

Searching for Solutions in Aquaculture: Charting a Sustainable Course

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Abstract

Aquaculture is currently the fastest growing animal food production sector and will soon supply more than half of the world's seafood for human consumption. Continued growth in aquaculture production is likely to come from intensification of fish, shellfish, and algae production. Intensification is often accompanied by a range of resource and environmental problems. We review several potential solutions to these problems, including novel culture systems, alternative feed strategies, and species choices. We examine the problems addressed; the stage of adoption; and the benefits, costs, and constraints of each solution. Policies that provide incentives for innovation and environmental improvement are also explored. We end the review by identifying easily adoptable solutions and promising technologies worth further investment.

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INTRODUCTION

The global demand for seafood¹ is rising rapidly with a growing population consuming larger amounts of fish in their diets. The world's population more than doubled between the early 1960s and 2008, rising from 3 billion to 6.5 billion, and over this same period, the average annual seafood consumption increased from 9 kg to 17 kg per capita (1). The global population surpassed the 7 billion mark in late 2011, and rising per capita incomes in many countries, especially in emerging

¹In this review, "seafood" includes food produced in fresh, brackish, and saltwater.

economies, spurred further growth in seafood consumption. Most of the additional demand for seafood is now met by aquaculture, as global catches from wild fisheries have stagnated or decreased since the mid-1980s (2, 3).

Aquaculture is currently the fastest growing animal food production sector and is poised to supply over half of the world's seafood in 2012 (3, 4). Global production of cultured finfish, crustaceans, and mollusks rose from 1 million metric tons (mmt) in 1950 to 52.5 mmt in 2008. The growth in aquaculture production has far outpaced human population growth; aquaculture production has increased by an annual average of 8.3% since 1970, while human population has increased by an annual average of only 1.6% (3). In 2008, the production of cultured aquatic plants reached 15.8 mmt in live weight equivalent, further enhancing aquaculture's contribution to world food production (3). Intensification of fish and shellfish production for human consumption will no doubt dominate any growth in wild catch volumes in the future, just as intensification of the world's agricultural and livestock systems—reflected in the use of advanced technology and added inputs to achieve high yields—has generated most of the growth in terrestrial food production during the past half century.

The question we pose in this review is whether or not the aquaculture sector can avoid some of the large resource and environmental problems that have plagued the agricultural and livestock sectors during the past several decades. What technological and management solutions are being developed, or have been adopted in commercial systems, to set the aquaculture sector on a more sustainable path? And what are the main socioeconomic, institutional, health, and technological barriers to adopting these solutions? Our goals are to review the available evidence on a wide range of solutions in aquaculture from the peer-reviewed literature and to identify some of the most promising pathways toward sustainable growth in the future. Our main challenge is to evaluate such a dynamic sector—one that is rapidly growing,

Aquaculture: the cultivation of algae and aquatic plants and animals

evolving, and improving—without being obsolete within the near future.

BACKGROUND

Trends in Aquaculture Production

Descriptions of the characteristics and trends in global aquaculture production can be found in recent reports by the United Nations Food and Agriculture Organization (3) and Bostock et al. (5) and are based on data from 2008. Most aquaculture takes place in freshwater systems in developing countries. Sixty percent of all aquaculture by tonnage is produced in freshwater, 32.3% is in seawater, and 7.7% is in brackish water. Most (88%) aquaculture is produced in Asia, including 62% in China.

Freshwater aquaculture is composed primarily of finfish (54.7% of all aquaculture production by tonnage), most of which are carp species (71% of freshwater production by tonnage) that are farmed in China. Freshwater fish are raised in ponds, lakes, canals, cages, and tanks that range from extensive operations with few inputs, low stocking densities, and little control over production to intensive production systems with comprehensive inputs, high stocking densities, and complete control over all aspects of production.

Marine and brackish aquaculture is composed primarily of mollusks (24.9% of all aquaculture production by tonnage including shell weight), finfish (9.7%), and crustaceans (9.5%) (3). Organisms are cultured in coastal ponds, tanks, cages, and rafts (5), and operations are mostly intensive systems, except for mollusks and seaweed aquaculture, which require few inputs (6, 7).

Although extensive production is currently dominated by small- to medium-scale enterprises with few employees and a relatively small market share, production by intensive operations is increasing rapidly, and consolidation can be seen throughout the supply chain of many internationally traded aquaculture products (5, 8, 9). Commercial aquaculture is still a nascent industry relative to other food

production sectors (10, 11), but the benefits and costs of farming seafood have become increasingly clear.

Social and Environmental Benefits

Aquaculture development has numerous social and environmental benefits. For example, it can play a vital role in ensuring access to affordable seafood and in generating income from the sale of seafood in both developed countries and developing countries (12–14). As of 2008, 10.8 million people relied on aquaculture as a source of income and livelihood, with 94% of them in Asia, and the value of global aquaculture harvests was estimated at approximately US\$98.4 billion (3).

Aquaculture can also provide ecosystem services, such as wastewater treatment (15), bioremediation (16), and habitat structure (17, 18). Aquaculture operations can help to rebuild depleted wild populations through stock enhancement (19) and spat dispersal (20), and scientific research conducted for aquaculture can have spillover benefits for fisheries and marine sciences (21). Because aquaculture can be done under highly controlled conditions, aquaculture products can be guaranteed to contain fewer contaminants and other health risks than wild seafood (22).

Environmental, Resource, and Social Problems

Although aquaculture has the potential to feed millions of people, some types of aquaculture production may severely degrade aquatic ecosystems, pose health risks to consumers, reduce incomes and employment in the capture fisheries sector, and diminish food resources for poor populations. The negative environmental impacts of freshwater and marine aquaculture have been reviewed extensively (e.g., 23–27). Major environmental problems include pollution of nearby aquatic and benthic ecosystems with excrement and metabolites, uneaten feed, herbicides, antibiotics, and other chemicals (28–30); destruction of coastal habitat and

FM: fish meal

FO: fish oil

ecosystems to build aquaculture infrastructure (31); salinization of groundwater and aquifers (32); use of large quantities of freshwater (33); disease and parasite transmission to wild populations (34–36); escaped or introduced organisms that interbreed with wild organisms of the same species or compete for resources with other wild animals (37–39); overfishing of wild fish populations that are caught to produce fish meal (FM) and fish oil (FO) used in aquaculture feeds (26, 40, 41); and depletion of wild fish populations to stock aquaculture operations (42). The severity of these problems varies depending on the type and location of the aquaculture in question (24, 25), but all can harm fishery resources and thus the livelihoods of fishing communities—some of which may also be affected adversely by price competition from the aquaculture sector (43, 44). In addition, the use of wild fish in aquafeeds can have food security implications for low-income households (particularly in sub-Saharan Africa and parts of Asia and Latin America) that depend on low trophic-level (LTL) fish as a key constituent of their diets (45). Finally, farmed seafood may be contaminated with natural and man-made toxins as a result of certain types of aquaculture practices (46, 47).

Solutions, Opportunities, and Limitations to Growth

Despite rapid increases in recent decades, growth in global aquaculture production may be slowing (3). Natural resource limitations and negative environmental impacts are two of the most significant impediments to continued growth in the aquaculture sector (21). There is a global trend toward intensification of farming systems as competition for land and water resources increases; this trend is particularly apparent in China and other Asian countries facing rapid economic growth, high population densities, and limited resource supplies. Life-cycle assessments of aquaculture production indicate higher energy dependency and greater environmental stress with high rates of intensification (48–50).

At the same time, aquaculture is a dynamic sector characterized by investment, technological innovation, market adaptability, and tremendous diversity. In the sections that follow, we examine the literature on current and proposed solutions to the most vexing resource constraints and environmental problems associated with aquaculture production: nutrient and chemical pollution; marine resource dependence via feeds; threats to wild species by farmed-fish escapes, parasites, and diseases; and limitations of freshwater and land resources for aquaculture growth. For each type of solution, we describe (a) the problem(s) it addresses; (b) the stage of adoption (early experimental development, precommercial trial, or adopted at a commercial scale); and (c) the environmental, technological, economic, institutional, and consumer/health benefits, costs, and constraints. The solutions we review fall broadly into three categories: changes to culturing systems, feed strategies, and species selection. In comparing different categories of solutions, our aim is to identify the low-hanging fruit for further development, as well as upstream investment opportunities that entail greater uncertainty but potentially high returns in terms of economic, social, and environmental outcomes.

CULTURE SYSTEM IMPROVEMENTS

Changing the systems in which fish and other organisms are cultured can reduce land use, water consumption, and nutrient and chemical pollution associated with the aquaculture industry. In this section, we review four culture systems that seek to (a) reduce land and freshwater use by recycling water, intensifying production, or moving into the ocean; and (b) reduce nutrient and chemical pollution by treating, converting, or diluting waste (**Figure 1**).

Conventional freshwater and brackish water aquaculture systems are extremely land intensive, but intensifying operations can help produce more fish and crustaceans per unit of land. For example, an extensive pond culture

operation with low stocking density and few inputs produces less than 2,000 kg of fish per hectare per year, but increasing production intensity with artificial feeds, aeration, 10%–40% water exchange per day, and active water mixing in ponds can increase production to 20,000–100,000 kg per hectare per year (33). Actual land use is likely much greater, as these values do not take into account the complete “ecological footprint” of production, including the land needed to grow feed inputs and the land required to absorb wastes from intensive pond production (51). As competition for land increases, aquaculture operations need to intensify production in a manner that reduces the land requirements for fish culture and waste processing.

Water use by conventional land-based systems is also high. Total water use for extensive ponds is about 45,000 liters/kilogram of fish produced, whereas intensive ponds with additional inputs use only 2,700 liters/kilogram (33). Conventional trout raceways use between 85,000–120,000 liters/kilogram, but mechanically aerating the water reduces water use to 16,000–42,000 liters/kilogram (52). Similar to land, competition with other sectors for available freshwater is increasing, and aquaculture operations must intensify in a manner that reduces water use per kilogram of production (3, 53).

Wastewater from aquaculture is composed of uneaten feeds, feces, and bacteria (particulate organic matter), as well as excreted ammonia, nitrite, nitrate, and phosphorus compounds (dissolved inorganic nutrients). If waste products remain in the aquaculture system, they can accumulate to levels that are toxic to fish and other organisms (54). If they are released into the environment, they can change (eutrophicate) aquatic ecosystems, which are often nitrogen and phosphorus limited (24, 55). Because fish are able to assimilate only 10%–50% of the nitrogen and phosphorus available in feeds (remaining nutrients are excreted as feces or diffused across gill membranes) (56), a key question in aquaculture is how to collect and remove or reuse the excess nutrients.

Recirculating Aquaculture Systems

One of the more intriguing strategies for intensifying production while simultaneously reducing wastes is the development of recirculating aquaculture systems (RASs). These systems are designed to collect and remove waste products, uneaten feed, and bacteria from the tank where the fish live so that water can be recycled back into the system (57). RASs can be designed around indoor or outdoor culture tanks or ponds (58). Systems vary in design and construction, but most perform the following key wastewater treatment functions: solid waste removal, nutrient removal or detoxification, carbon dioxide removal, dissolved oxygen supplementation, and bacteria and pathogen sterilization (57). Ongoing research in RASs is reviewed in Martins et al. (59).

Large solid particles of uneaten feed, feces, and bacteria are concentrated and removed by settling or mechanical filtration, and fine particles (<100 microns) are removed by foam fractionation or ozone treatment (solids removal techniques are reviewed in Reference 60). Dissolved nitrogenous wastes are removed in biofilters, which expose wastewater to beneficial bacteria, resulting in nitrification and denitrification. In nitrification, *Nitrosomonas* sp. and *Nitrosococcus* sp. bacteria oxidize ammonia into nitrite. *Nitrospira* sp. oxidize nitrite into nitrate (61, 62). Ammonia and nitrite are toxic to fish at low quantities, but fish can tolerate relatively higher levels of nitrate (56). Long-term exposure to nitrate can be harmful to some fish (63), so many systems rely on a range of different microorganisms to perform denitrification, converting nitrite into nitrogen gas (62, 64, 65).

Because fish and bacterial metabolism strip water of dissolved oxygen and increase concentrations of carbon dioxide, many operations run air through carbon dioxide-rich wastewater to degas carbon dioxide and increase oxygen concentrations (60). Ozone gas and ultraviolet lamps can also be used to kill many bacterial, viral, fungal, and protozoan pathogens before water reenters the culture tank or is discharged (as reviewed in References 66 and 67).

Recirculating aquaculture system (RAS): an aquaculture system that treats and reuses wastewater

RASs offer numerous advantages over conventional aquaculture systems. First and foremost, treating and recycling water allows both freshwater and marine RASs to reduce both water and land use substantially. Freshwater RASs may use as little as 50 liters/kilogram of produced seafood (including water use in feeds) (60). Water usage in marine RASs with artificial saltwater can be as low as 16 liters/kilogram of fish (68). In contrast, water intensity in conventional aquaculture systems ranges from 3,000–45,000 liters/kilogram of seafood (33). Coastal marine RASs that rely on saltwater intake require almost no freshwater inputs. Owing to their low water requirements, RASs can be located on land that is unsuitable for other types of food production, such as in deserts (69), on postmining land (70), and in urban areas (71). This flexibility allows RASs to operate close to markets, reducing shipping costs and transportation-related fossil-fuel emissions (59).

Furthermore, the intensive water treatment that occurs in most RASs protects farmed fish, reduces impacts on marine ecosystems, and produces by-products that can be used by other industries. By removing waste (uneaten food, excrement, and dead bacteria), RASs improve conditions for cultured fish, enhancing feeding efficiency (59) and allowing for higher stocking densities than most aquacultural systems (60, 68). By sterilizing water before it enters the system, RASs remove pathogens and reduce the risk of disease outbreaks (59). When wastewater is sterilized as it is discharged from the system, many RASs also reduce the possibility of fish escapes and the transmission of disease and waste to the surrounding environment (59, 71). Additionally, waste solids removed from RASs are rich in both nitrogen and phosphorus and can be used as agricultural fertilizers (53, 72) or in vermicomposting (73), polychaete production (74), or methane production (75).

The main constraints on developing a RAS at a commercial scale are its high costs of feed, labor, operations, and energy. The majority of RASs have been developed for small-scale operations [<50 metric tons (mt) of output per

year] (59, 60) for both hatchery production (including brood stock, larval, and juvenile rearing) and grow out around the world. Most existing commercial operations produce freshwater and marine species that can be niche marketed at a high-price point, including salmon smolts, ornamental and tropical fish, tilapia, hybrid striped bass, sturgeon, rainbow trout, arctic char, halibut, eel, sea bass, turbot, and African catfish (57). There are few large-scale (>50 mt per year) operations that are able to harness economies of scale in labor, processing, and infrastructure (60, 76). In general, the results have been mixed: Several commercial RAS operations of ~ 50 mt per year in the United States failed in the 1980s and 1990s (60), but some more recent operations have been profitable in Australia and the United States (77–79). High start-up costs combined with uncertain profitability have discouraged investments (59, 60). Despite these drawbacks, RASs do offer some promising economic advantages over conventional systems, including higher stocking densities, year-round production, and reduced water costs (78).

Another major constraint on RAS development is its energy intensity. Because electricity is required to run the recirculating systems, RASs consume much more operational energy than most other types of aquaculture systems (49, 80). Estimates of the total energy consumption of carnivorous-fish RAS facilities (including feed) range from 16–98 kilowatt hours per kilogram (kWh/kg) of fish produced, compared to 7.4 kWh/kg for net pen and 27.2 kWh/kg for flow-through farming of similar species (80, 81).

Other concerns associated with RAS include contaminant accumulation and fish mortality, as well as feed efficiency. Although two recent studies found that contaminants in RAS systems were either undetectable or below harmful levels (68, 82), water reuse may allow contaminants from feed and system components to accumulate in RASs, raising the risk of disease outbreak and potentially increasing farmed-fish mortality (83). Additionally, although controlled and optimized environments in RASs have been

shown to reduce feed conversion ratios, the high cost of building and operating RASs currently favors production of high-value carnivorous fish that require relatively large amounts of FM and FO (59, 60).

Overall, the most critical barriers to widespread commercial development of RASs are their low energy efficiency and the cost of waste removal. The goals to overcome these barriers include reducing energy use or the incorporation of alternative energy sources (e.g., solar and wind), removal of fine solids that reduce nitrification efficiency and water quality, improving nitrification and denitrification systems (including anammox systems that convert ammonia directly into nitrogen gas), and improving systems for the removal of phosphorus. These objectives can be achieved by altering feed inputs, improving energy efficiency, and optimizing conditions for beneficial bacterial growth (59). Other promising approaches include (a) bio-floc technology, whereby the flow rate is greatly reduced, and suspended communities of microbes, called flocs, convert toxic nutrients into biomass that can be consumed directly by fish or shrimp (reviewed in Reference 84); and (b) periphyton-based systems, whereby artificial substrates (e.g., bamboo shoots or poles) are added in a culture system to attract beneficial plant and animal organisms that remove nutrients and provide food for cultured organisms (reviewed by Reference 85).

Aquaponic Systems

Another emerging approach that combines intensive production with waste recycling and water conservation is aquaponic production. Aquaponic production systems join recirculating aquaculture with hydroponics to use nutrient waste from aquaculture as an input to plant growth. Traditional aquaculture systems treat or dispose of nutrient-rich wastewater, whereas hydroponic systems, which grow plants in water without soil, require nutrient inputs (86).

Fish in aquaponic production systems can be raised in ponds, tanks, or other containers. Plants are grown separately in hydroponic

tanks, submerged in water but suspended in gravel, sand, perlite, or porous plastic films, as well as on floating rafts (87). Systems vary greatly in design and construction, but most perform the following key functions: finfish and plant production, removal of suspended solids, and bacterial nitrification (86). Similar to RASs, aquaponic systems remove suspended solids by allowing solids to settle out of suspension in settling ponds or by passing wastewater through mechanical filters. Ammonia is oxidized to nitrite and then nitrate by the same bacteria used in RAS; however, in aquaponic systems, the bacteria are grown either in a designated biofilter (similar to a RAS) or in the hydroponic tanks, on tank substrate and in the roots of plants (87). The nitrate- and phosphorus-rich wastewater is transferred to the hydroponic tanks, where plants absorb the nutrients from the wastewater. The reduced-nutrient wastewater is then reused again in the fish grow-out tank. Aquaponic operations can achieve high fish production densities similar to those in RASs (88).

Nutrient removal and water-reuse rates in aquaponic systems vary widely, depending on the medium used to grow plants, the flow rate, the type of plant, and the ratio of plants to fish (89–91). Nitrate and phosphorus removal rates, for example, range from 9% to 93% and 0% to 53%, respectively (89–91). Water recycling rates as high as 98% have been reported in some systems, translating to water use of about 320 liters per kilogram of fish produced (92). Typical aquaponic systems produce about 7 kg of vegetables for every 1 kg of fish (90).

Recent estimates suggest that there are more than 1,500 aquaponic operations in the United States and an even greater number in Australia (93). This technology is used currently by commercial, research, educational, and not-for-profit organizations, as well as by private hobbyists. Most operations are small in scale (<50 mt per year) (86). Fish species grown in aquaponic aquaculture operations include tilapia, trout, barramundi, murray cod, and various species of perch and carp (94). Plants with low to medium nutrient requirements,

Feed conversion

ratio: measure of an organism's efficiency at converting food mass into body mass

Hydroponics: the culture of plants in water with dissolved nutrients instead of in soil

Aquaponics: the combination of recirculating aquaculture with hydroponics to use nutrient-rich waste from aquaculture as an input to plant growth

Integrated agriculture-aquaculture (IAA):

the combination of agriculture and aquaculture production to generate beneficial synergies

Integrated multitrophic aquaculture (IMTA):

the cocultivation of fed aquatic species and extractive aquatic species, where waste from fed species is utilized by extractive species

Trophic level (TL):

the position an organism occupies in the food chain

including lettuce, herbs, spinach, chives, basil, and watercress, do better in aquaponic systems than more nutrient-hungry species (86). Tilapia and lettuce is the most common aquaponic species combination (87, 93, 94).

One of the main technical obstacles to expanding aquaponic production is the difficulty of creating a system that offers optimal growth environments for fish, nitrifying bacteria, and plants (94). Nitrifying bacteria and most hydroponic plants thrive in different pH ranges, and more research is required to engineer around or find an optimal balance between varying pH requirements (94). Modification of feed ingredients has been proposed to obtain optimal proportions of nutrients for both fish and plants (91).

There are also economic constraints to scaling up aquaponic systems, including the lack of large-scale models and trained personnel available to operate commercial farms (93). In addition, although aquaponic systems achieve significant water-use reductions over conventional aquaculture systems, they require relatively large amounts of land. On average, a square meter of plant growth area is required to treat the water for each 60–100g of fish feed used (87). However, like RAS operations, aquaponic operations can be located on marginal and peri-urban lands, reducing the distance of fish and vegetable products to market. To date, few studies have evaluated the profitability of small- and large-scale operations (as reviewed by References 88 and 95).

Linked to the economic uncertainties of commercial aquaponic systems, there are additional concerns about food safety and consumer acceptance. There is increased risk of cross contamination, including spread of *Salmonella* and *Escherichia coli*, when growing fish and other animals near produce (96, 97), and consumers may also be wary of consuming vegetables grown in fish feces. Aquaponic products are currently ineligible for organics certification, reducing their attractiveness in some high-end markets and/or their profitability.

Similar to aquaponics, integrated agriculture-aquaculture (IAA) combines

two production systems, agriculture and aquaculture, to generate beneficial synergies. Examples include sequential systems (e.g., manure from chickens used to fertilize fish ponds, fish pond sediment and wastewater used as fertilizer for plants, and plant by-products used as fish feed) and polycultures (e.g., carp grown in rice paddies to reduce pests and weeds and to consume periphyton growth on rice stalks) (reviewed by References 5 and 98). Small-scale IAA operations in developing countries can increase household incomes relative to nonintegrated agriculture or aquaculture, but product quality and food safety issues limit IAA's scalability (98). Most research on IAA has focused on increasing production, but IAA operations may also be developed to improve freshwater and energy efficiency (5).

Integrated Multitrophic Aquaculture

A more diverse and less costly approach to waste treatment and ecological management of aquaculture is integrated multitrophic aquaculture (IMTA). IMTA uses coculture of organisms of different trophic levels (TLs) to reduce nutrient concentrations to a point where they do not cause ecological damage, such as eutrophication, harmful algal blooms, or green tides (99). In IMTA systems, various plant and filter-feeding organisms convert waste from fed aquaculture into growth (100, 101). Operations typically consist of a fish or crustacean species (usually finfish or shrimp) that relies on feed, one or two species that extract particulate organic nutrients, and a species that extracts dissolved inorganic nutrients (101, 102). At the top end, fish or shrimp consume feed and excrete organic particles and dissolved inorganic wastes (ammonia, nitrate, and phosphorus) (64). Organic extractive species, typically a shellfish or deposit-feeding invertebrate, are placed down current from the fed species and consume the particulate organic matter from uneaten food and excrement, resulting in higher growth rates than without the input (103, 104). Inorganic extractive species, such as macroalgae, are further down current and uptake nutrients

(ammonia, nitrate, and phosphorus) and carbon dioxide from the up-current species while growing and releasing oxygen (101).

The principles of IMTA can be applied to marine and freshwater operations on land, near the coast, or offshore (102, 105). Commercial, near commercial, or experimental on land and marine IMTA operations currently exist in over 40 countries, including Canada, the United States, the United Kingdom, Chile, South Africa, Israel, Japan, and China (28, 105–107). Numerous combinations of species have been tested in ponds, tanks, and at sea. Although most of these systems have yet to achieve proven commercial success, early results suggest that they may have strong potential. At sea, IMTA with finfish and shellfish can remove up to 54% of total particulate matter (108), and seaweed can remove up to 60% of dissolved inorganic nitrogen and phosphorus (109, 110). In on land IMTA systems, seaweeds have been shown to remove more ammonia than traditional biofilters, although seaweed requires a greater amount of surface area and land (111). The seaweed from IMTA systems can then be used as human food, fertilizer, or feed for other aquaculture species, such as abalone, and shellfish from IMTA can be used as human food. IMTA is economically beneficial in that it generates revenue from nutrients that are otherwise lost and helps farmers diversify their incomes by cultivating multiple species in the same system. Large “multipurpose integrated food and renewable energy parks” that combine IMTA with oceanic energy platforms (wind, underwater turbines) or on land biofuel farms have also been proposed (107). These systems would further incorporate the idea of using waste from one system as inputs for another and also seek benefits from economies of scale.

Despite improved system designs, IMTA still faces difficult constraints. First, the placement of different species in close proximity to each other can amplify pathogen exposure. Pietrak et al. (112) found that mussels bioaccumulate and shed harmful bacteria. Other studies show that some bivalves are not hosts; they can consume parasites (113) or inactivate pathogens

(114). More studies are clearly needed to understand the disease risks of IMTA. In addition, understanding water currents is a key obstacle to IMTA development in the ocean. IMTA relies on currents to move nutrient-rich water from fed species to extractive species. Coastal and pelagic currents can be variable and difficult to predict, depending on the location and time of year (105). Better oceanographic modeling could help improve IMTA siting and operation.

Finally, the economic viability of at sea and on land IMTA remains uncertain; culturing a single species can be difficult, but adding one or two more species increases the risk and uncertainty of production (as reviewed by References 28, 102, 106, and 107). A key obstacle to improving the economic viability of IMTA is assessing and recovering the value of biomitigation performed by IMTA (106, 115). IMTA would be more viable if non-IMTA finfish operations had to pay for discharge (116).

Consumer acceptability of or preference for IMTA-produced seafood would also improve profitability (117). Consumers may be reluctant to purchase shellfish and seaweed that are grown in the waste streams of finfish aquaculture owing to food safety concerns, but education about the risks and benefits of IMTA may change perceptions (107, 115). A growing number of consumers are interested in sustainable seafood products and are willing to pay a premium for them (118); this trend could help overcome the negative perceptions and enhance profitability if IMTA products are sold with ecolabels.

Offshore Aquaculture

On the basis of costs, food safety, and production uncertainties of integrated approaches, an alternative strategy to managing land and water scarcity and waste accumulation is to move aquaculture offshore. There is no broadly accepted definition of offshore aquaculture (119). Proposed definitions are based on various factors, including distance to the coast, remoteness from port, political boundaries,

and physical parameters such as depth and wave height (120–122). In this review, we define offshore aquaculture broadly to include all aquaculture operations that are situated in open ocean-like conditions.

Offshore aquaculture operations culture seaweed, shellfish, and finfish (as reviewed in References 7, 121, and 123–125). Structural components of offshore aquaculture operations vary depending on the species being cultured, but all offshore systems rely on water currents to remove waste and provide clean water and environmental conditions suitable for growth. Additionally, offshore systems must be designed to withstand challenging ocean conditions. There is a robust global commercial aquaculture industry in the coastal zone (125), but there are relatively few commercial farms located in offshore conditions (126). Universities also run or have run several offshore operations for research purposes (127).

Even in this experimental stage of development, it is clear that offshore aquaculture systems offer many advantages. Moving aquaculture offshore removes constraints of land and freshwater availability and reduces conflict with other near-coastal uses (e.g., view sheds, navigation, and commercial and recreational fishing). Although most offshore operations require port access and on land space for logistics, these land requirements are minimal relative to those of other forms of aquaculture. Moving marine aquaculture away from coastal ecosystems may also decrease pollution impacts, as flow rates and dispersal are greater and proximity to coastal flora and fauna is reduced (128). Finally, early evidence indicates that fish farmed offshore are healthier and grow faster (120).

Nonetheless, offshore aquaculture systems also present significant social, economic, and ecological challenges. Land-based aquaculture is typically located on private land, but marine aquaculture is often located in public coastal waters, creating use conflicts and equity issues with other public and private users, including the privatization of historical commons (129–131). The analyses of profitability of offshore aquaculture under present conditions

are mixed (127, 132–135). Offshore operations are capital intensive and have high production costs, which must be recouped in productivity or price increases if operations are to be economically viable (120, 122, 126). Investment is currently stymied by regulatory and operational uncertainties, including permitting, structural engineering, remote feeding tools, mortality retrieval systems, and communications and monitoring systems that allow operations to function offshore (120, 121, 131).

Offshore systems fail to fully resolve many of the environmental concerns associated with conventional coastal systems, including the risk of escaped fish interbreeding or competing for resources with wild fish, aggregation of other animals around offshore structures, and disease and parasite transmission to wild fish (reviewed in References 122 and 128). These problems, and the effects of releasing even diluted quantities of uneaten feed, wastes, and therapeutants, are likely to be reduced when farms move away from the coast and into oligotrophic environments, but to an uncertain degree (128). Although offshore seaweed and shellfish operations do not require feed (7, 123), resource efficiency remains an issue with offshore finfish operations because the high cost of building and operating offshore currently favors production of high-value carnivorous fish (11, 128). The high cost of production is also likely to rely on economies of scale for profitability, and thus favor large-scale operations or suites of operations that have not been evaluated for their impacts on marine ecosystems. Moving offshore increases the distances that support vessels must travel to reach aquaculture farms and therefore increases the fuel use and carbon intensity of production. Finally, the cost of labor may increase as managing offshore vessels and equipment requires skilled employees.

Moving aquaculture offshore is a “technology-driven enterprise” that will rely on research to improve operational and economic efficiency (124). Operating in offshore conditions complicates all aspects of aquaculture operations, and improved automated systems for feeding, grading, removal

of mortalities, monitoring, and harvesting are under development (as reviewed in Reference 124). Offshore operations can also be combined with wind energy or decommissioned oil platforms to reduce costs and capitalize on existing infrastructure (136–138).

FEED STRATEGIES

The efficiency of feed use and the sourcing of feed inputs for aquaculture are among the most important factors determining the economic profitability and environmental impacts of fish farming (41, 139–144). In particular, the use of wild fish in the form of FM and FO as inputs into aquaculture feeds relies on marine species that are renewable but often overexploited for human use. If aquaculture activities consume a greater volume of fish in feeds than they ultimately produce in the final product, they cannot be considered sustainable (41, 143). Not all farmed seafood falls into this category: Aquatic plant production and the culture of bivalve mollusks and some fish (e.g., certain carp species) extract ambient nutrients and planktonic food organisms from the water column and can thus be considered sustainable from a feeds perspective. Aquaculture systems that rely on FM, FO, or whole fish (e.g., tuna ranching) can use (to varying degrees) terrestrial plant- and animal-based proteins and lipids as substitutes, but other environmental issues arise. For example, the production of terrestrial feed ingredients can be associated with high nutrient and chemical input use and loss, land clearing in sensitive environments such as the Amazon, high energy-dependency ratios, and greenhouse gas emissions (144, 145). In short, as in all animal production systems, there is no free lunch regarding feeds for carnivorous and omnivorous fish, crustaceans, and other cultured aquatic animals such as turtles.

On the whole, the aquaculture sector has achieved significant progress in feed efficiency and feed inputs in recent decades. The ratio of wild fish input to total farmed-fish output (fish in to fish out) has fallen well below 1.0, feed conversion ratios have improved, and FM and

FO inclusion rates in feeds have been reduced throughout the aquaculture industry (139, 141, 146). Yet with continued growth in the total volume of farmed fish and crustaceans, the shares of global FM and FO consumed by aquaculture (as opposed to livestock and other industrial uses) were estimated at 60% and 74%, respectively, in 2008—roughly twice the shares that aquaculture consumed a decade earlier (141). Moreover, the proportion of omnivorous aquaculture species raised on diets with some inclusion of FM increased over this period, and FO has remained an important ingredient in aquafeeds for several carnivorous species to maintain fish health and provide long-chain (LC) omega-3 health benefits for consumers (139).

The aquaculture industry is now facing increasing competition for FO by humans consuming FO tablets and companies manufacturing pharmaceutical grade products with considerably higher levels of LC omega-3 fatty acids than have been used in the past. This competition is driving up prices for FO and hurting profits for certain segments of the aquaculture industry (particularly salmon and marine finfish), but also inducing more substitution in feed ingredients. The intersecting dynamics of the pharmaceutical, food supplement, and aquafeed industries is leading to a reversal in the share of global FO consumed by the aquaculture industry from a peak of over 80% in 2007, yet aquaculture still dominates global FO demand (141).

Some key questions loom regarding the ecological and economic sustainability of the aquaculture industry with respect to feeds. Will the demand for FM and FO for feeds, pharmaceutical products, and food supplements deplete wild fishery resources over time? If so, how will the decline affect humans and marine organisms that depend on fish for food? And how will those ecological effects translate to economic impact on different segments of the aquaculture industry?

Global FM and FO production has fluctuated between 5–7 mmt and 0.8–1.2 mmt per year, respectively, over the past few decades,

LC omega-3 fatty acids: the beneficial long-chain (\geq C20) n-3 polyunsaturated fatty acids, which consist mainly of eicosapentaenoic acid (20:5n-3) and docosahexaenoic acid (22:6n-3)

with variations driven mainly by climate variability related to El Niño-Southern Oscillation events and their impacts on forage fish stock abundance (143, 147). Between 20 to 30 mmt of reduction fish (one-quarter to one-third of the global fish catch) are removed from the marine food web each year to produce FM and FO (1). These fish are generally low on the marine food chain (LTL) and include small pelagic fish species, such as the Peruvian and Japanese anchovy, blue whiting, Atlantic herring, and chub and Chilean jack mackerel (147). An estimated additional 5–9 mmt (with a mean of 7.2 mmt) of low-value “trash fish” and other small pelagic fish are used in nonpelleted (farm-made) aquafeeds (148). These fish are also a key constituent of diets for low-income households in many parts of the world.

In natural systems, forage fish play an important role in converting plankton into food for higher TL species, including humans, larger fish, marine mammals, and seabirds. Although LTL fish are often characterized as fast-growing and resilient, analyses of stock assessment and global landings data for hundreds of species show that up to twice as many fisheries for small, LTL species have collapsed during the past half-century than for higher TL predators in the oceans (149). This result reflects high catch limits for LTL fish set by fisheries managers irrespective of large population fluctuations caused by climate variability (El Niño-Southern Oscillation events) and overfishing as fisheries managers often assume. Even temporary collapses can have widespread ecosystem effect (149). On the basis of ecosystem model results, Smith et al. (150) suggest that LTL catch volumes have to be reduced by 20% to protect higher trophic marine species in most regions. Today, most forage fish populations are either fully exploited, overexploited, or recovering from overexploitation (40). Addressing the threat of overexploitation of wild fisheries for reduction thus requires a focus on improving feed efficiencies and on replacing FM, FO, and other unsustainable fish inputs (such as trash fish) in aquaculture diets (139, 143, 151, 152).

Commercial Replacement of Fish Meal and Fish Oil

Three main categories of FM and FO replacements are available at commercial scales or are under commercial development: terrestrial crop products, rendered terrestrial animal products, and seafood and aquaculture processing wastes. Several recent reviews assess these alternative feeds in terms of their economic, ecological, and nutritional impacts (for example, References 139, 141, 143, and 153–156). To be a viable alternative for FM and FO, a candidate ingredient must possess certain characteristics, including nutritional suitability; ready availability; competitive pricing; and ease of handling, shipping, storage, and use in feed production. The nutritional quality of alternative feeds is important because it influences feed efficiency, fish growth, stress tolerance, and disease resistance—and hence the use of antibiotics in culture systems. Essential fatty acids in aquafeeds (in particular the LC omega-3 fatty acids) are a critical element for fish and human health and have been reviewed at length (154, 156, 157). Proteins and lipids in feeds are typically selected on the basis of fish health and performance, consumer acceptance, minimal pollution, ecosystem stress, and human health benefits. Economics also plays an important role, and prices for fish and nonfish feed have recently exhibited substantial volatility. Given limited supply and increasing demand, FM and FO prices are likely to rise in the long-term—a trend that is already facilitating the substitution of nonfish alternatives (139, 143).

Terrestrial plant alternatives. Partial replacement of FM by alternative plant proteins has been achieved in several omnivorous and carnivorous species at the commercial scale, and complete replacement has been achieved for numerous omnivorous species in research studies. FM inclusion rates in aquaculture feeds for some carnivorous species, such as salmon, trout, sea bream, and sea bass, have fallen by one-quarter to one-half since these species

began to be commercially farmed (143). In fact, recent feeding trials show that after the early juvenile stage, Atlantic salmon can grow just as well on all-plant protein diets as on combination plant-animal protein diets (158).

The range of plant-based protein concentrates suitable for aquafeeds includes products from barley, canola, corn, cottonseed, peas/lupines, soybeans, and wheat. Of these, soy-protein concentrates dominate the commercial market; wheat-protein concentrates are also suitable from a nutritional standpoint but have some processing constraints. Corn gluten meal is used widely in aquafeeds; however, owing to its limited amino acid profile and non-soluble carbohydrate content, it has limitations as a substitute for FM (143, 156). Dry distiller grains from corn-based ethanol production can also be used in aquafeeds, but their excess fiber, low solubility, and inadequate crude protein content make them noncompetitive in the culture of many carnivorous farmed species (143).

In general, plant feedstuffs tend to have a lower crude protein content than FM (with the exception of the more expensive, high-protein concentrates), and more indigestible organic matter in the form of insoluble carbohydrates and fiber, leading to higher levels of fish excretion and waste. Moreover, certain minerals in plant products, such as phosphorus, cannot be absorbed by fish. However, advances in fish nutrition, feeding, and dietary manipulations have substantially reduced waste production and increased the nutrient utilization and growth efficiency of farmed aquatic organisms raised on plant feeds (159). Improvements in this area continue to be made through classic breeding, transgenic manipulation, exogenous enzyme treatment, supplementation with additives to compensate for limiting nutrients, and postharvest processing technologies that enhance the quality of plant protein concentrates, as well as through advanced genetics and genomics techniques to develop modified strains of aquatic organisms that can tolerate higher levels of plant feedstuffs in the diet (as reviewed by References 139 and 160).

Terrestrial plant products can likewise be used to substitute for FO in aquaculture feeds. During the past decade, there has been a rise in the use of plant oils (e.g., canola, soy, flax, and palm oils) in aquafeeds. This rise has been driven largely by rising FO prices in world markets, although highly volatile crop prices have made price ratios between fish and vegetable oils unpredictable since 2005. Plant-based oils are an attractive FO substitute because they can be produced in large quantities to meet current and future demands by the aquafeed industry. On the down side, however, vegetable oils do not contain LC omega-3 (n-3) fatty acids; instead, they generally have high concentrations of the short-chain oleic (18:1n-9), linoleic (18:2n-6), and in some instances α -linolenic acids (18:3n-3) (156). The shift from LC omega-3 oils to oils containing short-chain (<C₁₈) fatty acids in fish diets has negative implications for both fish health (as reviewed by Reference 154) and consumer health. As a result, terrestrial plant oil and FO blends are commonly used in commercial aquaculture diets, with the blending ratio determined by price, stage of production, and desired consumer outcomes.

Rendered animal products. Another commercially viable substitute for FM and FO in aquafeeds is the suite of products rendered from terrestrial animals, such as meat and bone meal, feather meal, and poultry by-product meal (as reviewed in Reference 139). These products are readily available and economically competitive relative to plant- and fish-based proteins. Compared to vegetable proteins, animal by-product meals have a more complete amino acid profile (e.g., high levels of available lysine), and their digestibility has increased over the past 30 years owing to improved processing techniques. Lipids from terrestrial animals are also relatively inexpensive; however, they are high both in saturated fats and in short-chain omega-6-polyunsaturated fatty acids (as opposed to the healthy LC omega-3 fatty acids). Moreover, animal lipids have low digestibility at cold temperatures and must be

blended with polyunsaturated fats to facilitate digestion. Using an animal-plant lipid blend during grow out, in combination with finishing diets containing FOs high in LC omega-3 fatty acids, can help achieve the health benefits valued by consumers (139). Thus, the use of animal lipids in aquafeeds can contribute to a reduction in the use of FO but is unlikely to provide a complete solution.

Reports are mixed on the extent to which terrestrial animal by-product meals and oils are used in aquafeeds today. In Australia and New Zealand, there has been significant replacement of FM and FO by rendered animal products in aquafeeds (161). For example, it is estimated that poultry fat has replaced 75% of the FO formerly included in Australian farmed Atlantic salmon diets (personal communication, Richard Smullen, Ridley Aquafeed, January 31, 2012). Other accounts, however, suggest that rendered animal meals and oils contribute less than 1% of total compound feed production for aquaculture worldwide (not including farm-made feeds from livestock products) (141). Their low use in many areas, particularly the European Union, is attributed in large part to regulations and social concerns associated with the risk of disease transmission (i.e., mad cow disease or bovine spongiform encephalopathy) and the lower health value of the n-6 fatty acids as compared with LC omega-3 fatty acids. Although the risk of transmissible spongiform encephalopathy disease transmission via fish is remote (139), it is unclear how widely rendered animal products will be used as a replacement for FM and FO within the global aquaculture industry in the future.

Fish processing wastes and bycatch. Alternatively, a growing volume of aquaculture processing waste is now being used in aquafeeds in many locations. The recycling of wastes from the aquaculture sector has potential to reduce both fishing pressures on wild populations and pollution from the aquaculture industry. Any successful business that utilizes seafood processing wastes must have a stable supply of raw material (162), which the aquaculture industry

can provide. Although data on the global production of FM and FO from farmed- and wild fish and shellfish by-products are not readily available, it is estimated that ~6 mmt of trimmings from food fish are used for this purpose and that roughly one-quarter of commercial FM is now made from fish processing wastes (as reviewed by Reference 141). These numbers most likely underestimate the amount of trimmings available from the processing of farmed shrimp, crab, salmon, tuna, tilapia, trout, and catfish, as well as other major aquaculture activities worldwide (141). Indeed, the availability of processing wastes will increase significantly in the future as the aquaculture sector expands.

When aquaculture trimmings are combined with processing wastes and bycatch from wild fisheries, the available fish biomass for feeds is substantial (162). Estimates of fish wastes from industrial seafood processing plants range from 50% to 75% of the total catch volume (as reviewed by Reference 162); an amount that, aggregated over the entire global fishing industry, far exceeds the total biomass of forage fish captured each year (20–30 mmt) to produce FM and FO. However, despite the obvious potential for recovery of wild seafood processing wastes, barriers to its utilization still exist (163). Constraints include nutritional factors that limit farmed-fish growth and performance, infrastructure, transportation costs for moving processing wastes from remote locations (seafood by-products are highly perishable), and contaminants (polychlorinated biphenyls, dioxins, and heavy metals) in some seafood by-products that have the potential to bioaccumulate in farmed fish (139, 151). Moreover, using bycatch for feeds remains controversial because of its potentially deleterious effects on wild fisheries through relaxed bycatch regulations.

Fish Meal and Fish Oil Replacements in Experimental and Early-Development Phases

As the aquaculture industry continues to expand and consume the majority of global FM and FO production, novel technologies and products

fostering alternative protein and lipid sources are also on the rise. One category of innovations includes new genetic and metabolic engineering techniques to produce LC omega-3 fatty acids. Other categories encompass the development of single-cell organisms (SCOs), krill, polychaetes, insects, and other lesser-used feed inputs, such as macroalgae (139, 152). The most exciting innovations are aimed at producing FO replacements in aquafeeds to ensure a healthy product that will be valued by consumers. Although protein sources in feeds are a growing concern for aquaculture producers in a competitive and high-priced economy, replacing FO is likely to be more challenging, on a global basis, than replacing FM (139, 141).

The development of SCOs as a source of LC omega-3 fatty acids for feeds is one of the more promising areas of research (152, 164). SCOs, such as heterotrophic dinoflagellates, thraustochytrids, and some species from other algal groups, have been successful in shrimp feeds. However, the high cost of SCO and/or biomass production in large-scale fermenters currently constrains their widespread use in most aquafeeds—particularly for salmonids and marine finfish that have high oil requirements throughout their life history (139). A potentially cost-effective approach is to use SCOs in finishing diets for the final 6–12 weeks of fish growth, which enhances the LC omega-3 fatty-acid content and thus the value of the final product. There is also mounting interest by the biofuels industry in development of microalgae as a feedstock, which could help reduce production costs of SCOs to the aquaculture industry over time (139, 164). Linked to this area of research is the development of bacterial or yeast biomass for mariculture feeds (152). DuPont announced a new genetically modified (GM) yeast-based feed ingredient for salmon in 2011 and has partnered with AquaChile to scale this feed source to the commercial level (165). With multiple patents covering this new product, little public information is available on its cost or performance to date.

Genetic and metabolic engineering techniques can also be used to achieve the benefits

of LC omega-3 fatty acids with various other plant-based feeds. At the experimental level, the use of vegetable oils that contain biosynthetic precursors, such as the short-chain omega-3 fatty acid and stearidonic acid (18:4n-3), in aquafeeds can be used for salmonids to elevate this fatty acid in fish and also elevate levels of LC omega-3 fatty acids in tissues. However, conversion of stearidonic acid to LC omega-3 fatty acids varies among species (salmon > trout) and life stage (salmon fingerlings > postjuveniles in sea water), and this process is less efficient than obtaining LC-omega-3 fatty acids from FO in terms of elevating LC-omega-3 levels (151; personal communication, Ronald Hardy, University of Idaho, February 1, 2012). Early feeding trials were performed using *Echium* oil, and higher levels of stearidonic acid are now available in GM soybean (164).

Another approach under development is the GM (microbial gene insertion) of land plants, such as canola and soy, to produce LC omega-3 fatty acids (152, 164, 166). Such research initially led to modest increases in LC omega-3 fatty acids in a number of land plant species; more recently, much higher levels have been achieved in a range of model plants (167, 168). These developments indicate that the achievement of sufficiently high concentrations of LC omega-3 for substantial or even full replacement of FO may be anticipated within the coming decade (164).

A more immediate avenue for enhancing LC omega-3 fatty acids and proteins in aquaculture feeds is the use of marine zooplankton [e.g., herbivore copepods (red feed) and krill], polychaetes, other worms, and insects. Among these organisms, krill is the most widely developed in aquafeeds to date (141). Several species of krill, especially Southern Ocean *Euphausia superba*, have the potential to provide significant quantities of high-quality protein, lipids, and other nutrients. Constraints on expanding krill use in feeds include product variability, high perishability, and potentially serious ecosystem impacts (as reviewed in Reference 139). The fatty-acid profile of krill oil can vary by twofold depending on the

SCO: single-cell organism

GM: genetic modification or genetically modified

region, season of harvest, and interannual variability. Because these highly unsaturated fatty acids are prone to rapid oxidation—and hence perishability—suitable collection, storage, transport, and processing conditions are needed to prevent or minimize oil and meal degradation. In addition, marine zooplankton like krill and red feed are extremely sensitive to climatic variation and play a major role in supporting marine food webs (152). As a result, supply and price variability is a concern for feed manufacturers, and overharvesting is a concern for the environmental community.

Another innovation in aquafeeds is the use of polychaetes, or marine worms. In some sense, this feed source—the worm—is also one of the most traditional forms of bait in freshwater and marine fisheries. Research on polychaetes for aquafeeds is not new, yet its potential to supply LC omega-3 fatty acids is gaining recognition as aquaculture consumes the majority of global FO. Much of the published research on polychaetes has focused on shrimp feeds because of its suitable nutritional balance (169–171). Recent trials have also been conducted on trout, yet results are inconclusive to date and depend heavily on the feed formulation, as well as on how the worms are harvested and preserved prior to their use in feeds (personal communication, Ronald Hardy, University of Idaho, January 26, 2012). Although this area of research is still nascent, it can be incorporated into RAS and IMTA systems and also has promise to relieve pressure on marine fisheries by supplying a renewable source of protein and LC omega-3 fatty acids.

SPECIES SELECTION

Environmental impacts and resource constraints associated with effluents and feed requirements can also be addressed by changing the species being cultured. In this section, we review the advantages and disadvantages of selective breeding, GM, and culturing organisms at lower TLs. These practices are being pursued to varying degrees in both commercial and experimental systems.

Selective Breeding

In selective breeding, organisms with desirable traits are selected from a larger population and are interbred to produce offspring with similar or improved traits. Selective breeding techniques for fish have been reviewed extensively (e.g., 172, 173). Historically, breeding programs have focused on improving economically important traits, such as growth rate, feed conversion efficiency, age at sexual maturation, disease resistance, and product quality (e.g., muscle color, fillet size, and fat content), with the majority of research focused on increasing growth rates. Selection for faster growth has resulted in increases of 10%–20% per generation, effectively doubling growth rates in four to seven generations. The successes of breeding programs for several species, including salmon, tilapia, carp, catfish, and shrimp, are reviewed in Reference 172.

While selecting for increased growth, many correlated traits are altered that have environmentally beneficial implications, including increased feed conversion efficiency, improved digestion of alternative feed ingredients, and increased disease resistance. Feed conversion ratios in salmon decreased by 20% over five generations in breeding programs focused on growth rate (172). Breeding programs to select for growth and feed efficiency in FM and FO diets also work for selecting fish that perform better with soy-based feeds, reducing reliance on fish products as dietary inputs (174). Survival and disease resistance can be difficult to select for as fish must be exposed to pathogens to test resistance, but growth correlates positively with survival and resistance to many diseases. Increased genetic resistance to disease can help reduce the need to use antibiotics and other chemicals to treat disease and pathogen outbreaks (175).

Domestication of aquatic organisms for aquaculture is new relative to terrestrial organisms (176), and selective breeding is not widely used in aquaculture, despite a high cost-to-benefit ratio. It was recently estimated that only 10% of all aquaculture production uses

breeding programs (172, 177), meaning there are substantial opportunities for use of selective breeding to meet both economic and environmental goals.

Despite its potential, selective breeding also amplifies the ecological damages caused when selected fish escape and interbreed with wild fish of the same species (as reviewed in Reference 39). The risks to wild fish populations of interbreeding with selected fish include reduced genetic variability, which in severe cases can lead to extinction of wild genotypes, and outbreeding depression, which can produce wild-farmed hybrids with reduced fitness (as reviewed by Reference 178).

Molecular techniques are increasingly being applied to breeding programs to help improve the efficiency and precision of selection (179). Genetic markers can help identify parentage in breeding programs, helping to avoid inbreeding. Genetic maps can assist in the identification of genome sections that are related to important traits, further helping farms select fish with desirable traits. Microarray technology can also locate up- or downregulated genes under different culture conditions, which assists breeding programs identify genes associated with desirable traits (as reviewed by Reference 180).

Genetic Modification

Gene transfer technology, a form of GM, is currently under development for several fish to modify specific traits, although no commercial fish have gained regulatory approval. Unlike selective breeding, which relies on natural genetic variability, GM artificially alters the genome of one species with genetic material from different species. Several gene transfer methods have been tested on fish, but microinjection, whereby a DNA segment is inserted into a fertilized egg, is the most common (see Reference 181 for a review of gene transfer methods and results). Similar to selective breeding, most gene transfer programs have focused on improving commercially important traits (e.g., increasing growth rates, disease resistance, carbohydrate metabolism, and flesh shelf life) (181).

The most common form of GM in fish has been the insertion of growth hormone (GH) genes from mammals or other fish species. GH genes have been used extensively in carp, catfish, tilapia, and other commercially important aquaculture species, but the most substantial growth increase has come from salmonids, which have shown 5–30-fold increases in growth rates (180). For instance, Atlantic salmon, with a GH gene from Chinook salmon and an antifreeze protein promoter from ocean pout, is currently under regulatory review in the United States and reaches market size in half of the time required by nontransgenic salmon (182). Cold-water species, such as salmon, appear to respond better to GHs than warm-water species, which grow throughout the year and are likely less sensitive to GH regulation (180). Increases in growth rates are also greater when compared to wild fish than with selected strains (180), indicating that advanced selective breeding programs and GH gene insertion may be modifying similar cellular and physiological mechanisms to increase growth (181).

Insertion of GH genes typically alters other traits in addition to growth rate (due to pleiotropy); many of these traits have positive environmental and resource implications. Feed conversion efficiency increases have been shown in GH tilapia and salmonids, reducing use of FM and FO. Changes in immune system function and disease resistance can be both positive and negative, with some studies showing increased resistance to pathogens and others showing diminished resistance or no effect (as reviewed in References 181 and 183). Nutrient assimilation may also increase, resulting in nitrogen and phosphorus waste reductions of 50%–60% in tilapia with GH genes (184), reducing the nutrient concentrations of farm effluent.

There is substantial public opposition to development of GM fish because of the potential environmental and human health risks (185). GM fish can escape and interbreed with wild fish, resulting in three potential outcomes: The transgene can be disadvantageous and is eventually eliminated from the

GH: growth hormone

wild population; it can invade a population and eventually eradicate the wild genotype; or it can extirpate a population by dissemination of a nonviable “Trojan gene” (as reviewed in Reference 186). Pathogen-resistant GM fish could also accumulate and spread pathogens to wild populations (183). The risk of escaped GM fish interacting with wild fish can be reduced by building biosecure on land facilities and by sterilizing cultured fish (182). Although success rates of different sterilization techniques are high, a 100% sterilization rate is currently not viable (187–189). Depending on the nature of the modification, GM fish could produce toxins and allergens that are harmful to humans (as reviewed in References 183 and 190). The full benefits and costs of GM fish remain uncertain, complicating regulation and reducing investment in GM development (191, 192).

Farming Down the Food Chain

The culture of lower TL species is often advocated as a means to reduce FM and FO demand by the aquaculture sector, lower land and water requirements through greater stocking densities, and reduce wastes to the environment. Aquatic plants (TL 1), mollusks (TL 2), and herbivorous and omnivorous finfish (TL 3) make up the majority of aquaculture production (193). In many cases, omnivorous fish, such as carp, tilapia, and catfish, are fed small amounts of FM (146), but the majority of FM used by aquaculture is fed to shrimp (27.2%) and marine and anadromous fish (32.5%) that have higher TLs (141). Shrimp and marine and anadromous finfish consume almost all FO used in aquaculture (141).

Duarte et al. (11) estimate that a 0.4 unit decrease in the mean TL of marine aquaculture would afford a doubling of production for the same amount of primary productivity (and associated FM and FO). Reducing the demand for FM and FO by farming lower on the food chain would help support marine food webs, but calculating these effects based on mean TL alone can be misleading. When the range of (as opposed to average) TLs of fish in and fish out

are assessed, the most commonly farmed freshwater fish (carps, tilapia) and even most marine and diadromous farmed fish are roughly at the same TL as the fish from which a portion of their feeds is based (147). High-TL species have been widely identified in aquafeeds (194), raising concerns about the ecosystem effects and use of trash fish in feeds, but this also reflects some use of fish and shellfish processing wastes in feeds.

Lower-TL freshwater fish, such as carp and catfish, can also be cultured at greater densities than carnivorous marine and anadromous fish, as they have evolved in oxygen-poor and nutrient-rich environments (56). As a result, farming lower on the food chain reduces pressure on land and water resources used directly by aquaculture, not just the pressure on fisheries resources. Farming at the lowest TLs—aquatic plants and mollusks—also provides bioremediation services and lessens the overall effluent burden from aquaculture; however, filter feeders consume organic particles but excrete dissolved inorganic nutrients, such as ammonia and phosphate (7).

Production and consumption of freshwater fish, which are relatively of LTL, have increased substantially in China and other parts of Asia, while increases outside Asia have been moderate (3). Capture fisheries, which are generally of higher TL, make up the majority of seafood consumed in developed countries (3, 148). To shift tastes and preferences in developed countries from high to low TL organisms, some environmental nongovernmental organizations have begun campaigns in North America and Europe to highlight the health and environmental benefits of consuming lower-TL species. Campaigns have enlisted the support of celebrity chefs to convey their message (195), but their ability to shift cultural preferences remains uncertain.

POLICY AND INFORMATION APPROACHES

The aquaculture sector has a wide range of innovative technologies and management

strategies at its disposal to improve its overall environmental performance as it continues to expand. The question is: Will the industry take advantage of these innovations, particularly if the costs of adopting new approaches are initially high? Price signals often provide inducement for technological change and the adoption of improved management, yet capitalism fails to set a sustainable path when the social costs of aquaculture production—namely ecosystem damages—are not priced in the market. Substantial volatility in global commodity prices since ~2005 has further obscured market signals to producers. Policy interventions, international standards, labeling, and information strategies can help provide incentives to producers to adopt improved technologies and management practices, but they can also be counterproductive or confusing to producers and consumers (5).

To create the right incentives for widespread adoption of the innovations outlined in this review, governments promoting aquaculture need to establish enforceable standards that set clear limits on ecosystem damage, pollution, and resource use. Standards are required for aquaculture operations and siting, as well as for the flow and cumulative impact of nutrient and chemical effluents, pathogen transmission, fish escapes, and invasive species related to aquaculture activities (122). In addition, the establishment of a monitoring system, liability criteria for violations of standards, and a transparency process for public participation are needed to ensure the desired social outcome (122).

A wide range of scientific guidelines and information approaches has emerged to help policy makers and businesses set environmental standards and identify best practices and technologies for aquaculture development. Examples include the use of life-cycle assessments, the global aquaculture performance index, United Nations Food and Agriculture Organization codes of conduct, and business social performance standards (as reviewed by Reference 5). Numerous certification schemes are also available to producers to capture higher returns; although they provide a

valuable service to society, they can be extremely costly to producers because there is little coordination among the various schemes. As a result, firms trying to establish a socially responsible global business must meet the demands and inspections of multiple groups.² Organic certifications are also used in aquaculture when feed sources can be tracked (e.g., Reference 196) but are of limited value as they focus only on inputs to production and do not necessarily curb harmful outputs such as effluents, escapes, and pathogens.

Market prices play a more important role than policy in influencing aquaculture producers' choice of feed inputs. Despite high and volatile prices, an initiative funded by the European Commission, the AQUAMAX Project (197), has helped producers in the European Union reduce FM and FO use in feeds for Atlantic salmon, rainbow trout, gilthead sea bream, and cyprinids (147). This effort is important because globalization of FM and FO trade has reduced the traceability of the origin of feeds over time (198)—and hence the accountability by feed industries and producers for the pressure they place on wild fisheries.

In terms of regulations, it is more sensible to target the fishing sector than to regulate the aquaculture sector if the goal is to protect wild

²One example is HQ Sustainable Maritime Industries (in Hainan, China), a major global player in the production and value added of tilapia and its by-products. HQ is currently certified (or in the process of gaining certification) by about a dozen different groups for various practices along its value chain; some of these groups have conflicting standards. HQ's list of certifications includes: Hazard Analysis and Critical Control Points (HACCP) by the US foreign plant certification program; GLOBALGAP, which covers operations from fry to feed to grow out to processing; Global Aquaculture Alliance's Best Aquaculture Practices, encompassing certification for plant, pond, and feed mill operations; Ethical Trade Initiative, verifying fairness and workers' conditions; British Retail Consortium, the equivalent of HACCP in the United Kingdom; International Food Safety, a German food safety program; Aquaculture Stewardship Council, which sets standards for tilapia production; Chinese Inspection and Quarantine Services, the Chinese HACCP certification using mostly US Food and Drug Administration standards; and International Organization for Standardization 9,000 and 22,000 standards, verifying management controls and food safety protocols (personal communication, Norbert Sporns, CEO HQ Sustainable Maritime Industries, January 27, 2012).

fisheries from overfishing owing to FM and FO demands. Reducing FM and FO demand in one country for aquaculture use cannot prevent other countries or other sectors (livestock, pharmaceuticals, food supplements) from picking up the demand. Improving regulations and management of forage fisheries will be particularly important in the future as climate change creates greater uncertainties for the stability of forage fish populations (199).

THE PATH FORWARD

As shown in this review, there are a diversity of technological and management solutions available or under development to help reduce the resource constraints and environmental impacts of commercial aquaculture. We have examined the strengths and weaknesses of several promising culture systems, feed technologies, and species choices. The most viable and easily adopted solutions are those that are effective, profitable, and cause few additional problems, but no obvious technology stands out above the others. It is therefore advantageous to look at the efficacy of different solutions at meeting social goals, including food safety, pollution control, resource-use efficiency, and ecosystem protection.

Concerns regarding the safety of seafood products will likely remain or increase in the future, with consumers demanding seafood that can be guaranteed safe (22). RAS operations strive to control all aspects of production and can therefore remove or treat contaminants most effectively. Offshore and at sea IMTA operations will be the least secure in that they rely on increasingly impacted ocean environments for their water and feed sources (200). Aquaponic operations and IMTA operations also face the burden of having to demonstrate to seafood purchasers, consumers, and regulatory agencies that there is no contamination associated with using wastes from one aspect of production as inputs to another.

In striving to control all aspects of production, RASs are also able to guarantee reduced environmental impacts. All wastes

can be concentrated and treated or used as an input to other production systems (e.g., agricultural fertilizer or methane generation). RASs can be built in biosecure facilities away from water bodies, allowing farms to culture faster-growing fish that are selectively bred or GM without worries of escapes and biological invasion. Although a RAS serves as a favorable technological fix, it rarely works well economically, especially for large-scale commercial systems. The costs of infrastructure, labor, management, and energy can be prohibitively high. As a result, a RAS shows more promise for highly valued species, such as sturgeon, and little promise for catfish or tilapia.

One of the largest impediments to RAS technology is its energy inputs. A general conclusion from this review is that technologies that require substantial energy inputs—including RAS, offshore aquaculture, algae-based systems, and SCO-based feeds—are likely to be hampered by rising electricity generation and fuel costs. These technologies therefore remain risky from an economic and resource perspective, although innovations in integrated fuel systems could help alleviate the energy constraint. For example, renewable fuel technologies (solar, wind) could be used to power RASs; biogas emissions from RASs could be harnessed as an energy source for circulation and temperature control (68); and technological change in the biofuel industry using algae-based feedstocks could set the path for affordable production of SCOs as a healthy replacement of FO in feeds.

As the aquaculture sector continues to expand in a world in which water, land, and fishery resources are under pressure to meet multiple human demands, choices will have to be made carefully about which fish to raise, on what feeds, and in which ecosystems. There are clear advantages to culturing organisms lower on the food chain in terms of FM and FO requirements, stocking density potential, and effluents. But if consumers continue to demand high-quality seafood at high TLs, such as salmon, sea bass, shrimp, and tuna, there are three particularly attractive strategies for feeding

these animals. The first is the low-hanging fruit: using aquaculture trimmings or combining plant- or animal-based proteins and lipids with FM and FO at different rates during different periods of the life cycle to minimize FM and FO inputs and maximize health benefits to the fish and (human) consumers. The second strategy is to pursue research on polychaetes as a feed source, with specific attention to fish performance with different feed formulations and worm harvesting and preservation practices. Finally, the fields of SCO production and genetic engineering of plants to produce LC omega-3 fatty acids are quickly advancing and demonstrate great potential for reducing FO demand and thus relieving pressure on wild fisheries.

As competition for resources increases, integration of diverse food production systems will become increasingly attractive to improve the efficiency of resource use. Aquaponic and IMTA operations apply principles of ecological engineering to integrate waste streams from fed aquaculture into other forms of food production (51). As profit margins in aquaculture

become smaller, the attractiveness of using wastes as inputs to other profitable systems will grow as long as the food safety issues can be resolved.

More generally, rethinking aquaculture production with an integrated mind-set will be needed to tackle the simultaneous challenges of feed and energy demands; containment of wastes, pathogens, and escaped fish; land and water requirements; and consumer preferences. Like terrestrial crop and livestock systems, aquaculture production will become more intensive over time, and avoiding the environmental problems of intensification caused by crop and livestock systems will be key. The most effective strategy for achieving this goal will be reflected in diversity, as there are no silver bullet solutions in aquaculture. The most innovative, productive, profitable, and environmentally sound systems are likely to vary by species, country, and policies. Although a diverse aquaculture sector adds complexity, it might also enhance stability in the world food system if it can minimize environmental and resource damages.

SUMMARY POINTS

1. A range of technological solutions is available to help address the resource and environmental problems associated with intensification of aquaculture production, but each solution has strengths and weaknesses that must be addressed.
2. Aquaculture systems must remove and dispose of nutrients in an environmentally sound manner while reducing land and water intensity.
3. Reduced-cost, renewable energy inputs are needed to make some of the more promising aquaculture innovations (e.g., RAS, aquaponics, SCO-based feeds) economically viable.
4. Aquaculture feeds must become less reliant on FM and FO inputs from capture fisheries, yet whenever possible, they must incorporate ingredients that contain LC omega-3 fatty acids to augment health benefits to consumers.
5. Species can be bred to obtain traits that help reduce resource and environmental constraints. Farming species with lower TLs can also address resource constraints.
6. Environmental regulations, international standards, labeling, and information strategies can help provide incentives to producers to adopt improved technologies and management practices, but they need to be coordinated and promoted with care to prevent excessive costs to producers and confusion for consumers.

7. Rethinking aquaculture production with an integrated mind-set is needed to tackle the simultaneous challenges of feed and energy demands; containment of wastes, pathogens, and escaped fish; land and water requirements; and consumer preferences.

FUTURE ISSUES

1. Affordable, energy-efficient technologies are needed in recirculating aquaculture systems.
2. Improvements in waste measurement and management are needed in marine aquaculture systems.
3. Genetic technologies are needed to enhance LC omega-3 fatty acids in terrestrial aquafeed ingredients.

DISCLOSURE STATEMENT

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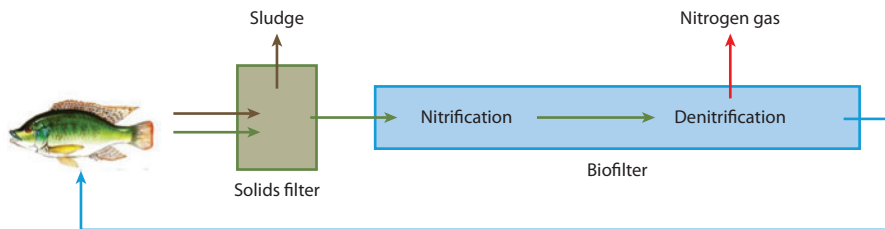
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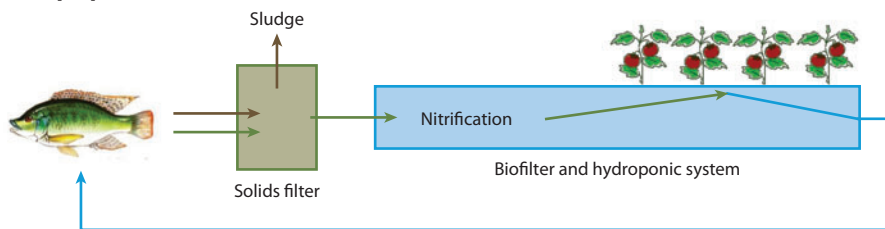
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a Recirculating aquaculture system



b Aquaponics



c Marine-based integrated-multitrophic aquaculture



d Offshore aquaculture

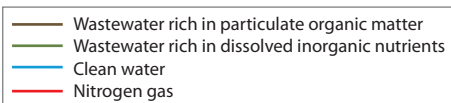
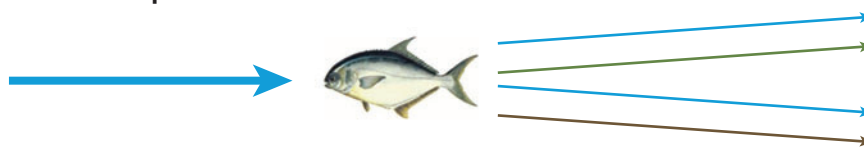


Figure 1

Simplified schematic of particulate organic matter and dissolved inorganic nutrient treatment in (a) a recirculating aquaculture system, (b) aquaponics, (c) marine-based integrated-multitrophic aquaculture, and (d) offshore aquaculture.



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