systems: ponds, extensive to super-intensive Feed: natural foods, fertilization, industrial feeds	20 (5–40)[h]	2 (0.5–10)	2.4 (2.1–3.0)	Omnivore, carnivore
Gigant tiger prawn *Penaeus monodon*	Systems: ponds, extensive to intensive Feed: commercial feed	20 (5-40)[h]	2 (0.5–10)	2.4 (2.1–3.0)	Carnivore, omnivore
Molluscs (all species)	Systems: long lines, many different constructions Feed: phytoplankton, detritus, zooplankton	10[a]	1[b]	2.2	Herbivore, omnivore
Marine macroalgae (all species)	Systems: long lines, many different constructions Feed: inorganic components and light	–	–	1	Primary producers

[a]Assumes 10% heterotrophs in natural diet. [b]Assumes 10% lipids in natural heterotrophic diet. [c]Mean values for carp. [d]Values for Norwegian production. [e]Global average for trout. [f]Values for Greek production. [g]Global value for marine fish. [h]Global average for shrimp

Table 2. Current percentages of fish meal and fish oil in feeds of fish farmed in Europe and the percentages targeted in AQUAMAX (taken from www.aquamaxip.eu/content/view/78/118/, last updated August 2008)

Species	Current levels (%)		Targets in AQUAMAX (%)	
	Fish meal	Fish oil	Fish meal	Fish oil
Atlantic salmon	35–45	25–33	12–16	8
Rainbow trout	30–35	20–25	5	5
Sea bream	40–45	15–20	15	10
Carp	20–25	5–8	0	0

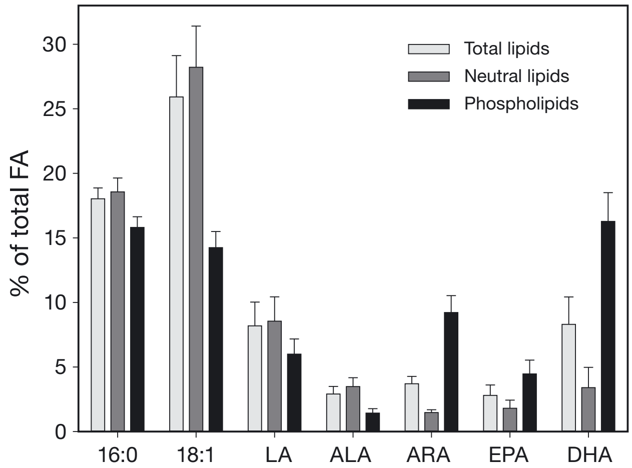

Fig. 4. Contents (%) of dominant total fatty acids (FA) in cultured Chinese carps in total lipids, phospholipids and in neutral lipids (mainly tri-acylglycerides) (data from Kaneniwa et al. 2000). LA: linoleic acid; ALA: α-linolenic acid; ARA: arachidonic acid; EPA: eicosapentaenoic acid; DHA: docosahexaenoic acid. Error bars = 1SE

(DHA, 22:6 n-3) and eicosapentaenoic acid (EPA, 20:5 n-3) of the n-3 family and arachidonic acid (ARA, 20:4 n-6) of the n-6 family that are essential fatty acids (EFA) for many marine animals, but these are not present in oils from higher plants (e.g. Glencross 2009, Venegas-Calerón et al. 2010). Some oils from higher plants can be rich in essential C18 EFA such as α-linolenic acid (ALA, 18:3 n-3), and most of these oils are rich in linoleic acid (LA, 18:2 n-6), which are the precursors of the HUFA synthesis of the respective n-3 and n-6 families. The species which require dietary HUFA for normal growth are those that cannot efficiently enough elongate and desaturate ALA to form DHA or EPA and LA to form ARA (Glencross 2009, Tocher 2010). HUFA are physiologically needed by all animal species as precursors in the synthesis of functional cell membranes, neural tissues (Morais et al. 2009) and eicosanoids, which are hormones with many regulatory functions (Tocher 2010). It is well known that many carnivorous species are incapable or inefficient in synthesising HUFA based on the C18 precursors, whereas many freshwater and diadromous species exhibit better capabilities (Glencross 2009, Olsen 2009, Tocher 2010).

The capabilities of, for example, carp to synthesise HUFA is illustrated in Fig. 4, which shows that DHA dominates in the cell membrane phospholipids of all carp species listed in Table 1 (data from Kaneniwa et al. 2000). The fatty acid composition of their membranes is comparable to those of marine species, although with a somewhat higher LA (18:2 n-6) and ARA (20:4 n-6) content (Kaneniwa et al. 2000, Olsen 2009).

It appears that, like carp, herbivore and detritivore species of shrimps and finfish can generally be cultured on a very high fraction of plant lipids (Table 1; Tacon & Metian 2008, Tocher 2010). As mentioned above, rearing in low-intensive pond systems makes some DHA and EPA available in the carp diets because they may consume some live prey, but it is still most likely that they are also capable of synthesising DHA and EPA from ALA quite efficiently (Radunz-Neto et al. 1996). Carnivore fish species such as rainbow trout and Atlantic salmon may be capable of growing normally with only C18 EFA in their feed, but fish health and viability increase when HUFA is included (Tocher 2010). Some marine fishes such as European turbot appear to be almost incapable of chain elongation and desaturation of C18 EFA (Rodriguez et al. 2002).

In conclusion, HUFA requirements appear to be species and stage dependent (Glencross 2009, Tocher 2010), suggesting that the metabolic capability of undertaking chain elongation and desaturation of ALA and LA to form the respective HUFA is likely a continuum among species rather than an on-off trait. Species with a high capacity for synthesis will likely be more suited in a further expansion of aquaculture as compared to species with an unconditional and high HUFA requirement. This will probably drive the species composition of global aquaculture production towards species with low HUFA requirements and extractive species if new HUFA resources cannot adequately be derived.

The option of producing transgenic carnivore fish and shrimps that no longer depend on a HUFA supply is an alternative strategy for overcoming the HUFA limitations. This approach is controversial, and it can also be a blind path. Tocher (2010) suggested that carnivore fish species generally have the genes needed for HUFA synthesis, but that the genes are inactive. It is therefore a more attractive and less controversial approach to learn how the inactive HUFA synthesizing enzymes of carnivores can be activated to make these species less HUFA dependent (Tocher 2010).

SOME MAIN PRESENT AND FUTURE BIORESOURCES FOR FEED

The above discussion has revealed that a further growth in intensive aquaculture production, and particularly the production of carnivorous marine shrimps and finfish, will require new feed resources containing HUFA-rich marine-type lipids. New research can increase the availability of plant proteins in the short term, but there is a long-term need for more protein resources as well. In my view, the main general challenges for developing mariculture to a major source of food for humans more comparable to agriculture are as follows:

- In the short term (2020), continue the efforts in research and development to substitute fish meal and fish oil with suitable terrestrial plant products to support a steady development in freshwater and marine aquaculture.
- Over a longer time period (beyond 2040), control the feed cycle of mariculture with the aim of steadily reducing the use of feed resources derived from pelagic forage fish and the agricultural food chain of humans.
- Over the short and long term, continue efforts to move the majority of cultured animals down in trophic level in order to increase production capacity and to reduce the required primary production needed per unit weight of animals produced.

The above scenario provides challenges that regrettably are quite ambitious, but the supply of healthy marine and freshwater food for humans cannot approach that supplied by agriculture unless we are able to move most of the mariculture production to a lower trophic level. This is because the metabolic losses through trophic transfers are substantial and because the global primary production that ultimately constrains production is limited (Duarte et al. 2009). Moving the carnivore species to a lower trophic level implies an increase in the fraction of ingredients from primary-producing organisms in the feed, meaning that the species, through adaptation of the feed composition or through metabolic manipulation, will become more and more herbivorous.

Table 3. Sources of fish meal produced globally (2002–2006) and dominant species in its manufacture. Source: International Fishmeal and Fish Oil Organisation (IFFO), www.iffo.net/

Country of production	Fish meal production (t)	Species
Peru	1 714 000	Anchovy
Chile	798 000	Jack mackerel, anchovy, sardine, other
Iceland	224 000	Capelin, blue whiting, herring (including trimmings)
Norway	198 000	Blue whiting, capelin, sandeel, trimmings, other
Denmark	246 000	Sandeel, sprat, blue whiting, herring, other
Other EU countries	210 000	Trimmings, sandeel, sprat, blue whiting, herring, other
China	348 000	Various
Thailand	402 000	Various
USA	300 000	Menhaden, Alaska pollack
South Africa	103 000	Anchovies, pilchard
Other	1 176 000	Mainly anchovy
Total	**5 719 000**	

Harvested feed resources

Fish

Fish meal and fish oil are produced mainly from planktivore fish stocks (pelagic forage fish) from global fisheries with a majority of the catches made in the Southeast Pacific fishing area (Tacon & Metian 2009, Kaushik & Troell 2010) (Table 3). The state of pelagic forage fisheries has been excellently reviewed by Tacon & Metian (2009); the global catches in 2006 were 27.3 million t, corresponding to 29.7 % of the total global landings. The major part of these landings are converted to fish meal and fish oil, which are mainly used as ingredients in feeds for pigs (24 %), poultry (22 %) and for aquaculture (46 %) (Alder et al. 2008). Tacon & Metian (2008) have comprehensively reviewed the use of these resources for species and countries in aquaculture (cf. Table 1). The amount of pelagic forage fish used directly for human consumption in 2006 was 4.6 million t, corresponding to 16.9 % of the landings (Tacon & Metian 2009). For some species and countries, e.g. for jack mackerel in Chile, there is an increasing trend in the production and exports of products for human consumption, but only 0.73 % of the major landing of Peruvian anchovy in Peru is consumed directly. It is my understanding that Tacon & Metian (2009) suggest that there is a general increase in food products as technology, buying power, and product alternatives increase, in agreement with FAO (2006) and Caddy & Garibaldi (2000).

Fish meal and fish oil are the ultimate sources of essential HUFA for aquaculture (Tacon & Metian 2008, Naylor et al. 2009), but the input has been reduced over the last decade, thanks to major research efforts. Cultured fish are gradually moved to a lower trophic level by replacing marine products with plant products. The input of marine resources per fish and shrimp produced have decreased (Tacon & Metian 2008, Naylor et al. 2009, Kaushik & Troell 2010), and the AQUA-

MAX project (www.aquamaxip.eu/) predicts that this process will continue (Kaushik & Troell 2010).

The exploitation of resources based on pelagic forage fish for farming of fish is controversial for many reasons, including environmental concerns about the function of small pelagic fish in the marine ecosystem, threats posed by global change to these stocks, and a broad complex of ethical, food security, and poverty issues (e.g. Alder et al. 2008). I will not go further into these discussions, but it seems clear that pelagic forage fish are taken out of the direct human food chain when they are reduced to fish meal and fish oil. There is apparently little if any significant direct human consumption of fish meal and fish oils (Alder et al. 2008). Fish meal and oil are put back into the human food chain through their use in animal feed, and low feed conversion efficiencies (feed used per fish produced) for many important species (Tacon & Metian 2008, Naylor et al. 2009, Kaushik & Troell 2010) secure at least an efficient use of these resources in aquaculture. With respect to the use of forage fish, Tacon & Metian (2009, p. 5) states that 'market economics and free market access are currently the main drivers that select whether small pelagic forage fish are fished for feed or fished for food', and they suggest that the market may take the best care of these resources, given improvement in fishing and onboard processing techniques. The alternatives proposed to the market approach can be national and international legislation that regulate fisheries, but any change in regime will probably have major socio-economic consequences for many fishing communities.

Discards from fisheries, estimated to be some 20 million t yr^{-1} (Hall & Mainprize 2005), and bycatches and wastes from processing, estimated to be 25 to 30 million t yr^{-1} (Naylor et al. 2009), are both potential sources for fish feed. None of these resources are easily available, but improved logistics in fish processing and an efficient international regime for managing marine catches can make better use of the resources available (Naylor et al. 2009). Nevertheless, none of these resources can alone support a major expansion in mariculture.

Large zooplankton stocks

The world's oceans have large stocks of herbivore copepods and krill that are abundant and potentially exploitable in regions where schools are formed. Siegel et al. (1998) reported a mean biomass of Antarctic krill *Euphausia superba* for the Elephant Island area (off the coast of Antarctica in the outer reaches of the South Shetland Islands, Southern Ocean) during 1977 to 1997 of 1.5 to 31 g^{-1} wt m^{-2}. The standing stock biomass of Antarctic krill is indeed very uncertain, but is estimated to be 500 million t (range 125 to 750 million t, Nicol & Endo 1997), meaning that the annual production must at least be well above 100 million t yr^{-1} (life span 6 yr). Antarctic krill has been harvested for a long time, but the landings are less than 1 million t yr^{-1}, well below the allowed quota of 6 million t yr^{-1} (Naylor et al. 2009). The biomass is now refined into various high- and low-valued products, among them products for fish feed (e.g. Qrill™, krill meal and krill oil products for aquaculture feed, www.akerbiomarine.com/).

The annual production of red feed *Calanus finmarchicus* in the Nordic Seas has been estimated to be in the range of 74 million t yr^{-1} (Aksnes & Blindheim 1996), and ongoing research will improve knowledge about the suitability of this species as a feed resource. The commercial harvesting of red feed is so far very limited, and harvesting is done mainly for research purposes. Research has shown that a general biological principle seems to apply for the *Calanus* species: growth rate of the population is inversely related to the biomass. Simulations using realistic 3D biological models have revealed higher food availability and a rapid restoration of the *C. finmarchicus* stock after a 90% simulated harvesting effort (<2 yr; D. Slagstad, SINTEF Fisheries and Aquaculture, pers. comm.).

It is noticeable that both the stocks of Antarctic krill and red feed exhibit an annual production comparable to the global catches of fish and squid (FAO 2006). Around 10 to 20% of this production represents a marine resource comparable to the landing of pelagic forage fish. Moreover, if herbivore zooplankton replaces fish products in fish feed for carnivore fish, this would imply that the cultured fish would be moved one trophic level down in the food chain (Olsen 2002).

Little data are available on Antarctic krill, but there are major concerns about the role of both Antarctic krill and red feed as food for fish, birds and marine mammals in the Antarctic Ocean and the Norwegian Sea, respectively (Alder et al. 2008, Tiller 2010). The fact that krill, and perhaps also red feed, are important for fisheries and as food for birds and mammals, means that the issue has management and political dimensions that must be thoroughly considered (Tiller 2010). These issues are controversial, but science should nevertheless thoroughly explore the possibilities, constraints and consequences of an alternative strategy for harvesting large zooplankton stocks in the oceans. The political, environmental and ethical concerns of krill fisheries are certainly relevant and important, but these aspects of zooplankton fisheries (Tiller 2010) are not covered here. A fish feed based on zooplankton resources cannot bring the cultured carnivore fish to the herbivore level that is being aimed for, and zooplankton is a limited resource that is harvested and not cultured. Zooplankton resources, however, can provide important ingredients such as HUFA, which are needed for the expansion of mariculture in the near future if such resources can be exploited with acceptable consequences for society and the marine ecosystem.

Farmed feed resources

Agriculture plants

Freshwater aquaculture depends mainly on highly diverse plant resources or wastes from agriculture, with small amounts of fish meal included (our Table 1; Tacon & Metian 2008). As mentioned above, major research programmes have been launched to increase the use of proteins and oils from higher plants in pellet feed for aquaculture (see www.aquamaxip.eu/). Among the important ingredients used to replace fish meal are, for example, corn soybean meal, gluten meal, wheat gluten, peas, and rapeseed meal (Gatlin et al. 2007, Naylor et al. 2009). Oils used to replace fish oil are, for example, rapeseed oil, linseed oil, and palm oil (Opsahl-Ferstad et al. 2003, Gatlin et al. 2007, Naylor et al. 2009; see www.aquamaxip.eu/). This strategy has been successful; it has allowed a further increase in aquacultural production despite a stagnant supply of marine feed resources. Agricultural oils contain only short C18 n-3 and n-6 fatty acids (i.e. ALA and LA) and cannot meet the HUFA requirements of carnivore species. This fundamental physiological constraint will regrettably at some point limit the further incorporation of higher plant oils in feed for carnivores. There is a point at which animal health, welfare and growth will be negatively affected (Tocher 2010).

Higher genetically modified (GMO) plants

Major research efforts have been made by companies and research organisations over the past decade to produce transgenic higher plants (GMO) with the ability to produce HUFAs such as DHA, EPA and ARA (Opsahl-Ferstad et al. 2003, Kim et al. 2009, Nichols et al. 2010, Venegas-Calerón et al. 2010). It is difficult to assess the current progress of this work, but Nichols et al. (2010) reports considerable progress in EPA production among the involved research groups (up to 26% of total fatty acids) whereas DHA yields are still relatively low (up to 3%). Progress has been fast, taking advantage of the modern tools available in molecular biology. An affordable DHA resource from higher GMO plants may completely change the perspectives for the development of global mariculture and animal production in general.

The production of GMO plants will regrettably require space and will therefore compete with the space requirements of agriculture needed for the production of human food. Reliable access to HUFA from GMO plants will, however, to a major extent, help move cultured carnivores to a lower trophic position, and therefore to a better utilisation of global primary production.

Marine plants:macroalgae

The cultivation of marine macroalgae has increased rapidly and was around 15 million t yr^{-1} in 2007 (Fig. 1). In addition, 1.0 million t were harvested from natural resources (FAO statistics; www.fao.org/fishery/statistics/global-capture-production/query/en). Harvested macroalgae have traditionally been used for the production of marine biopolymers, widely used as additives for food and for pharmacological and medical purposes, and for direct consumption by humans in Asian countries (Wikfors & Ohno 2001). Attention has also recently been drawn to macroalgae as a resource for bioenergy (Gao & McKinley 1994) and macroalgae have for a long time been used as feed for molluscs in mariculture (e.g. Robertson-Andersson et al. 2008). Most of the cultivation is undertaken in SE Asia, where one major location is Sanggou Bay, Shandong Province (60 000 t of *Laminaria japonica*; Zhang et al. 2009). The total production for China is 9.7 million t yr^{-1}, corresponding to 66% of the global production in 2007 (Fig. 1).

In contrast to higher plants, marine macroalgae contain HUFA (Radwan 1991, Burtin 2003, Guschina & Harwood 2006). Their lipid contents are relatively low, but macroalgae represent an almost unexploited resource which could serve as a substitute for marine fish oils in feed for marine carnivores. Macroalgae contain variable protein contents, depending on species and nutritional state (Fleurence 1999). They must be carefully refined before use as an ingredient in fish feed, and developments in this area are still to be made. It is worth noting that biofuels from macroalgae will come from polysaccharides, whereas lipids and proteins are the interesting ingredients for aquaculture feed.

Under the appropriate circumstances macroalgae can be produced in dynamic coastal and offshore locations without the addition of nutrients in many temperate or high-latitude regions, which have a short summer period and a high supply of nutrients from the deepwater. Nutrient uptake and growth of many species in these regions mainly take place in the winter and early spring (X. Wang unpubl. results). The warm season can be more important in other regions, and the options for utilising waste nutrient resources from aquaculture to produce macroalgae (integrated multitrophic aquaculture, IMTA) must be further explored

(Chopin et al. 2001). The use of macroalgae-derived compounds as the main ingredients in mariculture feed is very attractive, because it implies that mariculture could take a step towards being self-sustaining, based mainly on feed resources derived from marine plants (Duarte et al. 2009).

Industrially produced single cell biomass (SCB)

Biomass from microalgae

Microalgae can be produced in open culture and raceway systems in tropical regions exposed to high light intensities. A reliable large-scale production of biomass can also be undertaken in advanced photoreactor systems (Xu et al. 2009). For a long time microalgae have been produced as a health ingredient for direct human consumption and as extractable chemicals (Wikfors & Ohno 2001). Cultured microalgae are also an important ingredient in the hatchery production of juveniles of marine fish, shrimps and molluscs (e.g. Reitan et al. 1997, Wikfors & Ohno 2001). Microalgae appear to be nutritionally suitable as a resource for mariculture feed because many species have a high protein content and because the lipids may have a high HUFA content (Guschina & Harwood 2006, Gonzáles López et al. 2010). Their production costs are, however, relatively high, constrained by the ability to supply light as the energy source for biosynthesis. The efficiency of algae to convert light into biomass is low (a few percent; Walker 2009), and this cannot be compensated for by increasing the light intensity, because this will result in photoinhibition and ultimately damage to the photosystems (Falkowski & Raven 2007, Walker 2009). The biomass yields of photoreactors is lower than in algal cultures grown mixotrophically or heterotrophically based on organic substrates (e.g. Sijtsma & de Swaaf 2004).

Microalgae have recently attracted considerable attention as possible sources of bioenergy (Patil et al. 2008, Xu et al. 2009), and major research efforts made to explore these possibilities will probably also be useful for aquaculture. What makes microalgae attractive as an ingredient for aquaculture feed is that some species have high contents of HUFA, in particular of DHA (Sijtsma & de Swaaf 2004, Guschina & Harwood 2006, Mendes et al. 2009). It is possible that lipids from microalgae can be used as high-valued DHA and HUFA ingredients in aquaculture feed, but microalgae will hardly become a major bulk resource for feed. Microalgae can also be a genetic resource for producing transgenic higher plants, macroalgae or yeast (Guschina & Harwood 2006).

A taxonomically different group of DHA-rich microorganisms that can be produced in bioreactors are the thraustochytrids, which are fungoid protists (Rainuzzo et al. 2003, Guschina & Harwood 2006). Some strains can produce high biomass in culture, and oils from thraustochytrids can represent an alternative high-valued DHA source for mariculture in the future.

Biomass from bacteria

Other potential sources for feed in mariculture are bacterial or yeast biomass. A bacterial protein meal produced based on methane from natural gas is a new resource, and feeding experiments with rainbow trout *Oncorhynchus mykiss* using a feed containing up to 27% bacterial protein meal has produced positive results (Aas et al. 2006). The meal has also been found satisfactory for carnivorous warm-blooded animals (Skrede & Ahlstrøm 2002). The bacteria used did not contain HUFA.

An affordable nutritionally adequate SCB containing HUFA and grown based on a cheap carbon waste source, for example methane, could become a major feed ingredient for mariculture. The use of methane is not essential, but this concept for feed production is very attractive because it will close the human waste cycle by allowing food production based on waste deposits, sewage, and natural gas. The critical step is the organism; a suitable organism has apparently not yet been identified and cultured on a large scale, but it is indeed being searched for (Hinzpeter et al. 2006). It is perhaps most likely that a suitable organism will be transgenic and produced using modern genetic methods.

21st CENTURY SCENARIO AND THE WAY AHEAD

A scenario and a roadmap that can allow aquaculture to develop into a major supplier of food for people in the 21st century, comparable to agriculture, are described in this paper. The large aquaculture potential is in the oceans, and in particular in exposed areas of coastal and open seas, but freshwater will be important as well. The main challenge of this development is the availability of feed resources, or more specifically, the availability of lipids rich in HUFA, which are essential nutrients for marine carnivores. Other nutritional components such as proteins are needed as well, but proteins can be more easily made available.

In addition to the provision of HUFA-containing feed resources, there is a need to abandon as far as possible products that are part of the human food chain, because these will be needed directly for human food (Duarte et al. 2009). Second, to move carnivores to a lower trophic level, there is a need to replace most feed components that originate from animals with components from plants and SCB (assuming that bacteria are on Trophic Level 1). There is, finally, an unconditional need to secure the environmental, social and economic sustainability of the new feed resources.

In this scenario, a main priority in the decades to come should be to develop technologies to make HUFA-containing products available from transgenic higher plants, macroalgae and microorganisms. These products will also contain the other essential nutrients needed. Cultured macroalgae can serve as a bulk resource for all nutritional components whereas microalgae can produce selected HUFAs, such as DHA, and other high-cost ingredients for feed. SCB can become a bulk resource for animal feed provided that the nutritional quality is fully adequate and that the future price is affordable, and higher transgenic plants with HUFA can become a main bulk resource.

The above products are to different extents components in the human food chain. Macroalgae are to some degree consumed directly by humans, but SCB are outside the food chain, particularly if HUFA-containing SCB are produced based on methane. Transgenic HUFA-producing higher plants will compete for space in agriculture and will therefore be products in the human chain. Finally, as long as fish meal and fish oil are available, these resources are not direct parts of the human food chain.

The evolution of an aquaculture food chain that has little interaction with the human food chain will take a long time (>2050), and access to animal HUFA resources is paramount during that process. Meals and oils from pelagic forage fish, byproducts of processing, discards from fisheries and harvests of large zooplankton can contribute as HUFA sources towards a self-sustaining aquaculture production, and it is a challenge for science and industry to find the environmentally, socially and economically sustainable way ahead.

An absolute requirement for expanding the output of aquaculture to the levels now achieved in agriculture is to bring the major part of aquatic production to Trophic Levels 1 and 2, as is the case in agriculture (Olsen 2002). The production of macroalgae and molluscs in extractive aquaculture are already at low trophic levels. Fig. 5 illustrates 2 schematic aquaculture food chains and the importance of trophic levels for the future culture of carnivore fish (and shrimps). The food chain on the left-hand side of Fig. 5 is the traditional fish meal-fish oil food chain, common in the 1980s. The primary production input in this food web is that which is theoretically needed to produce the forage fish that are reduced to fish meal and fish oil and used for carnivore aquaculture. Energy is lost through 3 trophic transfers from primary production, ending on 2 units, or 0.2 % of the initial primary production. If, for

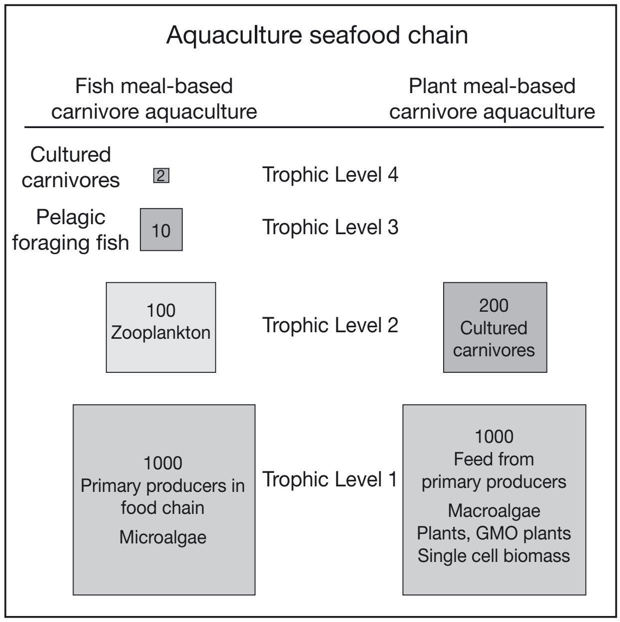

Fig. 5. Fish meal- (left) and plant-based (right) food chains for carnivore aquaculture. All values are relative. Trophic yields are assumed to be 10 % at the low level (Ryther 1969) and 20 % in the last phase that involves controlled culturing of the carnivore. Primary production of the fish meal-based food web should be understood as the primary production of the global ocean needed to produce the actual biomass of pelagic forage fish of Trophic Level 3 needed to culture carnivore species. GMO: genetically modified organism

example, we could double the primary production that is allocated to carnivore aquaculture through forage fish (1000 to 2000), we would still end up with a relative carnivorous production of 4 units, or 0.4 % of the primary production input. If we bring in discards from fisheries and byproducts from processing and double the resources on Tropic Level 3, increasing this from 10 to 20 units, this would have a similar effect. If we take both measures, the carnivore production potential is 6 units, corresponding to 0.6 % of the initial primary production. There is no other apparent way to increase the production beyond this level.

The situation is completely different when carnivores are fed food from Trophic Level 1, i.e. ingredients from plants and SCB (Fig. 5, right-hand panel). The produced carnivore biomass is then 200 units, or 20 % of the initial primary production, which is a 100 times higher yield than for the traditional forage fish food web. Any increase in the initial of primary production will enhance the production potential directly without costly trophic transfers.

These examples are oversimplifications, e.g. there will likely be some animal ingredients included in the plant-based food web, but they still demonstrate that aquaculture can only become as important as agriculture in human food production if the production is undertaken on Trophic Level 2, i.e. when ingredients from plants are the main feed components. This exercise also illustrates that the potential to produce carnivores on Trophic Level 4 is very limited.

The evolution towards a sustainable and self-sustaining aquaculture will be relatively slow, and there will likely be conflicts and competition for fish meal and fish oil in the future. What is important, however, is that there is a vision and a road map towards that vision that could potentially create a better situation for the marine environment, for society and for human welfare. The dependence of aquaculture on pelagic forage fish resources may lessen, but I am afraid that high demands will be made on these resources caused by other uses and driving factors.

The scenario described poses major challenges for policy makers, science and the private sector. There will likely be upcoming cascades of environmental, social, economic, and ethical questions and problems associated with the individual feed products. Optional shortcuts may become apparent, e.g. methods for chemical synthesis of HUFA or artificial photosynthesis of affordable biomass, but unpredicted ethical, health and environmental questions may emerge as well. In my view, science has a particular role to play and responsibility to explore the possibilities, constraints and consequences of the upcoming issues in an open-minded and transparent way as the process of the proposed scenario proceeds.

Acknowledgements. The early ideas behind the present paper were further developed together with European colleagues in the SAMI workshop in Menorca and later in a workshop in Mallorca during the past several years. Further motivation was gathered in the dialog and interactions with colleagues from different continents and with different perspectives in a project and workshop with FAO representatives to discuss challenges posed by the expanding mariculture in exposed waters. I thank these colleagues and others who have helped to stimulate my interests in developing our abiliy to produce more food from the ocean to help feed humanity.

LITERATURE CITED

Aas TS, Hatlen B, Grisdale-Helland B, Terjesen BT, Bakke-McKellep AM, Helland SJ (2006) Effects of diets containing bacterial protein meal on growth and feed utilisation in rainbow trout (*Oncorhynchus mykiss*). Aquaculture 261:357–368

Aksnes DL, Blindheim J (1996) Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. Ophelia 44:7–28

Alder J, Campbell B, Karpouzi V, Kaschner K, Pauly D (2008) Forage fish: from ecosystems to markets. Annu Rev Environ Resour 33:153–166

Burtin P (2003) Nutritional value of seaweeds. Elec J Environ Agric Food Chem 2:498–503

Caddy JF, Garibaldi L (2000) Apparent changes in the trophic composition of world marine harvests: the perspective from the FAO capture database. Ocean Coast Manag 43: 615–655

CAWMA (Comprehensive Assessment of Water Management in Agriculture) (2007) Water for food, water for life: a comprehensive assessment of water management in agriculture. Earthscan, London

Chopin T, Buschmann AH, Halling C, Troell M and others (2001) Integrating seaweeds into marine aquaculture systems: a key towards sustainability. J Phycol 37:975–986

Conceicao P, Mendoza RU (2009) Anatomy of the global food crisis. Third World Q 30:1159–1182

Duarte CM, Marbá N, Holmer M (2007) Rapid domestication of marine species. Science 316:382–383

Duarte CM, Holmer M, Olsen Y, Soto D and others (2009) Will the oceans help feed humanity? Bioscience 59:967–976

Falkowski PG, Raven JA (2007) Aquatic photosynthesis, 2nd edn. Princeton University Press, Princeton, NJ

FAO (Food and Agriculture Organization) (2006) State of world aquaculture. FAO Fish Tech Pap 500. FAO, Rome. Available at www.fao.org/docrep/009/a0874e/a0874e00.htm

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281:237–240

Fleurence J (1999) Seaweed proteins: biochemical, nutritional aspects and potential uses. Trends Food Sci Technol 10: 25–28

Gao K, McKinley KR (1994) Use of macroalgae for marine biomass production and CO_2 remediation: a review. J Appl Phycol 6:45–60

Gascuel D, Pauly D (2009) EcoTroph: modelling marine ecosystem functioning and impact of fishing. Ecol Model 220: 2885–2898

Gatlin DM III, Barrows FT, Brown P, Dabrowski K and others (2007) Expanding the utilization of sustainable plant products in aquafeeds: a review. Aquacult Res 38:551–579

Glencross BD (2009) Exploring the nutritional demand for essential fatty acids by aquaculture species. Rev Aquacult 1:71–124

Gonzáles López CVG, Garcia MCC, Fernandez FGA, Bustos CS, Chisti Y, Sevilla JMF (2010) Protein measurements of microalgal and cyanobacterial biomass. Bioresour Technol 101:7587–7591

Guschina IA, Harwood JL (2006) Lipids and lipid metabolism in eukaryotic algae. Prog Lipid Res 45:160–186

Hall SJ, Mainprize BM (2005) Managing by-catch and discards: How much progress are we making and how can we do better? Fish Fish 6:134–155

Hinzpeter I, Shene C, Masson L (2006) Biotechnological alternatives for omega-3 polyunsaturated fatty acids production. Grasas Aceites 57:336–342

Kaneniwa M, Miao S, Yuan C, Iida H, Fakuda Y (2000) Lipid components and enzymatic hydrolysis of lipids in muscles of Chinese freshwater fish. J Am Oil Chem Soc 77:825–831

Kaushik SJ, Troell M (2010) Taking the fish-in fish-out ratio a step further. Aquacult Eur 35:15–17

Kautsky N, Berg H, Folke C, Larsson J, Troell M (1997) Ecological footprint for assessment of resource use and development limitations in shrimp and tilapia aquaculture. Aquacult Res 28:753–766

Kim SH, Kim SY, Kim JB, Roh KH, Kim YM, Park JS (2009) Biosynthesis of polyunsaturated fatty acids: metabolic engineering in plants. J Appl Biol Chem 52:93–102

Marra J (2005) When will we tame the oceans? Nature 436: 175–176

Mendes A, Reis A, Vasconcelos R, Guerra P, Lopes da Silva T (2009) *Crypthecodinium cohnii* with emphasis on DHA production: a review. J Appl Phycol 21:199–214

Miller FP (2008) After 10,000 years of agriculture, whither agronomy? Agron J 100:22–34

Morais S, Monroig O, Zheng X, Leaver MJ, Tocher DR (2009) Highly unsaturated fatty acid synthesis in Atlantic salmon: characterization of ELOVL5- and ELOVL2-like elongases. Mar Biotechnol (NY) 11:627–639

Naylor RL, Hardy RW, Bureau DP, Chiu A and others (2009) Feeding aquaculture in an era of finite resources. Proc Natl Acad Sci USA 106:15103–15110

Nichols PD, Petrie J, Singh S (2010) Long-chain omega-3 oils—an update on sustainable sources. Nutrients 2:572–585

Nicol S, Endo Y (1997) Krill fisheries of the world. FAO Fish Tech Pap 367. FAO, Rome

Oki T, Kanae S (2006) Global hydrological cycles and world water resources. Science 313:1068–1072

Olsen Y (2002) MARICULT Research Programme. Background, status and main conclusions. Hydrobiologia 484: 1–10

Olsen Y (2009) Lipids. In: Likens GE (ed) Encyclopedia of inland waters, Vol 2. Elsevier, Oxford, p 774–782

Opsahl-Ferstad HG, Rudi H, Ruyter B, Refstie S (2003) Biotechnological approaches to modify rapeseed oil composition for applications in aquaculture. Plant Sci 165:349–357

Patil V, Tran KQ, Giselrød HR (2008) Towards sustainable production of biofuels from microalgae. Int J Mol Sci 9: 1188–1195

Radunz-Neto J, Corraze G, Bergot P, Kaushik SJ (1996) Estimation of essential fatty acid requirements of common carp larvae using semi-purified artificial diets. Arch Anim Nutr 49:41–48

Radwan SS (1991) Sources of C20-polyunsaturated fatty acids for biotechnological use. Appl Microbiol Biotechnol 35: 421–430

Rainuzzo J, Oie G, Alves-Filho O, Aasen IM (2003) Heatpump dried thraustochytrids for enrichment of rotifers. Biomol Eng 20:76

Reitan KI, Rainuzzo JR, Øie G, Olsen Y (1997) A review of the nutritional effects of algae in marine fish larvae. Aquaculture 155:207–221

Rie N (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J Shellfish Res 23:51–61

Robertson-Andersson D, Potgieter M, Hansen J, Bolton J and others (2008) Integrated seaweed cultivation on an abalone farm in South Africa. J Appl Phycol 20:579–595

Rodriguez C, Perez JA, Henderson RJ (2002) The esterification and modification of n-3 and n-6 polyunsaturated fatty acids by hepatocytes and liver microsomes of turbot (*Scophthalmus maximus*). Comp Biochem Physiol B Biochem Mol Biol 132:559–570

Ryther JH (1969) Photosynthesis and fish production in the sea. Science 166:72–76

Shahidi F, Miraliakbari H (2005) Omega-3 fatty acids in health and disease. Part 2. Health effects of omega-3 fatty acids in autoimmune diseases, mental health, and gene expression. J Med Food 8:133–148

Siegel V, Loeb V, Gröger J (1998) Krill (*Euphausia superba*) density, proportional and absolute recruitment and biomass in the Elephant Island region (Antarctic Peninsula) during the period 1977 to 1997. Polar Biol 19:393–398

Sijtsma L, de Swaaf ME (2004) Biotechnological production and applications of the ω-3 polyunsaturated fatty acid docosahexaenoic acid. Appl Microbiol Biotechnol 64: 146–153

Skrede A, Ahlstrøm Ø (2002) Bacterial protein produced on natural gas: a new potential feed ingredient for dogs evaluated using the blue fox as a model. J Nutr 132:1668–1669

Tacon AGJ, Metian M (2008) Global overview on the use of fish meal and fish oil in industrially compounded aquafeeds: trends and future prospects. Aquaculture 285: 146–158

Tacon AGJ, Metian M (2009) Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. Ambio 38:294–302

Tacon AGJ, Metian M, Turchini GM (2010) Responsible aquaculture and trophic level implications to global fish supply. Rev Fish Sci 18:94–105

Tiller RG (2010) New resources in old waters. The potential of national and international conflicts deriving from the future harvest of *Calanus finmarchicus*. PhD dissertation, Norwegian University of Science and Technology, Trondheim

Tocher D (2010) Fatty acid requirements in ontogeny of marine and freshwater fish. Aquacult Res 41:717–732

UN (United Nations) (2009) World population prospects: The 2008 Revision Population Database, available at http://esa.un.org/unpp (accessed Feb 28, 2011)

Venegas-Calerón M, Sayanova O, Napier JA (2010) An alternative to fish oils: metabolic engineering of oil-seed crops to produce omega-3 long chain polyunsaturated fatty acids. Prog Lipid Res 49:108–119

Walker DA (2009) Biofuels, facts, fantasy, and feasibility. J Appl Phycol 21:509–517

Wikfors GH, Ohno M (2001) Impact of algal research in aquaculture. J Phycol 37:968–974

Xu L, Weathers PJ, Xiong XR, Liu CZ (2009) Microalgal bioreactors: challenges and opportunities. Eng Life Sci 9: 178–189

Zhang J, Kupka Hansen P, Fang J, Wang W, Jiang Z (2009) Assessment of the local environmental impact of intensive marine shellfish and seaweed farming—application of the MOM system in the Sungo Bay, China. Aquaculture 287: 304–310

Editorial responsibility: Marianne Holmer, Odense, Denmark

Submitted: July 6, 2010; Accepted: January 31, 2011
Proofs received from author(s): March 1, 2011