

REVIEW ARTICLE



WILEY

Achieving sustainable aquaculture: Historical and current perspectives and future needs and challenges

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[The copyright line for this article was
changed on 04 July 2020 after original
online publication.]

Abstract

Important operational changes that have gradually been assimilated and new approaches that are developing as part of the movement toward sustainable intensive aquaculture production systems are presented via historical, current, and future perspectives. Improved environmental and economic sustainability based on increased efficiency of production continues to be realized. As a result, aquaculture continues to reduce its carbon footprint through reduced greenhouse gas emissions. Reduced use of freshwater and land resources per unit of production, improved feed

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management practices as well as increased knowledge of nutrient requirements, effective feed ingredients and additives, domestication of species, and new farming practices are now being applied or evaluated. Successful expansion into culture of marine species, both off and on shore, offers the potential of substantial increases in sustainable intensive aquaculture production combined with integrative efforts to increase efficiency will principally contribute to satisfying the increasing global demand for protein and food security needs.

KEYWORDS

future sustainability challenges, global sustainable aquaculture, recent advances toward sustainable aquaculture

1 | INTRODUCTION

During the past 20 years, global aquaculture enterprise has succeeded and continues to increase while achieving the critical goals of environmental, economic, and societal sustainability. The following collection of essays that compose this publication are written by a group of individuals who have significantly contributed to important advances and witnessed the positive changes that have resulted. This unique presentation was developed to honor the 50th Anniversary of the World Aquaculture Society and many authors are either Honorary Life Members, Past Presidents, Fellows, or hold more than one of these recognitions. The Society has held true to its mission statement of global dissemination of the results of basic and applied aquaculture research designed to increase sustainable global production. The collection of titles that compose this publication does not represent an array of exhaustive reviews of particular areas of investigation and application. Rather, they present opinion, concept, historical perspective, recent developments in different areas of research and their novel application that is contributing to the realization of the goal of sustainability. Not all areas recognized as critical components in achieving sustainable aquaculture are included in this publication format because of the prohibitive length and extensive effort that would be required to be that all-inclusive. Nonetheless, the essays are a decidedly representative mixture that offer insight and highlight advances that will have vital roles toward decisively achieving the critical goal of sustainable global aquaculture.

2 | THE OPERATIONAL CONCEPT OF SUSTAINABILITY—LORENZO M. JUAREZ

Aquaculture is the fastest-growing food-production technology, now globally accounting for more fish biomass than capture fisheries if non-edible amounts are included (Edwards, Zhang, Belton, & Little, 2019) and more total biomass than beef. Most of this development has occurred during the last 50 years, and thus sustainability, particularly environmental sustainability, has evolved into a growing concern. Attention has been increasingly devoted to enhancement of awareness of environmental issues and the corresponding implementation of practices designed to reduce the environmental footprint of aquaculture. Whereas degradation of the environment was not considered to be the most pressing concern of the industry five decades ago, it is now a vital focal point, whether academic, governmental, productive, or market based. In today's world, whether aquaculture production should be managed in an

environmentally responsible and sustainable fashion is no longer debatable (Engle & D'Abramo, 2018). Sustainability has evolved from an obscure idea, to the forefront of the considerations that govern the management of aquaculture firms and their regulation, public perception and their marketing of products.

Despite all its current recognition and relevance, the concept of sustainability as applied to aquaculture actually is not a clearly defined term and its use often results in confusion. Whereas public perception understands sustainability as the capacity of human activities to persist in time while maintaining a healthy environment, the most cited definition is that of the United Nations World Commission on Environment and Development. This Commission, better known as the "Brundtland Commission," defined sustainable development as "use of the environment and resources that meets the needs of the present without compromising the ability of future generations to meet their own needs" (World Commission on Environment and Development, 1987). This definition integrates environmental stewardship with social responsibility and economic gain, thereby presenting an understanding that exclusive focus on economic growth ignores and impedes social development and environmental protection, thus emphasizing the need to integrate various paths toward the improvement of conditions in the developing world (Hove, 2004). The "Brundtland definition" has been criticized for its lack of specificity and applicability and for leading to a false impression that development can proceed with only minor changes (Stefanovich, 2000). Regrettably, sustainability has become more of a clueless catchphrase and a marketing tool, rather than a clearly defined and useful concept.

Economic theory provides a more useful definition of sustainable development, stated as economic systems where the productive base, or total capital remains constant over time (Chapin, Kofinas, & Folke, 2009). In this definition, *Capital* refers to the comprehensive wealth of the system, including human, environmental, and economic components. This economic definition implies the impossibility of unlimited growth due to the planet's limited resources and presents the practical problem of assigning limits to the system and of quantifying consequences experienced by unrelated third parties; the so-called externalities.

Social sustainability is founded on the promotion of wellbeing within an organization's members. Focus is primarily directed to assurance of fair labor practices, but also includes the overarching goals of reducing social inequality, increasing the quality of life, and defending human rights. The predominant issues of social sustainability in aquaculture are connected to the elimination of abject poverty, child labor, modern slavery, and other unethical practices which unfortunately still prevail in some regions.

In ecology, sustainable biological systems are characterized as diverse, adaptable, resilient, and productive over time (Chapin et al., 2009). Examples of ecologically sustainable systems are healthy oceans, lakes, rivers, wetlands, and forests. This ecological definition is difficult to apply to food production systems such as agriculture and aquaculture.

Most countries have enacted sensible laws and regulations to protect the environment. Aquaculture is often regulated by multiple agencies that mainly address capture fisheries, agriculture, coastal management, water resources, and environmental protection. Whereas these compound bodies of regulation are often less than perfect, they do represent the country's legal interpretation of environmental sustainability.

Business owners and managers often interpret sustainability as the capacity of the business to be successful and persist in time. Central to this concept is the idea of permanence of profitability and predictability. Whereas the health of the environment is usually not the primary motivator of businesses, most leaders recognize that a healthy environment is required for successful operations. Seafood buyers and consumers increasingly play a role in demanding products that have been produced taking social and environmental responsibility into consideration. These guiding requirements have resulted in increased awareness and continuous improvements in the search and implementation of practices designed to manage the environmental footprint of aquaculture.

In practice, environmental sustainability becomes a question of selecting the best alternatives among different practices and procedures. Typically, when faced with an operating or investment decision an aquaculture venture can choose among solutions with different environmental consequences. Ideally, the best technologies allow a combination of producers increasing productivity while reducing environmental footprint. Engle (2019) recently summarized this approach in an editorial: "Perhaps it is time to bring the sustainability discussions down to earth and focus

on more pragmatic, empirical, outcomes-based approaches to choices related to species/production systems, their sustainability, and their contribution to human food security.” Industry groups, companies, organizations, and government institutions have developed sets of good management practices that aid in making such choices. Additionally, “green label” programs sometimes balance the cost of more expensive management practices by providing price premiums or access to specialty markets for aquaculture products raised under social and environmentally responsible practices.

Central to the concept of sustainability is the efficient use of resources such as energy, water, land, feed, and fertilizer. Reducing the use of these resources is key to providing healthy food for a growing population in an environmentally responsible manner. Because such judicious use can be quantified, benchmarked, and compared, this approach eliminates the subjectivity of stakeholders and turns established goals into a much more objective and scientific endeavor. Boyd and McNevin (2015) present an excellent review of this approach.

The global aquaculture community has been on a very steep learning curve over the past 50 years. During this time, environmental considerations have evolved from a sideline concept into an indispensable way of conducting business.

3 | THE PATH TO SUSTAINABILITY FOR THE INCREASINGLY IMPORTANT AQUACULTURE BASED SOURCE OF GLOBAL FOOD PRODUCTION—AARON A. MCNEVIN

Sustainability in food production is a subjective term used to describe how the planet allows for goods and services to be utilized and benefited by humans in a manner that does not harm the continued provision of these environmental services. In the effort to establish sustainable aquaculture globally, the pathway must consist of equivalent levels of achievement for both developed and developing nations for both domestic consumption and exports. The “three pillars” of sustainability are economic sustainability—the ability for humans to continue to support a living through an activity; social sustainability, that is, the societal acceptance of a specific activity; and environmental sustainability—the ability to conduct an activity without detrimental harm to the environment such that the resources needed for the activity are not compromised for future use. Sustainable development, therefore, requires incorporation of all of these pillars into a particular human activity. As humans are animals that seek to preserve their own kind, sustainable development tends to prioritize the pillars of sustainability such that the environmental component is tertiary to the more humanistic based economic and social pillars. Also, competing interests exist among a variety of stakeholders either in aquaculture directly or through allied industries. These stakeholders can be categorized as development institutions that seek livelihood generation, research institutions that operate through analysis and innovation related to aquaculture, and environmental nongovernmental organizations (eNGOs) that advocate and engage in the aquaculture sector to minimize the environmental burdens. “Sustainable aquaculture” is something that all of these stakeholder groups claim to support, but their institutional mandates and incentives are not always aligned with the altruism necessary for balancing the goals of these pillars of sustainability.

The goal of sustainable aquaculture is to provide a continued supply of farmed aquatic nutrients beneficial for human sustenance without harming existing ecosystems or exceeding the ability of the planet to renew the natural resources required for aquaculture production. However, the pillars of sustainability are not mutually exclusive and understanding this interface is critical. The justification of one pillar over another is conducive to unsustainable aquaculture and consequently has also impeded the development of sustainable aquaculture. When confronted with achieving the balance of the pillars of sustainability, the logical path is to seek answers to fundamental questions from experts or authority figures who are familiar with the subject matter such that informed decisions can be made. However, the use of information obtained to answer questions can become predisposed to serve a specific institution, and thus “science” in the form of unbiased research can consequently trend from a demand-based tool to a strategy of perpetuation of an institution. Research institutions are definitely not the only institutions that seek a

safeguarding strategy. However, the reason to highlight research institutions is to emphasize that science is a methodology for answering questions and understanding complexity and accordingly, humans look to them for objectivity. Science-based decision making has perpetually been contested, and this situation has accordingly influenced how one interprets the goal of sustainable aquaculture.

Aquaculture relies on the utilization of multiple natural resources to produce aquatic animals. The generalized classification of aquaculture with the capture of wild fish as seafood sources has produced a situation that is not shared with any other animal protein production sector. Transposing the procedure of evaluating wild fish stocks onto aquaculture has fundamentally skewed the public perception of aquaculture as an industry that is adversely affecting the freshwater and marine environment. Many critics of aquaculture ideally seek a culture environment that is more "natural," an environment that mimics the conditions in the wild. In contrast, aquaculture is based on the collective utilization of many natural resources to amplify the efficiency of protein production. And while recognizing that there are impacts of aquaculture that do harm to the environment, all food production has negative and positive impacts. Unfortunately, improving the production characteristics of aquaculture is not the path that is commonly practiced for management of wild fisheries where a balance of recruitment, growth, natural mortality and fishing mortality is sought. Sustainable aquaculture strives for continued progress on a path toward achieving optimization of use of natural resources to produce nutrients. Cumulative impacts and non-point source pollution require that sustainable aquaculture achieves greater control over and isolation of the negative impacts on the localized environment. Yet, some aquatic environments are so vast and devoid of human activity that aquaculture can be appropriately transposed into that medium where natural assimilative capacities to both dilute and process waste from production are operational.

While economic and societal pillars of aquaculture are addressed throughout the following text, much of the characterization and mischaracterization of the aquaculture sector rests in its association with environmental sustainability. The environmental sustainability of aquaculture consists of the environmental impacts of production within a specific locale (ecosystem-level impacts) combined with the natural resources utilized (natural resource extraction impacts).

Placing perspective on the magnitude of growth and general trends in categories of cultured aquatic organisms is necessary to understand the diversity of aquaculture. According to the United Nations Food and Agriculture Organization (FAO, 2019), approximately 84% of aquaculture is comprised of aquatic plants, mollusks and freshwater fish (Table 1). Mollusks and aquatic plants compose nearly half of global aquaculture volume, and one of the key attributes that allow aquatic plants and mollusks to continue to grow at magnitude scale (Figure 1) is that inputs are not necessary to farm these species groups. The second highest magnitude of growth in aquaculture production is identified by increases in popular, internationally traded products such as shrimp and salmon, marine fish, freshwater

TABLE 1 Global aquaculture production (m.t.) by species group separated by aquatic environment

Species group	Brackishwater	Freshwater	Marine	Total
Aquatic plants	1.20	0.07	30.54	31.81
Crustaceans	4.97	3.15	0.32	8.44
Diadromous fishes	1.57	1.21	2.86	5.65
Freshwater fishes	1.50	43.16	0.00	44.66
Marine fishes	0.80	0.05	2.25	3.10
Misc. aquatic animal products	<0.01	<0.01	<0.01	<0.00
Misc. aquatic animals	0.10	0.51	0.38	0.99
Mollusks	–	0.22	17.07	17.30
Total	10.14	48.38	53.43	111.95

Source: FAO, 2019

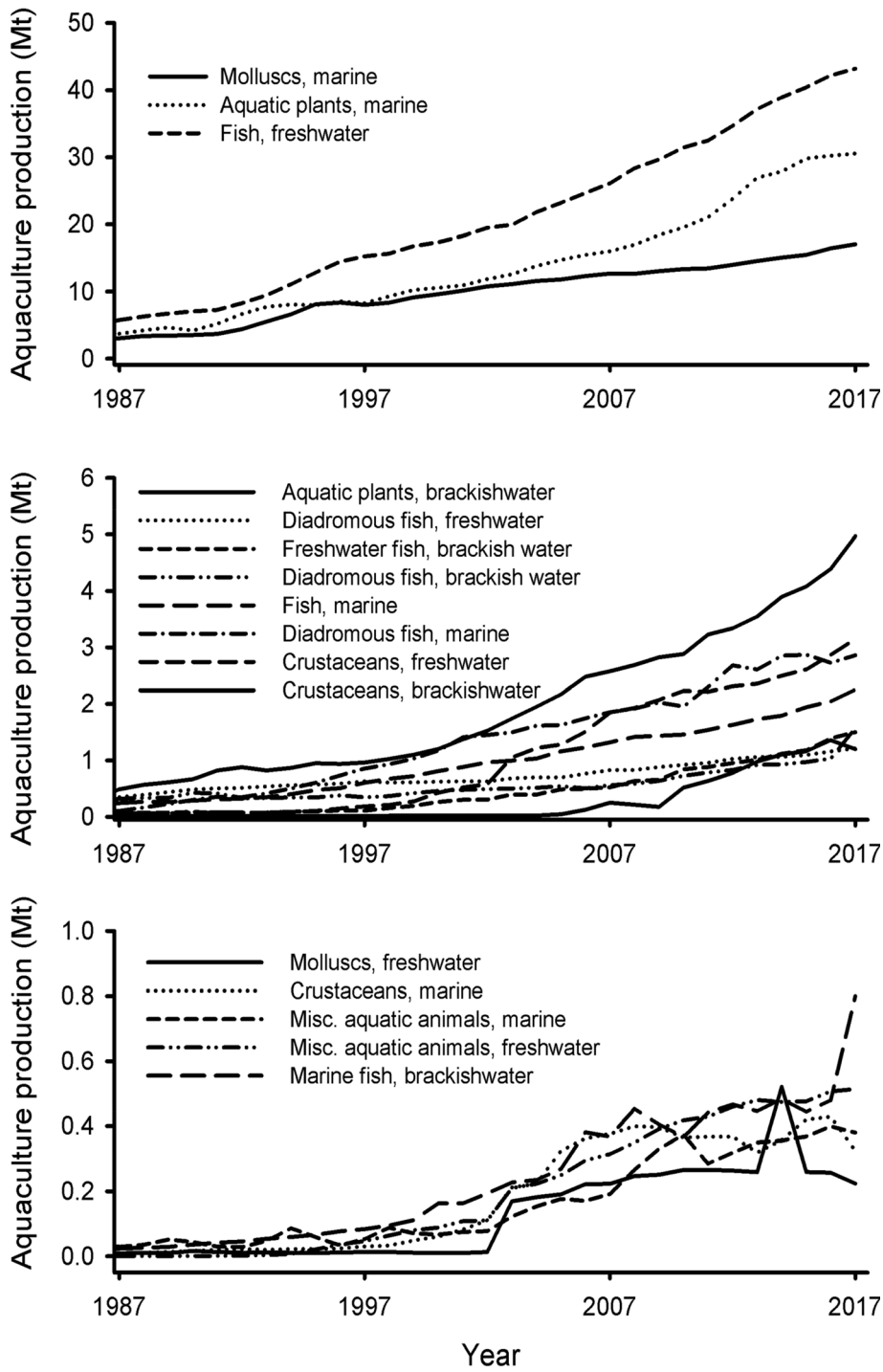


FIGURE 1 Global aquaculture production (m.t.) separated into three magnitudes of volume and by species groups and aquatic environment. Source: FAO, 2019

prawns and crayfish (embedded within their species groups). At a lower magnitude rate of growth, due to ambiguity in FAO data, the only demonstrable trend is limited to the increase in marine fish raised in brackish water environments.

Species, such as filter feeders or seaweeds, that have less resource demands than higher trophic level species or those that require greater amounts of manufactured feeds are being raised globally with beneficial water quality effects when sited appropriately. The comparatively large magnitude of this sector of global aquaculture sets it apart from other forms of animal production. However, in contrast, aquaculture, unlike other forms of animal production, commonly targets carnivorous species for culture. Aquaculture utilizes 20 million t of wild fish—roughly one-fifth of the world's wild caught fish species—as a source for amino acids and protein for feed (FAO, 2018), and this marine protein resource must be minimized and/or replaced or aquaculture's output will be limited. Progress in improving efficient use of marine proteins is occurring, but not at a pace that satisfies aquaculture production output (Fox, 2014). New trends in the development of novel animal feed ingredients such as algae, insect larva, single cell proteins, etc. continue to appear and ultimately should prove cost-effective.

Habitat conversion remains a challenge for the aquaculture sector because no greater change to ecosystem function probably exists than the conversion of terrestrial habitats to aquatic habitats (Boyd & McNevin, 2015). These changes remove and hinder species diversity from returning. In fact, mangrove conversion—a stigma that the aquaculture industry has earnestly tried to remove—keeps reappearing. Conversion of mangroves to ponds is still being practiced in southeast Asia. “Integrated mangrove shrimp,” a practice based on fragmenting mangrove habitat into strips and enclosing them in embankments to promote shrimp culture has, in fact, received support from a faction of the eNGOs (Bosma, Nguyen, Siahainenia, Tran, & Tran, 2016).

Use of appropriate terrestrial habitat for aquaculture remains under pressure and sites with proper soil and access to suitable water are few and far between. Many in the food production sector have come to acknowledge that producing more food (calories, proteins, amino acids) per unit of land area (intensification) will need to become the norm to support global population expansion and the corresponding demand for protein. Increasingly, our natural habitats are being adversely affected and the food production sector and food companies recognize the dramatic effect that climate change is and will be exerting on the availability of food (Sullivan & Gouldson, 2017). Thus, commitments to deforestation-free (D-free) and conversion-free (C-free) commodities are rising (New York Declaration on Forests, the Cerrado Manifesto, etc.) for the major suppliers of food and feed ingredients to the world. Approximately 70% of terrestrial biodiversity loss results from the production of food (Kok et al., 2014). Aquaculture no longer occupies a small and comparatively insignificant area in the space of animal protein. It has surpassed beef production in the past decade (Larsen & Roney, 2013), affirming that the greatest threats to our planet are cumulative rather than sector specific.

Land use and habitat conversion are shared impacts of aquaculture and terrestrial animal production, but unlike terrestrial animal production, aquaculture can expand into aquatic ecosystems. Cage culture (outside of ponds) and the culture of mollusks and aquatic plants are forms of aquaculture that are not directly responsible for habitat conversion. Cage culture can be carried out in a sustainable manner, but there is risk of pollution due to accumulation of waste. Crowding of cages in poorly mixed or constrained natural water bodies can result in hypoxic events and may also be accompanied by lethal concentration of reduced gases and unsustainable conditions. Cage culture, in recent years, has turned into a more industrious venture offshore where the social pillar and license to operate are less inhibiting. Any meaningful step-change in increased protein availability globally will be a result of offshore production enterprise (Gentry et al., 2017).

Continued consumption of fossil fuel as a primary source of energy is a key detriment to achieving sustainability of the aquaculture sector, as well as the food sector and humanity itself. Along with agriculture and societies in general, aquaculture must reduce and eventually eliminate its dependency on fossil fuels. Carbon dioxide is increasing in the atmosphere and correspondingly the global mean temperature of both the oceans and air is rising (Melillo, Richmond, & Yohe, 2014). Ocean acidification, caused by the increased diffusion of carbon dioxide into the ocean, is already adversely affecting the quality of shellfish products. Climate change and suspected consequences such as

changes in weather patterns causing droughts and flooding in addition to the loss of carbon storage capacity are the greatest threats to the overall physical and biological stability of the planet. For example, climate changes will definitely produce changes that will require modification of management practices in aquaculture enterprise (D'Abramo & Slater, 2019). However, the transition from fossil fuels to alternative, carbon neutral sources of energy also presents a challenge in maintaining sustainability of different production systems, such that the costs and availability must be at least equivalent.

Aquaculture has been subjected to an intense learning curve with a slope that no other food industry has had to climb. The trajectory for aquaculture to achieve the goal of sustainability is no different than any other form of food production, that is, limit, counteract, or isolate its pollution on the localized environment, and accelerate the efficiency of natural resource use. Aquaculture is likely better poised to meet these sustainability targets than many other forms of animal protein production because it is conducted in a uniform three-dimensional, as opposed to a two-dimensional, system. Aquaculture can utilize this third dimension of depth to increase output per unit water surface area, particularly in the open ocean.

Four areas of focus that should effectively coalesce in order for the goal of sustainable aquaculture to be realized are the preservation of intact habitat, efficient use of natural resources, traceability, and transparency. Traceability and transparency are fundamental to demonstrating accountability. Every stakeholder should be concerned with them because their accomplishment will produce clear economic, societal and environmental benefits.

3.1 | Preservation of intact habitat

Adverse modification of habitat, whether in a marine environment (through pollution) or in a terrestrial environment (through habitat conversion) is an issue of concern and corresponding need for study. Increased habitat degradation will commonly lead to challenges in the ability to efficiently produce. Unlike terrestrial animal or plant protein, aquaculture is the most appropriate animal protein sector to make a commitment to no conversion of intact habitat. Conversion-free aquaculture is a substantial asset to the animal and plant production sector and a key to future protein availability.

3.2 | Efficient use of natural resources

Natural resource efficiency is fundamental to halting further degradation of the planet. To maintain a conversion-free commitment, aquaculture must accelerate its efficiency in the use of natural resources by reducing the use of fossil fuel, water, land and wild fish use per unit of farmed product output. This goal requires changes in farming practices and feed production that will result in efficiency gains. Aquatic plants and mollusks can sequester carbon and a growing desire to utilize seaweeds at scale to help remove carbon dioxide content in the atmosphere by transfer to the oceans prevails. Alternative energy sources are saving producers operating capital. Cage operators and feed companies are being held to higher standards and being asked to recover the wastes that these aquaculture activities introduce into the environment. Water use in pond production has decreased, not due to specific environmental concerns, but rather for biosecurity considerations. New filtration, recirculation and water treatments are allowing for culture water to be reconstituted for successive uses. Land, however, is simply unavailable, restricted from access to suitable water sources or too expensive to convert to aquaculture systems.

Changes in feed, feed manufacturing and raw material production are required. Improvements in these areas such as utilization of alternative energy sources, utilizing primary production or other alternative ingredients that grow on waste and by-products of other human activities such as insects, algae, molds and fungi, bacteria, etc., should translate into better feed and feed delivery. Such an approach will reduce tight competition between aquaculture other animal production sectors for raw material for feeds.

Fundamentally, producers want to produce more product to sell from the resources in the area where they already operate. In turn, processors want to process more product to sell and feed companies want to sell more feed. These goals are clearly business-based and underscored by more efficient use of natural resources whereby intensification can be achieved. Intensification itself is not a panacea, and thus arguments cautiously call for a more responsible and less chaotic sectoral expansion, often termed "sustainable intensification." Yet, sustainable intensification is more of a vision and its definition is rightfully as ambiguous as the definition of sustainability itself. The future of aquaculture is the control of externalities or the attempt to isolate itself from an environment and optimize production. This intensification is better defined as "controlled intensification."

3.3 | Transparency and traceability

The practice of radical transparency and traceability by the aquaculture sector is the new norm because consumers that purchase aquaculture products to feed their families deserve the knowledge of where (traceability) and how (transparency) their food was produced. The aquaculture food production sector must be accountable. However, at least some of the opaqueness of this sector occurs because trade associations compromise accountability by focusing on the desire for convenience and low cost of the imported product. For example, the National Fisheries Institute refuted the need for traceability of shrimp products through the Seafood Import Monitoring Program created by the National Oceanic and Atmospheric Administration (NOAA). The International Marine Ingredients Organization consists of the fishing industry that in turn certifies the fishmeal industry. The Global Aquaculture Alliance owns and operates the Best Aquaculture Practices certification and certifies its own board members. The demonstrated and potential conflicts of interests that exist within these trade associations have led to several disservices including a cover-up of the human rights abuses in Asia, the environmental devastation in the West African reduction fisheries and the clear lack of traceability of many seafood products. Trade associations that fail to disclose all of the shortcomings of the aquaculture sector are consequently becoming a pronounced liability for the industry.

The growing public acceptance of the negative impacts of aquaculture has constructively and usefully contributed to part of a path to sustainable food in the future. Radical transparency is about owning both your farmed product as well as its associated impacts while challenging others to help in finding solutions to increase sustainable features of products. The advocacy and implementation of traceability demonstrate the acceptance of accountability and its proof would likely lead to more credible certification and verification act programs that are advocated by NGOs. These programs must demonstrate credibility by inclusion of a corresponding high level of enforcement to deter fraud, thereby leading to improved public policy and public opinion.

3.4 | Final considerations

A general sense of focus by stakeholders (producers, academics, researchers, development institutions, industry trade associations, eNGOs, consultants, philanthropy, certification entities, chemical companies, drug companies, etc.) engaged in aquaculture is needed. An inherent dilemma exists relative to the selection of a limited number of stakeholders with a specific direction toward the realization of sustainably viable production. Choice of participants must be founded on combining expertise and experiential knowledge to produce meaningful collaborations and progress leading to impactful guidelines and policy. The outcomes must transcend corporate social responsibility pet projects, eNGO "transformations" of companies, novel schemes to further tax the supply chain, or academic research that produces more questions than answers. A selfless or rather "institutionless" based agenda must prevail to advance the sector and achieve the goal of sustainable aquaculture. Realistically, achievement of this ideal may not be entirely possible in principle, but nonetheless needs to be an overriding goal.

4 | THE ROLE OF MECHANICAL AERATION AND WATER CIRCULATION IN THE INTENSIFICATION OF SUSTAINABLE AQUACULTURE—CLAUDE E. BOYD

Fish farmers learned centuries ago that livestock manure and other types of farm wastes could be used to fertilize ponds and increase fish production (Boyd, 2018). Moreover, meat processing waste, table scraps, and grain were commonly used as feed for fish. These early fish farmers on some occasions presumably added more organic matter than certain ponds would be able to assimilate, resulting in low dissolved oxygen concentration or other water quality aberrations. It was not until fish farmers began to use manufactured feeds in the 1950s and 1960s that low dissolved oxygen concentration became a common problem in achieving success in pond aquaculture.

Ictalurid catfish farming in the southeastern United States provides a good example of the relationship of feeding to water quality. Those feeds initially used were nutritionally incomplete and natural food in ponds served as a supplemental source of nutrients. Production was limited to 1,500–1,800 kg/ha, and feeding waste usually did not depress levels of dissolved oxygen excessively. But, feeds improved and greater production became possible. The amounts of feed added to ponds frequently caused depletions in levels of dissolved oxygen. When this condition occurred, farmers often (if possible) flushed ponds with oxygenated water in an attempt to prevent fish mortality. They also drove boats with outboard motors or jet skis over ponds to stir and oxygenate water. Some placed tractors with bush hogs in shallow water edges of ponds and stirred the water with the bush hog, and reports of farmers hiring helicopters to hover over ponds so that the air currents from the rotor stirred the surface water to oxygenate it also exist (Anonymous, 1979). These attempts were sometimes successful, but fish mortality due to oxygen depletion remained common.

Two fish farmers in Alabama, USA (Perez, 2006) invented the tractor-powered paddlewheel aerator (Figure 2) that consisted of a trailer on which was mounted the differential and axles of a truck. A paddlewheel was placed on the ends of the axles and a shaft was extended to the power takeoff of the tractor. The trailer was backed into the water and the paddlewheels were then engaged to splash a large volume of water into the air to produce an exchange of oxygen in the air with the water. Strong currents induced by the paddlewheels drove the water across the pond and this device was highly effective in preventing fish mortality from oxygen depletion (Boyd, Steeby, & McCoy, 1979; Boyd & Tucker, 1979). The shortcoming of use of such a device was that each required a 50-hp or larger tractor and was suitable only for emergency use.

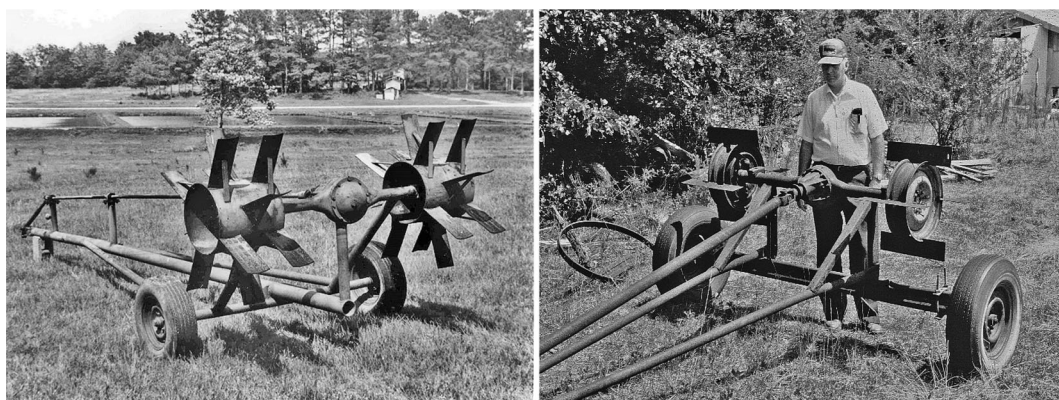


FIGURE 2 Left: a tractor power take-off (PTO)-powered paddlewheel aerator built in Greensboro, AL, in the early 1970s. Right: A tractor PTO-powered paddlewheel built and used in northwest Mississippi (the “Delta”); handwritten on the original 35-mm slide was, “first paddlewheel in Mississippi, 1974” (photograph by Thomas Wellborn)

By using tractor-powered emergency aerators, feeding rates of up to 40–50 kg/ha/day were possible, and maximum standing crops of 2,000–2,500 kg/ha were attained. In their quest for greater production, farmers often exceeded safe feeding rates. As a result, the ability to successfully manage dissolved oxygen problems became increasingly difficult, particularly at night, using tractor-powered paddlewheel aerators.

A movement arose toward the use of floating electric aerators of various types. However, due to the small sizes of the aerators available at the time, the first attempts at employing electric aerators were disappointing. The experience with small electric aerators, however, led to the development of an efficient, floating, electric paddlewheel aerator through research at Auburn University in close collaboration with several machine shops interested in manufacturing fish-farming equipment (Boyd, Torrans, & Tucker, 2018).

The development of more nutritionally adequate feeds and the floating, electric paddlewheel aerator resulted in a remarkable intensification of catfish production with annual yields increasing from around 1,500 kg/ha in the 1960s and early 1970s to 5,000–10,000 kg/ha (average \approx 6,500 kg/ha) at present. Tractor-powered emergency aerators did not become completely obsolete. Under occasional circumstances, particular ponds on a catfish farm may develop oxygen demands exceeding the dissolved oxygen transfer capacity of floating, electric paddlewheel aerators dedicated to ponds. Therefore, most catfish farms have one or more tractor-powered, paddlewheel aerators available for emergency use.

Improvement in the efficiency of aerator operation can reduce the cost of mechanical aeration and be a contributor to economic sustainability. Dissolved oxygen concentrations in ponds oscillate over a 24-hr period with the highest concentrations usually being in the daytime and the lowest concentrations at night. Automatic aerator control systems have been developed whereby aerators are activated and deactivated in response to signals from a dissolved oxygen monitoring probe positioned at a selected location in the pond. In catfish farming, aerators often are activated when dissolved oxygen concentration is around 4 mg/L and shut off when the concentration rises above 6 mg/L. Automatic aerator controllers are becoming more reliable and the cost of these devices is declining as this technology continues to improve. Nonetheless, presently, a dissolved oxygen monitoring program is still necessary to assure proper functioning of aerator control systems.

Fish suffering from nutritional deficiency and/or chronically stressed by low dissolved oxygen concentration are more susceptible to disease. Better feeds and aeration have improved fish health that is an important component to ensuring economic sustainability. Feeding, aeration, and fish health are intricately related in aquaculture and should not be considered as independent factors.

The development of better feeds and aeration techniques were not limited to catfish farming in the United States; rather it has become the norm in several types of pond aquaculture leading to greater intensification and contributing much to the rapid increase in global aquaculture production during the past 50 years. In marine shrimp farming, levels of production in the 1970s and early 1980s seldom exceeded 500–1,000 kg/ha per crop. Today, single crop production from heavily aerated ponds often falls between 8,000 and 10,000 kg/ha (Boyd, McNevin, & Davis, 2018). Similar increases in production intensity have occurred with other species.

The electric paddlewheel aerator design developed for catfish farming in the United States (Figure 3) and smaller paddlewheel aerators of various designs developed in Asia (Figure 4) are the most common mechanical aerators used in pond aquaculture. In most raceways, water recirculating production systems, and other types of highly intensive culture units, electric paddlewheel aerators are not applicable. For such production units, pure oxygen contact systems (Boyd & Watten, 1989), diffused-air aeration systems, jet aerators, and other types of aerators are used (Boyd, McNevin, & Davis, 2018).

Although mechanical aeration has become a common practice, and aerators that are efficient in transferring oxygen to water and of excellent mechanical reliability have been developed, the knowledge of efficient aerator use to contribute to sustainable production systems is poorly developed. Minimum dissolved oxygen concentrations that can be maintained without causing a decrease in feed consumption and feed conversion efficiency and greater susceptibility to disease need to be determined for the different aquaculture species. The placement of aerators in ponds also deserves additional investigation.

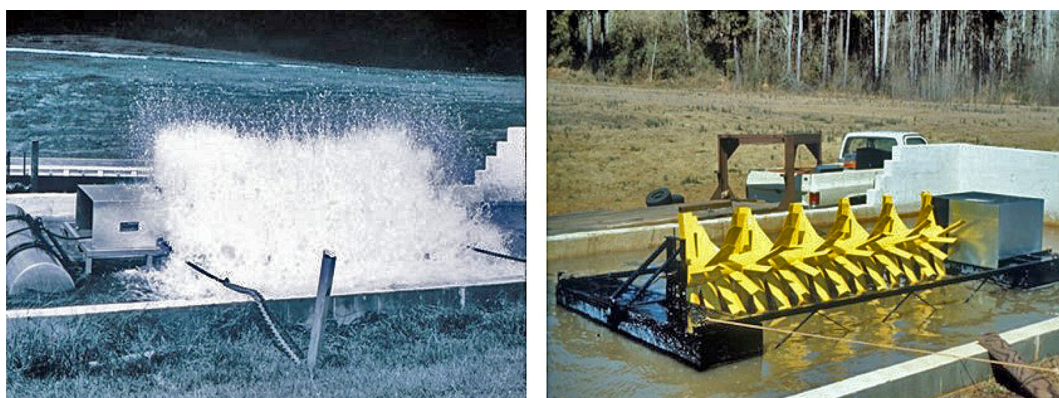


FIGURE 3 The full-size (7.5 kW) prototype paddlewheel aerator based on research conducted at Auburn University

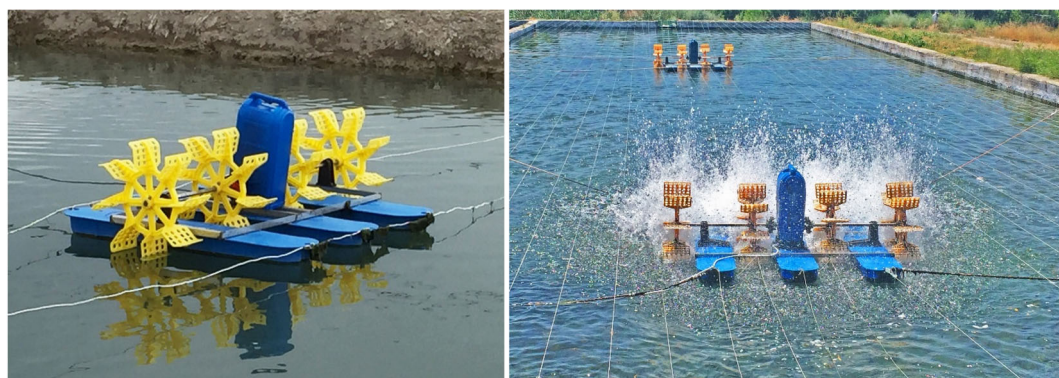


FIGURE 4 A "Taiwan-style" paddlewheel aerator on a fish farm (photograph courtesy of Wikimedia Commons)

Pond depth is an important factor because aerators must generate sufficient water circulation to prevent thermal stratification. Surface aerators are most commonly used in ponds, and the ideal depth of ponds with surface aerators is about 1.5 m. Generally, these devices usually can prevent thermal stratification in ponds with depths up to 2–2.5 m. In such ponds, thermal stratification can be avoided through maintenance of a constant movement of oxygenated water across the pond bottom. In the absence of adequate dissolved oxygen at the pond bottom, anaerobic conditions develop at the soil-water interface, resulting in the possible release of potentially toxic microbial metabolites into the water column. Avoidance of anaerobic conditions at the pond soil-water interface is especially critical in shrimp culture, because shrimp spend much of their time on the bottom.

An especially critical research need for dissolved oxygen management in ponds is the investigation of the relationship between aeration and water circulation. Most aerators, and particularly floating electric paddlewheel aerators, were designed for maximum oxygen transfer efficiency, and the characteristics of water currents produced by aerators have not been thoroughly studied. Devices that induce water circulation in ponds have been designed, fabricated, and tested (Howerton, Boyd, & Watten, 1993). A preliminary study suggested that the combination of aerators and water circulators might be more efficient in maintaining dissolved oxygen concentrations in ponds than that achieved by application of aeration alone (Tucker & Steeby, 1995). Research to determine the conditions under which water circulators could be efficiently used to enhance aeration practices should be highly prioritized.

Both fish and shrimp cannot hold position in ponds if water currents become too strong, and in laboratory studies, shrimp grow best at water velocities of 0.63–2.78 cm/cm (Dai, Zhang, & Zhang, 2008). In earthen culture ponds, shrimp avoided areas where water velocity was <3 cm/s (apparently because of sedimentation) and tended to avoid areas where water velocities were >5 cm/s (Wijesekara, Nomura, & Matsumura, 2005). Water velocities in aerated fish and shrimp ponds have been reported to range from <1 cm/s to >50 cm/s depending on the place of measurement (Delgado et al., 2003; Kang, Lee, Choi, & Sin, 2004; Moore 1992; Peterson & Pearson, 2000). Assuming that different cultured animals avoid areas based on specific preferences for current velocity, a large area (and volume) of culture systems may not be inhabited, creating crowding in areas of acceptable current velocity. Of course, if currents are excessive and no refuge of lower water velocity is available, the additional energy required for culture animals to maintain their position in currents will detract from growth (Dai et al., 2008) and adversely affect levels of production that potentially could be achieved. More information about the effects of water circulation on culture species must be obtained to formulate and establish the best management practices for using aerators or aerator-water circulator combinations.

Aerator-generated water currents also can cause serious erosion of pond bottoms and especially the insides of embankments. The soil particles suspended by erosion usually settle in quiet zones in the pond (Avnimelech, 2001; Boyd, Munsiri, & Hajek, 1994; Peterson & Pearson, 2000). Better means of protecting pond earthwork from erosion by aerator-generated water currents are needed. Improved aerator design and placement could likely result in reducing the potential for aerator-induced erosion relative to what currently exists.

The aeration rate (power per unit area or volume) in wastewater treatment basins is determined by solving the aerator performance equation (Tchobanoglous, Burton, & Stensel, 2003) in concert with information on the hourly oxygen demand of the wastewater; hourly oxygen transfer rate of the aerators used; minimum acceptable dissolved oxygen concentration, water temperature, and a few other characteristics of the wastewater. After much effort to apply this methodology in pond aquaculture, Boyd, Torrans, and Tucker (2018) concluded that the large daily variability in pond oxygen budgets and the inability to calculate the hourly oxygen demand accurately rendered the aerator performance equation for estimating aeration rate to be inapplicable to aquaculture ponds.

Experience in shrimp culture has revealed that for each additional horsepower of aeration produced by Asian-style paddlewheel aeration, 400–500 kg more shrimp can be reared. In catfish culture in the United States, the increase in production possible per increase in 1 hp of aeration is likely to be 600–700 kg, presumably because the aerators used in the United States are more efficient than those used in Asia. Tilapia is more tolerant to low dissolved oxygen concentration than marine shrimp or ictalurid catfish, and possibly up to 1,000 kg of tilapia production is possible per horsepower of aeration. Nevertheless, due to the variability of pond dissolved oxygen budgets, the accuracy of the production to aerator horsepower ratio selected in a pond should be continually verified by monitoring the dissolved oxygen concentration.

In the interest of the promotion and achievement of sustainable aquaculture production, the reduction of resource use per unit of aquaculture production is a pervasive goal. Ultimately, direct resource use is conserved by reducing inputs per unit weight of aquaculture production as well as the quantity of waste generated per unit weight of production (Boyd et al., 2017; Chatvijitkul, Boyd, Davis, & McNevin, 2017a). In addition, less inputs per unit of production reduces the amounts of embodied resources used as well as the waste generated in producing the necessary inputs (Chatvijitkul, Boyd, Davis, & McNevin, 2017b). Aeration also allows much greater efficiency of land and water use at the farm level than possible in unaerated ponds, thereby favoring sustainable production practices. Land and freshwater are embodied in feed, but a large reduction in total land and freshwater use can be realized for production levels up to 10,000 kg/ha/crop (Boyd et al., 2017). In some cases, an increase in energy use per unit of aquaculture production with greater production intensity may result, but the trade-off of less land and water in exchange for somewhat more energy seems acceptable.

5 | POND MANAGEMENT SYSTEMS: STRATEGIES FOR SUSTAINABILITY

CRAIG S. TUCKER

The history of pond aquaculture is defined by continuous intensification of culture. Early farmers discovered that fish production could be improved by fertilizing ponds to increase plant growth—the base of the food chain. Fertilizers often were locally available waste products, which integrated pond aquaculture with other human activities. Fish were consumed within the household or traded locally, and for millennia the goal of intensification was simply to grow a greater number of fish.

In the last quarter of the 20th century, wild seafood harvest began to no longer increase as ocean fisheries reached (or exceeded) maximum sustainable yield. Almost simultaneously, goals and incentives to intensify production shifted as new profit opportunities arose. Production systems and management practices were developed to earn more money and produce higher-value products, often for export. The new practices, especially the introduction of pelleted feed to support intensification, had higher rates of resource use and imposed greater (or at least different) environmental impact than extensive, fertilized or lightly fed pond aquaculture (Edwards, 2015).

All these changes occurred during a time of heightened environmental awareness and advocacy. The seemingly unrestrained charge to generate profits was slowly tempered by an awareness that aquaculture systems must be developed with improved resource-use efficiency and reduced environmental impacts. Nonetheless, profit-making remains the key driver of technology innovation and adoption because farms must be profitable to continue operation. But recent experience shows that melding what would often be characterized as contradictory goals of profit-making and sound environmental performance is, in fact, possible because improved resource-use efficiency—a key indicator of sustainability—can also lead to lower per-kg production costs and improved profitability (Bosma & Verdegem, 2011; Boyd et al., 2017; Engle et al., 2017). Recent advances in pond aquaculture technology are good examples of that positive relationship, showing that productive and profitable systems with dramatically improved environmental performance can be developed.

5.1 | Pond aquaculture intensification

Growing more fish involves overcoming a series of limiting factors, which are similar for all aquaculture systems. Assuming some minimum initial set of environmental conditions (such as proper water temperature, salinity, and pH), the limitations on productivity progressively shift from providing more food, to providing more oxygen, to removing growth-limiting waste products (Tucker & Hargreaves, 2012).

Food availability can be increased by enhancing natural food production inside the pond or by adding feeds external to the pond. Natural productivity is increased by fertilizing ponds with organic or chemical fertilizers that stimulate growth of plants (usually phytoplankton) that are the base of pond food chains. Yields from most fertilized ponds are modest—less than 0.5 to 2 tons/ha—but can be surprisingly high, up to 4 to 6 tons/ha, depending on length of growing season, the species cultured, and the type of fertilization program.

Production from fertilized ponds is ultimately limited by solar radiation, which sets an upper limit to how much plant material can be produced. To increase aquaculture yield past that attainable through fertilization, nutrients for growth must be obtained from outside the pond and formulated into a palatable and nutritious feed. In effect, sunlight energy is harvested from outside the pond to overcome the constraints of the limited sunlight-harvesting area inside the pond.

Providing increasing amounts of food does not translate into ever-increasing fish production because most of the feed consumed is not converted to harvestable crop but rather is lost to the water as waste, with potentially negative impacts on the culture environment. Waste nutrients (nitrogen, phosphorus, and other minerals) and waste organic matter (feces and uneaten food) stimulate biological activity that exerts an oxygen demand inside the culture system. At some point in the attempt to intensify production by stocking more fish and adding more food, total pond

oxygen demand will become too high to be offset by natural oxygen inputs (oxygen diffusing into the water from air and produced in daytime photosynthesis) and dissolved oxygen concentrations will fall to levels that stress or kill the cultured animal. The deficit between oxygen production and oxygen consumption must be offset by using mechanical aeration to keep animals alive, healthy, and growing. Supplementing the natural supply of oxygen allows a big step in fish production. Static-water ponds with feeding and aeration can produce 8–10 tons/ha, or more, again depending on length of growing season and physiological characteristics of the animals under culture.

After the system's oxygen demand is met and adequate dissolved oxygen is available to meet the needs of the animal under culture, growth is limited by accumulation of ammonia, carbon dioxide, or other potentially toxic waste products. Ponds have a surprisingly large capacity for waste treatment, as evidenced by the impressive productivity of static-water ponds with feeding and aeration. But the capacity of pond ecosystems to provide waste-treatment services is limited and this, in essence, defines the upper limits of intensification of conventional fed and aerated aquaculture ponds. To go beyond that point, waste products must be removed by other means.

One approach to increasing the rate of waste removal from ponds is to exchange waste-laden water with high-quality water. Water exchange rates in fish and shrimp "ponds" vary from essentially none to several volume-exchanges per day. If water exchange is the principal process used to manage water quality, then the system is functionally no longer a pond, even if cultured animals are held in something that otherwise looks like a pond. Using this criterion, some "ponds" used to grow marine shrimp or pangasid catfishes are not ponds at all because they rely on high rates of water exchange to support high levels of production. Systems that are managed with water exchange have a characteristically different set of environmental impacts than true ponds with no or limited water exchange. Water exchange increases water use, increases the risk of escape and spreading infectious disease, and transfers the ecological and economic burden of waste treatment from inside the pond to other water bodies, which has ethical repercussions and may be subject to legal regulations.

Intensifying pond aquaculture without resorting to water exchange is a daunting technological challenge. One approach is to increase the pond's internal waste-removal capacity by either redesigning the pond to enhance phytoplankton growth (the dominant ecological process in conventional ponds) or by radically changing the internal biological processes responsible for waste treatment. This internal-enhancement concept of waste removal spawned two innovative technologies—partitioned ponds and biofloc ponds. Another approach to address intensification is to enhance waste-treatment capacity on a whole-farm basis rather than in individual ponds. These disparate management technologies have broken the barriers that limit productivity in conventional ponds while improving land- and water-use efficiencies and reducing pollution.

5.2 | Partitioned ponds

Partitioned ponds were developed in the 1990s to integrate fish culture with zero-discharge wastewater treatment (Brune, Schwartz, Eversole, Collier, & Schwedler, 2003; Tucker, Brune, & Torrains, 2014). The original partitioned aquaculture system (PAS) confines fish at high densities in concrete raceways that comprise about 5% of the total pond area. Wastes produced during fish culture are circulated through a large, well-mixed pond based on "high-rate algal ponds" originally designed for domestic wastewater treatment (Oswald, 1963). Potential fish production increases as a result of the system's improved waste treatment capacity. In theory, if you double the rate of net algal photosynthesis, you can double the removal rate of ammonia and other waste products, thereby doubling both the maximum safe feeding rate and fish production.

Net algal photosynthesis is optimized by using a shallow (<0.5 m) basin to reduce the volume of water below the photic zone, ensuring continuous turbulence so that algal cells are continuously swept up into the well-lit surface waters, and removing algal cells from the system using planktivorous tilapia. Continuous algal cropping is necessary before they die and consume oxygen and generate ammonia during decomposition. Net photosynthesis increases by three- to fourfold compared with deeper, unmixed, catfish monoculture ponds. As system management continued to

be refined over time, annual channel catfish *Ictalurus punctatus* production increased to about 20 tons/ha, with an additional crop of 5 tons/ha of Nile tilapia *Oreochromis niloticus*. Catfish production in the PAS is about three- to four times greater than that achieved in conventional catfish ponds, levels that are proportional to the increase in net algal photosynthetic rate. This result is exactly as predicted from the original premise.

The original PAS developed for ictalurid catfish culture has been expanded to greenhouse-enclosed versions for penaeid shrimp aquaculture. The system has produced up to 35 tons/ha of Pacific white shrimp *Litopenaeus vannamei* in temperate, inland regions of the United States at costs competitive with imported farmed shrimp (Brune, Tucker, Massingill, & Chappell, 2012).

The PAS represents the ultimate degree of intensification for ponds where phytoplankton metabolism is the dominant process affecting the environment. However, the original PAS was not widely adopted by fish farmers because the system is operationally complex and costly to build. Two variations of the PAS were developed to make the partitioned pond concept more commercially attractive.

In-Pond Raceway Systems (IPRS) confine fish at high densities in flow-through tanks installed within an existing pond. Aerated water is pumped through the raceways from the pond, which provides the same waste-assimilation functions as the algal basin in the PAS. In-pond raceways similarly benefit from certain features of the PAS, such as facilitating feeding, harvesting, and protecting the fish crop, but are less expensive to build. Although the IPRS was originally designed for catfish aquaculture in the southern United States, use has rapidly expanded for carp and tilapia culture in China, India, Thailand, and other countries.

Split-ponds are another PAS variant, and were developed for ictalurid catfish farming in the southern United States. The concept was based on the sound ecological principles of the PAS but with the goal to reduce the inherent risk of the system and take advantage of existing catfish ponds as a starting point for construction (Tucker et al., 2014). Split-ponds are built by dividing an existing fish pond into two unequal sections by construction of an earthen levee, with water circulated between the two sections with high-volume pumps (Figure 5). In comparison to PAS or IPRS, split-ponds have a relatively smaller algal basin (about 80–85% of the total area) and a larger fish-holding basin.

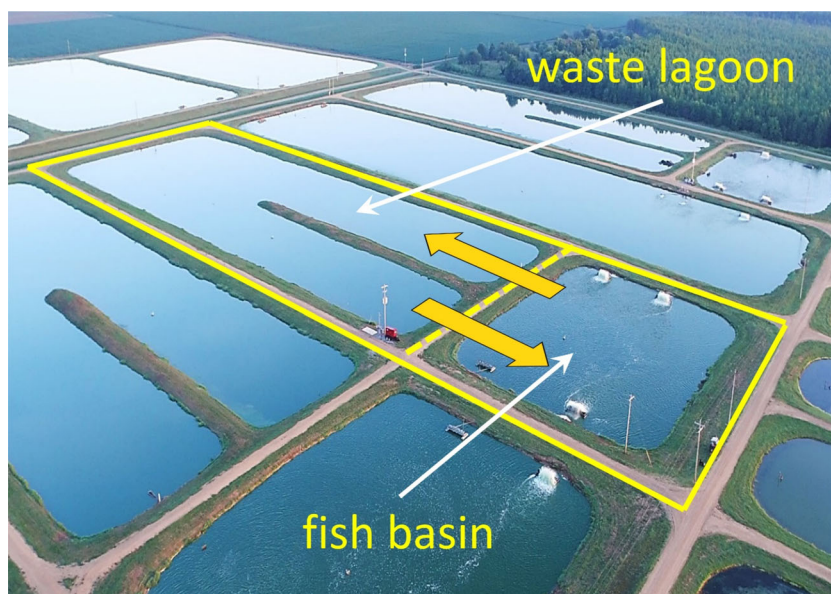


FIGURE 5 Split ponds for ictalurid catfish in Mississippi, USA. The middle pond is highlighted to show partitioning of the original 3.2-ha pond into a 0.6-ha fish-holding basin and a 2.6-ha algal waste-treatment lagoon. Arrows show direction of daytime pumped-water circulation through culverts. Photograph by Danny Oberle

The larger fish-holding basin holds fish at much lower densities than those within the raceways of the IPRS or PAS. The reduced density affords a margin of safety against sudden oxygen depletions during unexpected loss of electrical power.

Unlike the original PAS, the algal basins in IPRS and split-ponds are existing fish ponds with no modifications to enhance algal productivity. Thus, net photosynthetic rates of algae in split ponds and IPRS are not as high as those in the PAS, thereby reducing the system's waste-treatment and fish-production capacity. Nevertheless, fish production in either IPRS or split-ponds can be impressive; for example, ictalurid catfish production in commercial-scale split-ponds in the southeastern United States ranges from 14 to 18 tons/ha, nearly as good as production originally achieved by PAS.

5.3 | Biofloc ponds

All previously described pond-based production systems are "photoautotrophic" because algal metabolism is the dominant process affecting the environment. Photoautotrophic systems are difficult to manage because algal metabolism is affected by weather and other uncontrollable external factors. Of utmost importance is the waste-treatment capacity of photoautotrophic systems, being ultimately limited by the energy available from solar radiation. To intensify pond aquaculture beyond that achievable in photoautotrophic systems and provide better control of the culture environment, intensive pond-based systems have been developed in which oxygen is supplied almost entirely by mechanical aerators and wastes are jointly removed by complex communities of autotrophic and heterotrophic microorganisms (Avnimelech, 2014).

The key ecological feature of these mixotrophic systems is the formation of bioflocs, which are suspended aggregations of algae, bacteria, protozoans, fecal matter, and uneaten feed. In addition to the waste-treatment function provided by biofloc communities, bioflocs are a nutritious food resource produced entirely from recycled waste products. Intensive mixing and aeration are critical to successful operation of biofloc systems because flocs must be suspended in the water column to function properly and effectively counteract the very high respiration rates (Figure 6). Biofloc systems are expensive to build and operate, requiring considerable technical expertise. These systems appear to be most effective and applicable to the culture of animals such as penaeid shrimp, tilapia, and the nursery phase of certain fish which are grown at very high densities and use bioflocs as a nutritional supplement to manufactured feed.

5.4 | Farm-level water recirculation

This concept considers the unit of production to be the whole farm (or blocks of ponds on a farm) rather than individual ponds. Instead of partitioning and optimizing ecological functions within each pond, as in the PAS, different functions are partitioned among separate, outdoor "unit processes," much like a scaled-up, outdoor version of an indoor water-recirculating system. The concept is evolving, and various configurations exist. In high-density shrimp culture, ponds serve primarily as a container, with high densities allowing efficient feeding, aeration, and water treatments. Many modern intensive shrimp ponds have central drains or conical sumps to collect and remove solids. These collected wastes are transferred to anaerobic settling areas where denitrification controls nitrate accumulation and non-oxygen-consuming fermentations reduce the organic load. Water from the treatment pond passes to an aerobic pond or canal where tilapia or other sanitary species are held to graze the excess algae. Throughout the linked system of ponds and canals, water is treated for reuse and return to the shrimp pond. The treatment pond area consists of about 10% of the production pond area in relatively low-intensity culture, but may exceed four times the production pond area on high-intensity farms. A significant benefit of farm-level water recirculation is improved



FIGURE 6 An intensively aerated biofloc shrimp pond in Guatemala. Photographs by John Hargreaves

biosecurity in comparison to conventional ponds with water exchange. Shrimp production differs according to overall system design and management but can be as high as 30–40 tons/ha.

5.5 | Intensification and sustainability

Pond aquaculture productivity varies over at least two order of magnitude, ranging from less than 0.5 ton/ha per year in some fertilized ponds to more than 50 tons/ha in biofloc systems. The magnitude and nature of environmental impacts vary as production intensifies, and the environmental impacts of ponds have a greater range than those of other aquaculture systems (Tucker & Hargreaves, 2012). Many impacts of aquaculture are independent of the type of production system, but ponds have unique attributes that make land and water availability key issues for future expansion of pond-based aquaculture.

Aquaculture production must increase to provide efficiently produced protein to meet the demand of the world's ever-increasing population. Assuming that a large proportion of the additional protein will come from pond production, how, then, should pond aquaculture change to meet that challenge while remaining sustainable? Fertilized ponds, particularly those fertilized using wastes from other activities, are appealing animal production systems because there is little reliance on outside resources for food, energy, and waste treatment. Ecologists and environmentalists often embrace extensive pond aquaculture for its intuitive appeal, but production is relatively low, which undermines the goal of attaining the highest efficiency of land and water use. Although considerable land area in certain regions of the world is available to allow expansion of extensive pond aquaculture (Edwards, 2015), pond aquaculture principally occurs in sensitive wetland or coastal habitats that should be spared to the extent possible. Furthermore, development in some regions is constrained by user conflicts and issues with habitat conversion (Hargreaves, Brummett, & Tucker, 2019).

Full assessment of land use in animal agriculture includes total facility area and all land needed to produce plant feedstuffs. Sometimes included in the overall "ecological footprint" is the area needed to treat wastes. Ponds are unique because waste treatment is principally achieved via internal processes rather than transferring this burdensome process to outside ecosystems. Land use for plant feedstuff procurement usually is the largest part of the ecological footprint for most fed-animal cultures, including ponds. For example, Boyd et al. (2017) calculated land areas needed to produce Pacific white shrimp in Thailand. Average annual shrimp production is 17.3 tons/ha. Each hectare of pond water requires 1.1 ha for facility support (buildings, road, levees, etc.) and 6.4 ha for feed procurement.

With so much land outside the pond devoted to resource procurement, this system would appear to be inefficient. However, the key in the assessment of efficiency is to determine whether increased animal production in intensive systems offsets the increased land area required to support that production. Boyd et al. (2017) examined that relationship and demonstrated that land-use efficiency in shrimp farming improves as production intensifies. The study revealed that improvement in total land use is rapid up to a point, and then changes to a gradual increase at higher levels of intensification but continues to improve over the entire range of production intensification examined.

The large surface area of ponds imposes another liability: Water use in freshwater pond aquaculture can be extraordinarily high. Ponds, even when operated with zero water exchange, offer large surface areas for water loss due to evaporation and seepage. The average annual water use index for inland pond aquaculture is about 15 m³ of water/kg fresh weight of production and may be as high as 45 m³/kg for freshwater fish grown in fertilized ponds. These estimates include water used in all phases of production as well as water used to grow grains used in feeds and are among the highest for any animal agriculture (Costa-Pierce et al., 2010; Verdegem & Bosma, 2009; Verdegem, Bosma, & Verreth, 2006). Intensification can dramatically reduce water use in pond aquaculture. For example, the overall water-use index (including water used in all production phases and water used to produce feeds) for ictalurid catfish fed and grown in conventional aerated ponds in the southern United States may be as high as 12 m³/kg but can be reduced to less than 3 m³/kg by using intensive partitioned ponds, genetically improved fish, and aggressive water conservation practices (Tucker, Pote, Wax, & Brown, 2017). That level of performance compares favorably with total water use for swine (4.7 m³/kg) and poultry (2.7 m³/kg).

Ponds also offer a potential advantage over other culture systems because waste nutrients can be recycled back into a crop, greatly increasing feed-use efficiency. A minority of the feed nutrient content is recovered in the fish crop and the remainder is released to the water as waste. In most net-pen and flow-through systems, these wastes are transported outside the culture unit, where they impose a waste treatment burden. Waste nutrients in ponds are assimilated by endogenous microflora (phytoplankton, zooplankton, and bacteria), thereby transforming wastes into a potential food source at no cost to the farmer. Pond polyculture systems that include fish capable of grazing on plankton can increase overall production and improve nutrient-use efficiency in photoautotrophic systems. Likewise, nutrient recycling into edible bioflocs can increase waste-nutrient recovery and feed-use efficiency in mixotrophic systems.

Low-input, rain-fed or tide-flooded ponds will continue to be an important part of food production in rural, developing regions. Farmers in those regions typically do not use fertilized or lightly fed management practices with

the objective of reducing inputs for environmental benefits, but rather because they lack resources needed to intensify production. Sustainable increases in global food production from ponds will largely depend on improving resource-use efficiency (inputs/kg of production) and not by reducing inputs per hectare and expanding extensive pond aquaculture (Bosma & Verdegem, 2011; Boyd et al., 2017; Boyd, McNevin, & Tucker, 2019; Edwards, 2015). Land- and water-use inefficiencies that are characteristic of older technologies can be addressed through intensification. Ponds also internalize waste treatment to a large degree and offer an array of opportunities to effect waste-nutrient recovery that are easier than those used for other commonly used aquaculture systems. These attributes, together with prudent facility site selection and improvements in resource-use efficiency, ensure that ponds will continue to provide a large share of global aquaculture production well into the future.

6 | SUSTAINABLE FEEDS AND RESPONSIBLE FEED MANAGEMENT— ALBERT G. J. TACON

The rapid growth and development of farmed fed fish and crustacean production over the past two decades has been due in-part to market availability and provision of feed inputs within the major aquaculture producing countries. It follows therefore that if the sector is to sustain its current average annual growth rate of 5.70% (fish) and 9.91% (crustaceans) since 2000 (FAO, 2019), then the external provision of nutrient and feed inputs will have to grow at a similar rate. While this goal may have been readily attainable when the industry remained in its infancy, corresponding growth of needed amounts of nutrient and feed input may not be possible in the future as the sector matures and grows into a major consumer and competitor for feed and food (fish oil) resources with the continuing and larger terrestrial animal feed manufacturing sector (Tacon & Metian, 2015) and humans (in the case of fish oil). Thus, despite its relatively small size (total global aquaculture production reported at 111.95 million tons in 2017 (FAO, 2019), the finfish and crustacean aquaculture sector consumed over 69% of the total global fishmeal production and 75% of the total global fish oil production available in the market place in 2016 (Hua et al., 2019).

According to the latest statistical information from the FAO it is estimated that about 61.8 million tons of farmed fish and crustaceans or the equivalent of 55.2% of the total global aquaculture production in 2017 (FAO, 2019) is currently dependent on an external supply and provision of exogenous nutrient inputs, either in the form of commercially manufactured feeds (the majority), or to a much lesser extent fresh feed inputs. Examples of fresh feed inputs would be the use of lower value trash fish species in the culture of highly valued piscivorous fish and crustacean species or lower-cost farm-made supplementary feed inputs.

6.1 | Rapid growth of commercial aquaculture feed production

Total estimated commercial production of aquaculture feed was approximately 51.23 million tons in 2017 (Table 2). During the period of 2000 to 2017, the commercial aquaculture feed sector has grown over three-fold, from 13.84 to 51.23 million tons. This increase represents an average percentage rate of 8.0% per year since 2000, and is expected to reach 58.85 million tons by 2020 and 73.15 million tons by 2025, respectively (Tacon, unpublished data).

6.2 | Increasing global demand for sustainable sources of feed ingredients

Commercial aquaculture feeds are composed of mixtures of different plant and animal feed ingredients. However, the aquaculture sector has to successfully compete with other terrestrial users for the procurement of these feed ingredients, including the rapidly growing and profitable pet food sector that will commonly pay higher prices. Feed ingredient availability continues to offer the use of the same conventional feed ingredient sources that include plant

Chinese carp feeds	13.55 (26.4%)
Tilapia feeds	9.20 (17.9%)
Shrimp feeds	7.58 (14.8%)
Catfish feeds	5.81 (11.3%)
Marine fish feeds	4.32 (8.4%)
Salmon feeds	3.35 (6.5%)
Freshwater crustacean feeds	2.59 (5.0%)
Miscellaneous freshwater and diadromous fishes	1.82 (3.5%)
Milkfish feeds	1.53 (3.0%)
Trout feeds	1.10 (2.1%)
Eel feeds	0.381 (0.7%)
Total estimated compound aquafeed production	51.23

TABLE 2 Estimated total compound aquafeed production (million tons) by major species group (x) = percent of total

oilseed meals, protein concentrates and oils; captured and aquaculture fishery by-products meals and oils; terrestrial animal by-product meals and fats; cereal by-product meals, protein concentrates and oils; and microbiologically produced single-cell proteins (SCP), including algal, bacterial, and yeast SCP, the feed industry has made significant progress toward the increased use of lower-cost, locally sourced feed ingredients, typically with lower nutrient content and digestibility. For example, the successful reduction in the dietary inclusion level of fishmeal and fish oil within aquaculture feeds has been due to the realization that fish and crustaceans (like all other farm animals) have a dietary requirement for 40 or more essential nutrients (including essential amino acids, fatty acids, sterols, vitamins, minerals and trace elements, etc.) and not for specific feed ingredients such as fishmeal or fish oil. The upshot of the above has been the increased use by aquaculture feed manufacturers of the above mentioned conventional feed ingredient sources combined with the use of specific essential nutrients and feed additives (depending upon the ingredients used), including limiting essential amino acids (i.e., lysine, methionine, threonine, etc.), essential fatty acids (i.e., DHA, EPA, etc.), and/or trace elements (these essential nutrients having been previously supplied by using high-quality fishmeals and fish oils), and more recently specific feed enzymes (i.e., phytase, protease, xylanase, etc.), emulsifiers (i.e., lecithin derivatives, taurocholic acid), acidifiers (i.e., organic acids), and prebiotics and/or probiotics depending upon the cultured species (Huan et al., 2018; Novelli et al., 2017; Tacon, Hasan, & Metian, 2011).

Complementing these efforts, the feed ingredient sector itself has also been introducing innovative processing techniques with the goal of improving the nutritional value of existing conventional feed ingredients through the use of aerobic/anaerobic fermentation technologies and enzymatic acid stabilization/digestion techniques. In particular, fermentation technologies are effective in the destruction/removal of many of the antinutritional factors present within conventional plant oilseed meals and/or through enrichment. Moreover, new emerging feed ingredients sources such as high protein bacterial SCP produced from readily available hydrocarbon substrates, insect protein meals produced from seafood and/or agricultural waste products, and algal SCP rich in *n*-3 highly unsaturated fatty acids (including DHA and EPA) offer the feed industry many new opportunities for reducing its reliance on supply of marine protein meals and oils and increasing the long-term sustainability of the sector (Rossi Jr., Newcomb, & Gatlin III, 2017; Zhuo, Liu, & Lin, 2014).

Notwithstanding the above, whereas ingredient selection in the past was based solely on nutrient level, nutrient digestibility, and cost exclusively, other selection criteria are now being considered by many aquaculture producing countries and consumers within key export markets. Thus, sustainability of use of feed ingredient production, including specific considerations related to feed and food safety (i.e., use of genetically modified feed ingredients, terrestrial ruminant meals, potential feed adulterants, etc.), environmental footprint, and possible import dependency and food security concerns are also increasing becoming important (Tacon et al., 2011; Tacon & Metian, 2008; Tacon & Metian, 2015).

6.3 | Need for responsible on-farm feed management

With over 83.6% of total global farmed fish production being freshwater fish species, 44.66 million metric tons in 2017 (FAO, 2019), and an increasing proportion of these species reared under intensive net-cage based farming systems within public water bodies, including lakes, reservoirs, and rivers (Halwart, Soto, & Arthur, 2007), concern about the potential negative environmental impacts of these intensive open farming systems is growing. This foundations for these concerns reside in uneaten feed and feed and nutrient loss from feed, water pollution and fecal sediment build-up under the cages, fish disease outbreaks and transfer to natural fish populations, and overall ecosystem stability and health (Herath & Satoh, 2015). Therefore, the aquaculture sector will be confronted with an increasing need to ensure that these intensive net-cage farms are operated in an environmentally responsible and sustainable manner. The water in which the fish are reared is a shared public resource used by other stakeholders, including for municipal, agricultural, and/or recreational uses (FAO, 1997). It is clear that future farming systems will have to be increasingly more self-contained, not only in terms of farm biosecurity and potential disease exclusion/impacts, but also in terms of water reuse and minimizing nutrient discharge (Badiola, Mendiola, & Bostock, 2012; Bregnballe, 2015). The role and responsibility of local feed manufacturers in guiding the resident aquaculture sector toward the development of more environmentally friendly production systems and feeds will be of paramount importance in guiding the long-term sustainable development of the fed finfish and crustacean aquaculture sector.

7 | BEYOND JUST NUTRIENT SUPPLY: PERSPECTIVES ON THE USE OF FEED ADDITIVES AS CONTRIBUTORS TO SUSTAINABLE AQUACULTURE— DAVID C. HUYBEN, BRETT D. GLENCROSS

In modern aquaculture feeds, a variety of additives are frequently used to supplement the primary nutrients on which they are based. In addition to the essential nutrients and energy supplied by feeds, a range of additives has become common place for an array of reasons. Additives that mitigate variability in the quality of ingredients, reduce the impact of antinutrients and also strengthen the immune system are now seen as the added value in feeds and constitute a key point-of-difference among many of the marketplace products available to the fish grower (Ringo, Olsen, Vecino, Wadsworth, & Song, 2012).

The use of additives in aquaculture feeds is not a new story. Arguably, among the original “additives” were crystalline amino acids, which were used to make up shortages in essential nutrients not provided by the main protein sources in the diet. However, more recently the use of additives has moved to the use of “functional ingredients” that affect metabolism and physiology either directly (e.g., nucleotides) or indirectly (e.g., prebiotics). The inclusion of such additives has also grown in synergy with an increasing level of intensification of aquaculture systems over the past 20 years. Intensification of culture has notably challenged the health and immune systems of many farmed species while farmers (and by extension the feed sector) are seeking management practices to enhance the immunocompetence of their stock. Some additives have a more beneficial role than others, and their applicability and effectiveness may be species-specific and subject to culture conditions.

7.1 | Prebiotics

Prebiotics are “nondigestible food ingredients that beneficially affect the host by selectively stimulating the growth and/or activity of one or a limited number of bacteria in the colon,” essentially acting as food for probiotics (Gibson & Roberfroid, 1995). Prebiotics are dietary fibers composed of complex carbohydrates that bypass acidic digestion (i.e., the stomach) and act as a substrate for the fermentation and proliferation of probiotic bacteria farther within the intestinal tract. Prebiotics are typically oligosaccharides that are composed of a saccharide polymer

containing only a small number (3–10) of monosaccharides (Gibson & Roberfroid, 1995). Two common oligosaccharides used in aquaculture studies include mannan-oligosaccharides (MOS) and fructo-oligosaccharides (FOS), while lesser common prebiotics include xylooligosaccharides and galactooligosaccharide. In addition to nondigestible oligosaccharides, nonstarch polysaccharides (NSPs) can act as prebiotics, for example, inulin and glucans. Most prebiotics are derived from the cell walls of plants, bacteria, or yeast (e.g., chicory root and oat hulls). Beta-glucans, composed of β -D-glucose polysaccharides, occur naturally in high proportions within yeast cell walls along with MOS, which has led to the common application of disrupted yeast cells (extracts), thereby inducing a combined effect of both prebiotics. Several commercial prebiotics exist in aquaculture and include yeast extracts, barley, or yeast-derived beta-glucan and MOS products, and a mixture of yeast extract and dairy components.

Based on a short review of prebiotics used in intensive systems with common aquaculture species, MOS and beta-glucans were found to be the most used prebiotics followed by yeast extract, inulin, and FOS. Over 10 studies have found that feeding MOS increased growth performance (i.e., growth rate, weight gain, and/or feed efficiency) of Atlantic salmon, gilthead seabream, European sea bass, Nile tilapia, rainbow trout, and whiteleg shrimp (Table 3). Several theories have been presented concerning the mode of action that enables MOS to increase growth performance by stimulating feed intake and nutrient digestibility (Torrecillas, Montero, & Izquierdo, 2014). Studies have found that beta-glucans and MOS improved gut integrity, such as microvilli density and absorption which enhance enterocyte functionality and the transport of nutrients across the intestine (Dimitroglou et al., 2009; Dimitroglou et al., 2011; Refstie et al., 2010). In contrast, the lack of increased growth in non-MOS prebiotic studies is partly due to the exclusive focus on immune response and disease resistance, although several studies have found no effect on growth performance (Bagni et al., 2005; Luna-González et al., 2012).

In some management practices, antimicrobial agents have been eagerly used in excessive amounts to reduce the introduction and establishment of pathogenic microbes via the skin, gills, or gut of aquatic animals (Ringø et al., 2007). Supplementation of prebiotics in aquafeeds has been recognized as the sustainable alternative in effecting an increase in disease resistance by either stimulation of the immune system or proliferation of beneficial bacteria in the intestine that directly or indirectly antagonize pathogenic microbes (Torrecillas et al., 2014). Prebiotics of beta-glucans and MOS have been the most cited for increasing the immune response based on an elevated serum lysozyme activity, oxidative burst, nitric oxide, bactericidal activity, and phagocytic activity of head kidney leukocytes in several aquaculture species, especially European sea bass and rainbow trout (Table 3). Prebiotics can stimulate the gut-associated lymphoid tissue (GALT) and reduce the translocation of bacteria in the intestinal tract, resulting in elevated disease resistance (Torrecillas et al., 2007; Torrecillas et al., 2011). Beta-glucans and MOS supplementation have significantly reduced mortalities in Atlantic salmon, European sea bass, Nile tilapia, rainbow trout challenged with several pathogens including *Aeromonas hydrophila*, sea lice, and *Vibrio* spp. (Dimitroglou et al., 2011; El-Boshy et al., 2010; Refstie et al., 2010; Rodriguez-Estrada et al., 2013).

The intestinal tract is inhabited by microbes, mainly bacteria and yeast, that contribute nutrients and energy to the host while interacting with the GALT and innate immune system to reduce or inhibit pathogenic microbes (Llewellyn, Boutin, Hoseinifar, & Derome, 2014). Farmed fish and shrimp generally have a core microbiota permanently inhabiting the gut (autochthonous bacteria) or transient in the digesta/feces (allochthonous bacteria) represented by the Proteobacteria, Firmicutes, Bacteroidetes, Actinobacteria, and Fusobacteria phyla (Cornejo-Granados, Gallardo-Becerra, Leonardo-Reza, Ochoa-Romo, & Ochoa-Leyva, 2018; Llewellyn et al., 2014). Recent advances in the efficiency and affordability of next-generation sequencing (NGS) technology has provided an advanced tool in identifying bacteria, especially in the gut of aquaculture species. However, the majority of previous research on the effects of prebiotics on the gut microbiota has relied on inaccurate fingerprinting or culture-dependent techniques that only identify a small percentage of gut bacteria (Zhou et al., 2014). For this reason, the previous findings that feeding prebiotics to salmonid fishes resulted in lower or unchanged counts of cultured bacteria may not be an accurate depiction (Bakke-McKellep et al., 2007; Dimitroglou et al., 2009; Ortiz et al., 2013). This finding may be due to shifts in gut bacteria that were not culturable or identifiable by the older techniques. In terms of NGS, two studies have been performed to date using the Illumina MiSeq platform and found that feeding MOS increased the bacterial diversity and the abundance of Firmicutes

TABLE 3 Examples of prebiotics and their effects on common aquaculture species

Prebiotic	[Prebiotic]	Species	Effects	References
Beta glucans	1 g/kg	European sea bass	↔ growth, ↔ FCR, ↑ immunity	Bagni et al. (2005)
Beta glucans and yeast extract	10 g/kg glucans or yeast extract	Nile tilapia	↑ immunity, ↑ disease resistance	El-Boshy, El-Ashram, Abdelhamid, and Gadalla (2010)
Beta glucans and MOS	0.5–1 g/kg glucans or 1–2 g/kg MOS	Atlantic salmon	↑ growth (only MOS), ↑ disease resistance (only glucans)	Refslie, Baeverfjord, Seim, and Elvebø (2010)
FOS and MOS	10 g/kg FOS or MOS	Atlantic salmon	↔ growth, ↑ E retention, ↑ immunity (only MOS)	Grisdale-Helland, Helland, and Gatlin (2008)
FOS	0.25–8.0 g/kg	Whiteleg shrimp	↑ immunity, ↓ gut bacterial composition	Li et al. (2007)
Inulin	75 g/kg	Atlantic salmon	↓ bacterial counts, ↓ gut bacterial diversity	Bakke-McKellep et al. (2007)
Inulin	1.25–10 g/kg	Whiteleg shrimp	↔ growth, ↑ immunity, ↑ disease resistance	Luna-González et al. (2012)
Inulin and FOS	5–10 g/kg inulin or FOS	Rainbow trout	↑ growth, ↓ gut bacterial composition (only inulin)	Ortiz et al. (2013)
MOS	4 g/kg	Atlantic salmon	↔ growth, ↑ N retention, ↑ disease resistance	Dimitroglou, Reynolds, Ravnoy, and Johnsen (2011)
MOS	2 or 4 g/kg	Gilthead sea bream	↑ growth, ↑ N and C digestibility	Gultepe, Salnur, Hossu, and Hisar (2011)
MOS	2.5 or 5 g/kg	Rainbow trout	↑ growth, ↓ FCR, ↑ N retention, ↑ immunity, ↑ disease resistance	Rodriguez-Estrada, Satoh, Haga, Fushimi, and Sweetman (2013)
MOS	0.2 or 0.4 g/kg	European sea bass	↑ immunity, ↑ disease resistance	Torrecillas et al. (2007)
MOS	2.4 or 6 g/kg	European sea bass	↔ growth, ↓ FCR, ↑ immunity	Torrecillas et al. (2011)
MOS and yeast	6 g/kg MOS or 5 g/kg yeast	Rainbow trout	↑ bacterial composition, ↑ gut bacterial diversity (NGS)	Gonçalves & Gallardo-Escárate, 2017
Yeast extract and MOS	10 g/kg extract or 4–10 g/kg MOS	Rainbow trout	↔ growth, ↔ FCR, ↓ gut bacterial composition (NGS)	Betiku et al., 2017
Yeast extract	5 g/kg yeast extract or powder	Rainbow trout	↑ immunity, ↑ disease resistance	Tukmachi and Bandboni (2014)

Abbreviations: N, nitrogen (protein); E, energy; C, carbohydrate; FCR, feed conversion ratio; FOS, fructo-oligosaccharides; MOS, mannan-oligosaccharides; NGS, next-generation sequencing.

in the gut of rainbow trout (Betiku et al., 2017; Gonçalves & Gallardo-Escárate, 2017). Most studies covered in this review have found that prebiotics reduce pathogenic bacteria, such as *Aeromonas* and *Vibrio* spp. (Proteobacteria phylum), while increasing lactic acid bacteria, such as *Lactobacillus* and *Enterococcus* (Firmicutes phylum). This finding is largely regarded as beneficial to the host, although more NGS studies are required.

7.2 | Probiotics

Probiotics consist of living bacteria or yeast that are orally consumed by the animal, colonize the intestine and benefit the host organism (Fuller, 1989). This review only focused on common probiotics in aquaculture that include bacteria species of *Bacillus*, *Enterococcus*, *Lactobacillus*, *Lactococcus*, and *Pediococcus* as well as brewer's yeast *Saccharomyces cerevisiae* (Table 4). Of these probiotics, *Bacillus subtilis*, *Lactobacillus rhamnosus*, and brewer's yeast were the most cited in aquaculture studies with a particular focus on Nile tilapia and rainbow trout. Most probiotics are gram-positive, lactic acid bacteria (Lactobacillales order) and are generally considered as favorable microbes due to their abilities to stimulate host GI development, digestive function, mucosal tolerance, immune response, and disease resistance (Ringo et al., 2018). In addition, yeast are part of the normal gut microbiota and are known to produce enzymes, such as phytase, that benefit the host as well as produce antimicrobial peptides that reduce the incidence and proliferation of pathogens (Navarrete & Tovar-Ramírez, 2014). Beta-glucans and MOS in the cell walls of yeast can provide a source of prebiotics, but yeast cells must be lysed, thereby inactivating yeast and voiding any probiotic effects. Previous studies have found that feeding live rather than inactivated probiotics, such as yeast and *Lactobacillus rhamnosus*, achieved increased effects on the immune system and gut microbiota of Nile tilapia (Panigrahi et al., 2005; Panigrahi, Viswanath, & Satoh, 2011; Ran et al., 2015; Taoka et al., 2006), confirming the positive effects of live probiotics. In practice, feeding live probiotics is accomplished by using cold-pressed feeds or adding probiotics after extrusion (e.g., during lipid coating) in order to avoid inactivation of probiotics by high temperatures and pressure.

Several studies have found that feeding probiotic bacteria and yeast can increase growth rate, weight gain, and/or feed efficiency (i.e., feed conversion ratio [FCR] and nutrient retention) for several aquaculture species, especially Nile tilapia and rainbow trout (Table 4). The increased growth performance produced by use of probiotics is achieved via enhancing metabolic pathways by contributing vitamins (e.g., K and B₁₂), short-chain fatty acids (acetate and butyrate) and enzymes (protease and amylase) that are either not normally produced by the host or sufficiently included in their diet (Merrifield, Bradley, Baker, & Davies, 2010). In addition, probiotic yeast have been shown to increase development of the digestive system in young rainbow trout fry by elevated leucine-aminopeptidase and alkaline phosphatase activity (Waché et al., 2006). Growth performance was particularly increased in studies that used probiotics of *Bacillus* spp., *Lactobacillus* spp., and yeast, although some studies were not successful, especially those fed *Pediococcus acidilactici* (Abid et al., 2013; Ingerslev et al., 2014; Standen et al., 2013; Telli et al., 2014).

Over the years, probiotics have served as a tool to increase growth of aquaculture species. However, focus has been principally directed to their ability to modulate the immune system and increase disease resistance, especially given the increasing problem of antimicrobial resistance (Nayak, 2010). Probiotics interact with the immune cells, such as mononuclear phagocytic cells (monocytes, macrophages), polymorphonuclear leucocytes (neutrophils), and natural killer (NK) cells to enhance the innate immune response in fish as well as interact with the GALT (Nayak, 2010). Many studies have found a significant effect of several probiotics on the immune response of fish that includes; elevated levels of lysozyme, respiratory burst, bactericidal, peroxidase, and/or complement activities as well as leucocyte counts and gene expression of inflammatory cytokines (Table 3). Probiotic improvement of the innate immune system has led to increased survival during exposure to several fish pathogens, especially *Aeromonas anguillarum*, *A. hydrophila*, *Aeromonas salmonicida*, *Streptococcus iniae*, and *Yersinia ruckeri* (Table 4). In addition to fish, a few studies have found that feeding *Bacillus* and *Lactobacillus* spp. to whiteleg shrimp reduced loads of pathogenic *Vibrios* and led to improved water quality, growth rates, immune response, and disease resistance against white spot syndrome virus (Franco et al., 2017; Li, Tan, & Mai, 2009; Nimrat, Suksawat, Boonthai, & Vuthiphandchai, 2012; Zuo, Shang, Shao, Li, & Sun, 2019).

TABLE 4 Examples of probiotics and their effects on common aquaculture species

Probiotic	[Probiotic]	Species	Effects	References
<i>Bacillus amyloliquefaciens</i>	10 ⁴ or 10 ⁶ CFU/g	Nile tilapia	↑ immunity, ↑ disease resistance	Selim and Reda (2015)
<i>Bacillus amyloliquefaciens</i> or <i>Lactobacillus</i> spp.	10 ⁸ CFU/g	Nile tilapia	↑ growth (only BA), ↔ FCR, ↑ immunity, ↑ gut bacterial counts	Raida, Larsen, Nielsen, and Buchmann (2003)
<i>Bacillus coagulans</i>	10 ⁶ , 10 ⁷ or 10 ⁸ CFU/g	Whiteleg shrimp	↑ growth, ↓ FCR, ↑ immunity, ↑ disease resistance, ↑ gut bacterial diversity, ↓ gut bacterial composition (NGS)	Amoah et al. (2019)
<i>Bacillus licheniformis</i>	10 ⁴ CFU/g	Whiteleg shrimp	↑ growth, ↑ immunity, ↑ water quality, ↑ survival	Franco et al. (2017)
<i>Bacillus subtilis</i>	10 ⁷ CFU/g	Gilthead Sea bream	↓ gut bacteria diversity, ↓ gut bacteria composition	Cerezuela et al. (2013)
<i>Bacillus subtilis</i>	10 ⁷ CFU/g	Rainbow trout	↑ immunity, ↑ disease resistance, ↓ bacterial counts	Newaj-Fyzul et al. (2007)
<i>Bacillus subtilis</i> and <i>Bacillus licheniformis</i>	10 ⁸ , 10 ⁹ or 10 ¹⁰ CFU/g	Rainbow trout	↑ growth, ↓ FCR, ↑ N retention, ↑ gut bacterial counts, ↑ survival, ↓ gut bacterial composition	Bagheri, Hedayati, Yavari, Alizade, and Farzanfar (2008)
<i>Enterococcus faecium</i>	10 ⁷ CFU/g	Nile tilapia	↑ growth, ↑ immunity	Wang, Tian, Yao, and Li (2008)
<i>Enterococcus casseliflavus</i>	10 ⁷ , 10 ⁸ or 10 ⁹ CFU/g	Rainbow trout	↑ growth, ↓ FCR, ↑ immunity, ↑ gut bacterial counts, ↑ disease resistance	Safari, Adel, Lazado, Caipang, and Dadar (2016)
<i>Enterococcus faecalis</i>	2.5 or 5 g/kg	Rainbow trout	↑ growth, ↓ FCR, ↑ N retention, ↑ immunity, ↑ disease resistance	Rodriguez-Estrada et al. (2013)
<i>Lactobacillus acidophilus</i>	10 ⁷ CFU/g	Nile tilapia	↑ immunity, ↑ disease resistance	Villamil, Reyes, and Martinez-Silva (2014)
<i>Lactobacillus plantarum</i>	0.05–0.2 g/kg	Nile tilapia	↑ growth, ↓ FCR, ↑ N retention, ↑ immunity, ↑ disease resistance	Hamdan, El-Sayed, and Mahmoud (2016)
<i>Lactobacillus rhamnosus</i>	10 ⁹ , 10 ¹⁰ or 10 ¹¹ CFU/g	Rainbow trout	↑ immunity, ↑ gut bacterial counts	Panigrahi et al. (2004)
<i>Lactobacillus rhamnosus</i>	10 ¹¹ CFU/g (heat-killed, spray-dried or freeze-dried)	Rainbow trout	↑ immunity (only SD and FD), ↓ gut bacterial counts (only SD and FD)	Panigrahi et al. (2005)
<i>Lactobacillus rhamnosus</i>	10 ¹⁰ CFU/g	Nile tilapia	↑ immunity, ↑ disease resistance	Pirarat, Kobayashi, Katagiri, Maita, and Endo (2006)

(Continues)

TABLE 4 (Continued)

Probiotic	[Probiotic]	Species	Effects	References
<i>Lactococcus lactis</i>	10 ⁶ , 10 ⁷ or 10 ⁸ CFU/g	Whiteleg shrimp	↑ growth, ↓ FCR, ↑ N retention, ↑ gut bacterial counts, ↑ survival, ↑ disease resistance	Adel, El-Sayed, Yeganeh, Dadar, and Giri (2017)
Mix of <i>Bacillus subtilis</i> , <i>B. licheniformis</i> , and <i>Lactobacillus</i>	1–8 g/kg	Whiteleg shrimp	↑ growth, ↓ FCR, ↑ immunity, ↑ gut bacterial diversity, ↓ gut bacterial composition (NGS)	Xie et al. (2019)
Mix of <i>Bacillus subtilis</i> , <i>Enterococcus faecium</i> , <i>Lactobacillus reuteri</i> , and <i>Pediococcus acidilactici</i>	1.5 or 3 g/kg	Nile tilapia	↑ growth, ↔ FCR, ↑ immunity, ↑ gut bacterial counts, ↓ gut bacterial composition	Standen et al. (2016)
Mix of <i>Bacillus subtilis</i> , <i>Lactobacillus acidophilus</i> , <i>Clostridium butyricum</i> , and yeast	10 g/kg	Nile tilapia	↑ immunity, ↑ disease resistance	Taoka et al. (2006)
<i>Pediococcus acidilactici</i>	3.5 or 7 g/kg	Atlantic salmon	↔ growth, ↔ FCR, ↑ immunity, ↑ gut bacterial diversity, ↓ gut bacterial counts	Abid et al. (2013)
<i>Pediococcus acidilactici</i>	10 ⁶ CFU/g	Rainbow trout	↔ growth, ↑ immunity, ↓ gut bacteria composition, ↔ gut bacterial diversity (NGS)	Ingerslev et al. (2014)
<i>Pediococcus acidilactici</i>	10 ⁶ CFU/g	Nile tilapia	↔ growth, ↔ FCR, ↑ immunity	Standen et al. (2013)
<i>Pediococcus acidilactici</i> or yeast	10 ⁶ CFU/g	Rainbow trout	↔ growth, ↑ disease resistance, ↓ gut bacterial counts (only PA)	Aubin, Gatesoupe, Labbe, and Lebrun (2005)
Yeast	0.5–5 g/kg	Nile tilapia	↑ growth, ↓ FCR, ↑ N and E retention, ↑ immunity, ↑ disease resistance	Abdel-Tawwab, Abdel-Rahman, and Ismael (2008)
Yeast	5 g/kg	Rainbow trout	↑ gut bacterial diversity, ↓ gut bacterial composition (NGS)	Gonçalves & Gallardo-Escárate, 2017
Yeast	214 g/kg	Rainbow trout	↔ bacterial counts, ↑ bacterial diversity, ↓ bacteria composition (NGS)	Huyben et al. (2018)
Yeast	10 ⁷ CFU/g (live and inactivated)	Nile tilapia	↑ growth (only live), ↔ FCR, ↑ immunity, ↑ disease resistance, ↓ gut bacterial composition (NGS)	Ran et al. (2015)
Yeast	10 g/kg	Rainbow trout	↑ digestive enzymes, ↑ immunity, ↓ gut bacterial composition	Waché et al. (2006)

Abbreviations: CFU, colony-forming unit; FD, freeze dried; N, nitrogen (protein); E, energy; FCR, feed conversion ratio; NGS, next-generation sequencing; SD, spray dried.

The development of NGS technology has increased our knowledge of the minute changes in gut bacteria that occur with and without probiotic supplementation. The only confounding problem is that large variations in bacterial community composition that exist for different time points (Ingerslev et al., 2014), feed compositions (Huyben et al., 2018), fish life-cycle stages (Llewellyn et al., 2016), rearing systems (Lyons, Turnbull, Dawson, & Crumlish, 2017), water temperatures (Huyben et al., 2018), and several other internal and external factors. As measured by older culture-dependent techniques, feeding probiotics tended to increase bacterial counts in a few studies (Adel et al., 2017; Bagheri et al., 2008; Panigrahi et al., 2004; Safari et al., 2016; Standen et al., 2016), while the opposite was also found (Li et al., 2009; Newaj-Fyzul et al., 2007; Panigrahi et al., 2005). In NGS studies, feeding probiotics typically increased bacterial diversity and altered the proportional composition of bacteria phyla in the gut of Nile tilapia, rainbow trout, and whiteleg shrimp (Amoah et al., 2019; Gonçalves & Gallardo-Escárate, 2017; Huyben et al., 2018; Xie et al., 2019). However, there was no clear trend in the effect of probiotics on the relative abundance of bacteria at the phyla level as Proteobacteria were found to both increase and decrease, although two studies found that probiotics reduced the abundance of *Photobacterium* and *Vibrio* that are genera known to include opportunistic pathogens (Amoah et al., 2019; Huyben et al., 2018). Only a small number of probiotic studies that analyze gut microbiota using NGS exist and additional data are needed to evaluate the effects of probiotics on a range of aquaculture species, especially given the confounding internal and external factors mentioned above.

7.3 | Enzyme additives

The use of enzymes as feed additives has been relatively commonplace in the terrestrial animal feed sector for some time, but is definitely less established in the aquafeed sector (Bedford, 1995; Castillo & Gatlin III, 2015; Ravindran, 2013). One of the key challenges for use in aquaculture feed has been the effective addition of enzymes to feed ingredients whereby they do not become denatured and inactivated during extrusion processing or are rendered easily solubilized and lost from a simple top-coating process once delivered into the water. Presently, most commercial enzyme additive use in aquaculture feeds is based on one of three primary functions (Castillo & Gatlin III, 2015):

- increasing the digestion of NSPs (e.g., xylanase),
- reducing the negative effects of antinutritional factors (e.g., phytase),
- accentuating protein digestion (e.g., proteases).

Considerable investigation has been devoted to the use of exogenous enzymes in feeds for a variety of aquaculture species (Cao et al., 2007; Castillo & Gatlin III, 2015; Kumar, Sinha, Makkar, De Boeck, & Becker, 2012). Most of the evaluation of the different enzyme preparations has focused on the efficacy of various carbohydrases/polysaccharidases preparations as well as different phytase preparations to enhance phosphate digestion and mitigate effects of the antinutrient phytate. Therefore, application of these enzymes has been in conjunction with the use of dietary plant protein to mitigate the adverse effects of the additional polysaccharides and phytate.

Studies on carbohydrase/polysaccharidase preparations in aquaculture species have examined a range of different enzyme types including; cellulases, α -galactosidases, β -glucanases, and xylanases (Dalsgaard, Bach Knudsen, Verlhac, Ekmann, & Pedersen, 2016; Glencross, Boujard, & Kaushik, 2003; Jacobsen et al., 2018; Jacobsen, Samuelsen, Girons, & Kousoulaki, 2018; Jiang et al., 2014; Lin, Mai, & Tan, 2007; Yigit & Olmez, 2011) (Table 3). In most cases these various enzymes have been used to increase the digestion of the dietary polysaccharide content of diets where substantial plant protein sources have been included. The effects of the different enzyme preparations have had somewhat mixed effects. The addition of α -galactosidase to feeds containing lupins fed to rainbow trout improved the protein and energy digestibility of the diet (Glencross et al., 2003). The use of cellulases, β -glucanases, and xylanases has been examined with several salmonid species fed diets containing soybean, sunflower, or rapeseed meals with mixed effects observed (Dalsgaard et al., 2016; Jacobsen, Samuelsen, et al., 2018). Some studies have

reported significant benefits from β -glucanase when applied to soybean-based diets, whereas xylanases had limited benefits in such diets (Dalsgaard et al., 2016). In contrast, the addition of a range of enzymes (phytase, protease, xylanase, and cellulase), pre- and postextrusion, showed no benefit compared to when no enzyme was added to the control feed fed to Atlantic salmon (*Salmo salar*); however, the inclusion levels of the enzymes appeared to be somewhat less than that used by other researchers (Jacobsen, Samuelsen, et al., 2018). The addition of exogenous preparations of xylanase and β -glucanase when added to diets for tilapia has produced better results than those observed in salmonids (Lin et al., 2007; Maas, Verdegem, Dersjant-Li, & Schrama, 2018). In many cases improvements in both growth and feed conversion have been observed. In some studies improvements in nutrient digestibility in diets have also been reported (Maas et al., 2018). As a general rule, it seems that the impacts of carbohydrases appear to be dependent on the type of ingredients used in the feeds and also have a greater benefit when fed to tropical rather than cooler water species. The effects of many studies also appear to be complicated by the inclusion of multiple enzymes which does not allow isolation of specific effects.

There has been a relatively long history of demonstrating that phytases provide a dual benefit of mitigating the antinutritional impact of phytate as well as increasing the accessibility of phosphorus from plant meals when fed to aquaculture species (reviewed by Cao et al., 2007; Kumar et al., 2012) (Table 3). The addition of phytase to diets containing high levels of soybean meals has provided demonstrable benefits including improvements in digestibility of protein, phosphorus, and most other minerals when fed to a range of salmonids (Rodehutscord & Pfeffer, 1995; Sajjadi & Carter, 2004; Storebakken, Shearer, & Roem, 1998; Sugiura, Gabaudan, Dong, & Hardy, 2001). Interestingly, Sajjadi and Carter (2004) also found the addition of phytase improved growth irrespective of whether there was phytate in the diet or not. However, recent studies with Atlantic salmon (*Salmo salar*), by Jacobsen, Samuelsen, et al. (2018), found little benefit from the addition of a multi-enzyme complex that contained phytase to any critical parameters of performance, adding to the evidence that suggests the benefits of phytase are quite dependent on dose and raw material choice in the diets used. In other species, studies examining the use of supplemental phytase in diets for Tilapia (*Oreochromis niloticus*) have noted somewhat clearer effects with a greater magnitude of benefit (Liebert and Portz (2007); Maas et al., 2018). Importantly, Liebert and Portz (2007) noted that there were differences between different preparations of phytase. A distinct observation among all these studies has been the predominance of soybean meal as the base ingredient. There are clear reasons for this (e.g., the dominance of supply of soybean as an ingredient globally), but further work examining the utilization of other ingredients is clearly warranted.

In contrast, the number of published studies concerning the application of the other main groups of enzymes, exogenous proteases, or other enzyme types has been somewhat less (Table 4), despite studies reporting their evaluation as far back as the 1970s. Most of the early workup until the past 20 years has been with larval fish (Dabrowski & Glogowski, 1977; Kolkovski, 2001). In salmonids, use of a dietary protease/carbohydrase mix has reported some benefit (Dalsgaard et al., 2016; Drew, Racz, Gauthier, & Thiessen, 2005), although studies by Jacobsen, Samuelsen, et al. (2018), showed limited value of a dietary protease on protein digestion by Atlantic salmon. The addition of a protease to soybean meal based diets fed to Nile tilapia and Gibel carp has also shown some promise as observed by improvements in digestibility, growth, and FCR (Lin et al., 2007; Shi, Li, Chowdhury, Chen, & Leng, 2016). However, studies on the application of proteases in fish are generally lacking and more work is needed in this area.

7.4 | Other additives

A variety of other feed additives are also used in the aquafeed manufacturing sector. They are commonly included in feeds to functionally achieve fortification of the immune system, enhancement of digestion or improvement of quality attributes (Ringo et al., 2012). Most of these additives have already been the subject of other reviews, and detail about their roles as functional ingredients in modern aquaculture feeds will be limited. Moreover, what follows is not exhaustive as other additives exist and are appearing in the marketplace.

Nucleotides are organic molecules that are the simplest units composing the structures of nucleic acids such as DNA. They are abundant in dietary ingredients like fishmeals, but recent studies have largely been based on fortifying diets with exogenous sources. The possible roles of nucleotides in fish diets initially focused on the stimulation of feed intake and fish feeding behavior, whereas more recently, attention has turned to their ability to enhance immunity and disease resistance of a variety of aquaculture species (Li & Gatlin III, 2006; Ringo et al., 2012). Dietary nucleotides have been found to positively influence an array of immune functions, including lymphocyte maturation, activation, and proliferation, macrophage phagocytosis and immunoglobulin responses (Burrells, Williams, & Forno, 2001; Burrells, Williams, Southgate, & Wadsworth, 2001; Do Huu et al., 2012; Li & Gatlin III, 2006; Ringo et al., 2012).

Bacterial peptidoglycans have been the subject of little investigation but are reputed to provide some stimulation of the immune system in fishes (Casadei, Bird, Vecino, Wadsworth, & Secombes, 2013; Casadei, Bird, Wadsworth, Vecino, & Secombes, 2015; Rattanachai, Hirano, Ohira, Takahashi, & Aoki, 2005; Ringo et al., 2012). The beneficial addition of other products from deactivated bacteria have also been reported for other species (Glencross, Arnold, & Irvin, 2015; Sellars et al., 2015), though these additives are less defined in their characterization. Further work is warranted in this area.

Carotenoids are widely used as additives in the salmonid, shrimp, and aquarium fish feed sectors to principally manage muscle and skin coloration (Sales & Janssens, 2003; Torrisen & Christiansen, 1995; Wade, Gabaudan, & Glencross, 2017). The sources of dietary carotenoids are of either natural or synthetic origin and appear to have equal functional activity (Bories et al., 2007; Wade, Gabaudan, & Glencross, 2017). Synthetic astaxanthin is the most widely used pigment in aquaculture, although natural sources from green algae *Haematococcus pluvialis*, red yeast, *Phaffia rhodozyma*, and crustaceans are gaining interest (Wade, Gabaudan, & Glencross, 2017). Carotenoids are used extensively throughout the salmonid sector, principally as a pigment to ensure that certain quality (color) characteristics in the meat are obtained (Torrisen & Christiansen, 1995). Similar objectives of producing pigmentation are obtained in aquarium species (Sales & Janssens, 2003) and in shrimp to meet consumer preference. Dietary carotenoids have also been reported to enhance growth and immunocompetence of shrimp (Wade et al., 2017; Wade, Budd, Irvin, & Glencross, 2015).

7.5 | Challenges and possible future direction of dietary additives for sustainable aquaculture

Interest in pre- and probiotics seems to be at its highest level and commercial products are becoming available around the world for a range of aquaculture species. For prebiotics, many aqua-feeds already contain low levels (less than 1%) of MOS, beta-glucans, or yeast extract because this low level of inclusion is both affordable and effective. Brewery yeast is often readily available to feed producers due to its use in baking and brewing industries, as well as the energy industry that uses yeast to produce bio-fuels. Root vegetables, such as chicory, beet, and onion, contain low levels of prebiotic fibers that are readily available and affordable for easy inclusion in aquafeeds, and this trend will most likely continue.

In contrast, probiotics have to be fed in their live form at a high concentration (e.g., above 7 or 8 logs colony-forming units/g of feed) to aquaculture species to yield beneficial effects. This need incurs more technical costs so that a high live count during feed manufacture, storage, and feeding is maintained. Despite these added costs, probiotics may be characteristically able to target the local immune system and increase resistance against specific diseases. For example, isolation, cultivation, and dietary inclusion of probiotic bacteria derived from individual farms may be more effective than a commercial source of probiotics, which commonly consist of multiple species to increase the chances of success derived from at least one effective probiotic. However, this targeted "pond source" approach would be difficult to manage on an array of small-scale farms, and also underscores the difficulty in finding

commercial sources that are effective in certain aquaculture systems. In addition, the combined use of pre- and probiotics, referred to as “synbiotics,” can further increase the specificity of these feed additives.

There has been substantial progress in the past 20 years aimed at improving our understanding and efficient use of pre- and probiotic in aquaculture, although several shortcomings need to be addressed. Both pre- and probiotics can exist in different forms, doses, microbial species, strains, carriers, sources, and other factors that can influence their effectiveness on growth performance, immune response, disease resistance, and gut microbial communities in aquatic species. In addition, internal factors, such as aquatic species, life-stage and health status, as well as external factors, such as environment and other internal factors of the aquatic animal can influence the effectiveness of pre- and probiotics. Therefore, the following suggestions may lead to improved research and application of pre- and probiotics:

- Consolidated selection of commercially available pre- and probiotics that are specific to individual fish species, life stages, and/or culture conditions.
- Paired testing of individual probiotics with and without prebiotic supplemented feeds rather than cocktails of several pre- and probiotics together.
- Comprehensive studies that include combined analyses of growth performance, immune response, intestinal histology, metabolic pathways, and gut microbiota.
- Analyses of gut microbiota communities using advanced sequencing technologies (e.g., NGS) rather than fingerprinting or culture-based techniques.
- Standardized methodologies for 16S rRNA gene sequencing (e.g., similar DNA extraction, polymerase chain reaction primers, and bioinformatic pipelines) for better comparison.
- Inclusion of environmental samples (e.g., diet and tank biofilm) as well as blank or mock samples in NGS studies to identify potential contamination and biases.
- Rigorous record keeping and reporting of rearing conditions (e.g., temperature) to compare external factors across different studies.

The specific efficacies and benefits of these feed additives must be keenly understood to efficiently improve the growth performance and health of aquaculture species.

A clear opportunity for promoting the potential of carbohydrase enzymes will be their potential to improve the consistency of the nutritional value of plant protein resources (Castillo & Gatlin III, 2015). As the presumed utility of carbohydrase enzymes gains further acceptability across the aquaculture feed sector, the focus on other potentially beneficial enzymes is likely to occur. Prospects for proteases to improve the utility of low-grade protein resources and increase their digestibility, and lipases and esterases to increase the digestibility of lipids in species traditionally unable to metabolize higher levels of lipids are future opportunities (Bedford, 1995; Ravindran, 2013). Identification of such enzymes must be accompanied by technologies that will preserve their activity under commercial feed manufacture conditions.

The use of other functional additives, particularly those that stimulate the innate immune system, will be of increasing importance (Ringo et al., 2012; Vallejos-Vidal, Reyes-López, Teles, & MacKenzie, 2016). While there are a range of existing molecules that are now well known to stimulate the immune system of aquatic animals (e.g., nucleotides), a search for other novel immunostimulants should continue. Application of phytobiotics is a particularly interesting area relative to such investigations (Cristea et al., 2012; Vidanarachchi, Mikkelsen, Sims, Iji, & Choct, 2005).

Additionally, with increasing intensification of aquaculture production, an inevitable increase in the demand for such functional additives to feeds is highly likely. Other future roles for functional feeds and the concomitant use of additives will include the role of environmental benefits, such as improved fecal integrity and reductions in nitrogen and phosphorus discharge. Whereas the role of product quality and expectations with respect to what consumers

demand will continue to rise and thereby increase pressure on the use of additives to maximize quality of the product, whether it be color, taste, or shelf-life (Claret et al., 2014; Haard, 1992).

8 | PROSPECTS OF OFFSHORE MARINE FISH AQUACULTURE AS A VITAL CONTRIBUTOR TO SUSTAINABLE AQUACULTURE AND GLOBAL FOOD SECURITY—LORENZO M. JUAREZ

In a 1971 interview Jacques Cousteau famously stated that... “we must plant the sea and herd its animals ... using the sea as farmers instead of hunters. That is what civilization is all about—farming replacing hunting” (cited by Elizabeth Brubaker in Schneider, 2008). Offshore, or “open-ocean” aquaculture refers to marine aquaculture production systems located at sites characterized by exposure to high energy elements such as winds, waves, storms, and currents, and by lack of protection from land masses (O’Shea et al., 2019). Offshore aquaculture is a relatively new development which did not exist as such in 1968 when the World Mariculture Society was founded; nevertheless, open-ocean farming was already in the imagination of visionaries.

Open ocean aquaculture has its foundation in near-shore fixed cages located in shallow, protected areas. Modern net pen aquaculture probably originated in Japan, where the first commercial culture of yellowtail, *Seriola quinqueradiata*, commenced in 1957 (Milne, 1972). This enterprise was followed by commercial net-pen farming of Atlantic salmon, *Salmo salar*, during the 1960s in Norway (Beveridge, 1987) and then by multiple systems of similar construct for various marine fishes in the United Kingdom and elsewhere. With time, it became evident that ideal, near shore locations were limited and their lack of availability was accentuated by high competition for other uses. Coastal land for support sites was also expensive, and poor water quality was a shortcoming at some sites due to runoff from human activities on land (Cicin-Sain et al., 2005). Additionally, localized effluents and bottom deposits could potentially become problematic. In contrast, deeper, better flushed locations provided better environmental conditions for the growth and survivability of fish and allowed the opportunity to expand farming to highly suitable areas that were not beset by the limitations of near shore sites.

Despite most of the environmental concerns associated with net-pens being attributed to open-ocean aquaculture, the enterprise has developed, and continues to develop with the aid of risk mitigation technologies to address these concerns. Most often, the risks relate to accumulation of wastes on the bottom under the cages, water pollution, transfer of diseases to/from wild fish, and escapes of farmed fish into the wild. The sector continues to build on capabilities and techniques developed by other industries, such as offshore oil and gas exploitation, to allow improved cage performance and survivability. These solutions utilize a combination of better materials, more robust modeling, and careful siting.

Deterioration of water quality and the benthos around farms can occur when nutrient inputs exceed the physical, chemical, and biological capacity of the ecosystem to assimilate them (Pearson & Rosenberg, 1978). Solid wastes from excess, uneaten feed and fish wastes can accumulate on the sea floor in the vicinity of net pens and the oxygen demand created by this organic matter can overwhelm the ocean’s normal aerobic bacterial assimilation processes thereby resulting in anoxic conditions. Effects of net pens on water quality can include increases in levels of nitrogenous compounds and phosphorus, turbidity, oils (from feed), and reductions in dissolved oxygen. During the last few decades, knowledge as to the best ways to manage and minimize these effects has notably increased through proper site selection and by incorporating improved inputs and procedures; for example, research showed that organic matter tends to accumulate beneath net pens in sites of less than 15 m depth and low current velocities (Weston, 1986), so these issues can be avoided by siting farms in waters of adequate depth and current speed. When cages are properly sited, water quality impacts are typically not detectable beyond the immediate vicinity of the cages (Mantzavarakos, Kornaros, Lyberatos, Kaspiris, & Lekkas, 2005; Nash, Burbridge, & Volkman, 2005; Tlusty, Pepper, & Anderson, 2005). The same has been found for benthic deposit accumulation (Cross, 1990; Paramatrix, 1990; Weston, 1986). Feed, normally the greatest operating cost in net pen aquaculture, is a paramount consideration.

Improved feeds that leach less nutrients to the water and are better assimilated by the fish minimize waste and improve the efficiency of feed utilization, benefiting both the environment and the farm's bio-economic results.

Locating farms in deeper waters at least three times the depth of the cages favors waste dispersion and processing by the ocean's natural bio-assimilation processes. Combining deeper waters with sites characterized by moderate, steady currents normally results in minor or no deposition of solid wastes on the bottom. Sophisticated models are now available for siting net pen farms based on the local current velocity, depth, loading rate, and other factors that minimize adverse benthic impacts. Monitoring of benthic quality before startup, and then routinely during operation, is a good management practice that has become a part of environmental regulations in most countries.

Disease transmission and amplification are concerns whenever animals are farmed at high densities. Managers of aquaculture facilities now prevent and control disease events with improved biosecurity measures, effective vaccines, probiotics as dietary additives, appropriate nutrition, use of genetically resistant strains of fish, appropriate rearing densities, and other proven aquatic animal health management strategies. Improved engineering and management have reduced escapes of fish from offshore cages, and our understanding of the genetic consequences of escaped fish has also advanced to the point where models can be used to identify and manage those risks (Rust et al., 2014).

The learning curve for offshore marine aquaculture has been a steep one. Advances in technology during the last few years have led to the acceptance of offshore farming as a highly productive technology with the capacity to produce substantial amounts of fish and become a significant contributor to the world's seafood supply. Better understanding of proper siting requirements has made offshore farming environmentally sustainable through solutions that maintain benthic communities and preserve water quality. Other advances include the development of feeds which can be assimilated more efficiently, and which contain reduced amounts of fish meal and fish oil. Improved health management has greatly reduced the risk of diseases and therefore enhanced economic sustainability. Welch et al. (2019) have shown that a well-sited, properly sized and efficiently operated offshore aquaculture facility has a negligible impact on its environment.

Further development of offshore farming technology will occur as more and more farms operate successfully from both the economic and environmental standpoints. In parallel, improved aquaculture and food security policy, including rigorous but straight-forward permitting processes, would make investment into the sector more inviting. Today, there are multiple offshore farms producing fish commercially. Most are ramping production to support achieving long-term financial viability and market impact.

A recent study (FAO, 2018) shows that open ocean aquaculture has the potential to meet the growing global gap between fin fish supply and demand, while realizing this potential remains an open question. The solution to increased seafood needs will probably be a combination of methods, including properly managed wild-capture fisheries, near-shore farms, offshore farms, and land-based facilities. All these approaches are the subject of significant R&D efforts, and production facilities are in operation and volumes continue to grow. Their ultimate future state is yet to be determined, but their development will be interesting to watch as the market determines the most efficient solutions for specific sites and situations.

9 | A POTENTIAL SCENARIO FOR SUSTAINABLE MARICULTURE USING THE GULF OF MEXICO, USA AS AN EXAMPLE—JOSEPH R. TOMASSO

Mariculture exists throughout the world in different forms (e.g., offshore cages, onshore ponds, and onshore raceways). The type of production system is determined by the needs of the species being cultured and its corresponding economic viability. Some locations are well suited for mariculture. For example, the deep, protected fjords of Norway are ideal for net-pen farming of salmon. Other locations, such as the Gulf of Mexico (GoM), present challenges. Here, I will describe the GoM and present some ideas on how GoM mariculture might be economically and

environmentally sustainable. While limited to the GoM, these thoughts may apply to similar situations found elsewhere in the world.

The GoM is a 1.6 million km² basin with 2,700 km along the southern shoreline of the United States and 2,243 km along the eastern shoreline of Mexico. A wide continental shelf and several large bay systems characterize the GoM (Briney, 2018). This discussion focuses on the U.S. portion of the GoM because mariculture enterprise there will probably be developed as a source of live and fresh product to the nearly 100 million people who live within the five GoM states (Texas, Louisiana, Mississippi, Alabama, and Florida) and nearby states (Georgia, North Carolina, Tennessee, and South Carolina). Most of the Gulf coast of the United States is highly developed (tourism, retirement communities, shipbuilding, oil and gas facilities in support of offshore fields, and shipping). Periodically, highly destructive hurricanes come ashore. The combination of a high level of development and risk of a hurricane strike cause concern about the long-term viability of production facilities along the coast or in the shallow waters of the continental shelf.

In 2016, the U.S. Department of Commerce/NOAA finalized regulations to allow net pen aquaculture in the GoM (Federal Register, 2016). However, in 2018, a federal court held the regulations to be invalid (Alexander, 2018). NOAA has appealed the ruling, and a decision is pending. If eventually approved, offshore aquaculture in the GoM would probably use submerged cages to avoid damage from storms (Alexander, 2018). This approach potentially presents challenges founded in complexity, expense, and risk.

The combined siting of production facilities a few kilometers inland and pumping seawater to the facility may be an alternative to coastal or offshore production. All that would be needed on the coast is an appropriate site to locate a pump station. Thus, by siting the facility inland, very little expensive, environmentally sensitive, and exposed coastline is occupied. Pumping costs should be predictable and can easily be built into a business plan. An inland production site would commonly have the advantage of being located at an altitude higher than that of waterfront property and can offer some protection from the disastrous effects of storm surge. The altitude where the farm might be located would depend on what is available for reasonable purchase and the cost of pumping.

Inland siting of a production facility will not be without challenges, in particular, the securing of a shoreline pumping site and pipeline right-of-way near suitable land where the proposed production facility would be located. Moreover, the mechanics of screening and pumping large volumes of seawater will need to be thoroughly evaluated in association with respect and understanding of local conditions. As with the introduction of new activities in most coastal areas of the United States, the potential emergence of multiple use conflicts will likely result in the need to obtain an array of permits from a diverse group of agencies.

The type of production system used on a farm would be determined by the species selected for culture and the local effluent regulations, often highly restrictive in U.S. coastal regions. Also, because pumping seawater inland can potentially contaminate freshwater aquifers, a thorough investigation of the hydrogeology of the prospective production areas is essential. Inventory control, feeding, and harvesting are easily accomplished in raceways, but raceways generate a constant effluent. Recirculating systems can offer near zero water exchange; however, investment and operating expenses are comparatively higher. Also, recirculating systems do not need a ready source of seawater, so there is no advantage to being located on or near the coast. Thus, ponds probably offer the best option despite also having fundamental challenges. Ponds built near the coast often need to be lined if the soil is sandy. Predatory birds can also potentially create noteworthy problems and their management may be difficult due to possible protected status (Barras, 2007; Barras & Godwin, 2005). Ponds have the advantage of low investment costs relative to raceways and recirculating systems and essentially no effluent except during draining.

The split-pond system (Kumar, Engle, & Tucker, 2016) that has recently been developed may serve as the best production system for nearshore production facilities. The split pond actually consists of two ponds that work together each serving a different purpose. Water circulation between the two ponds is achieved by means of very efficient, low-head water movers. One pond, approximately four times the area of the other, contains no fish or other culture animals and functions as a water treatment facility. The culture animals are held in the smaller pond. At night, when dissolved oxygen levels are low, water flow between the ponds is stopped and the smaller pond is

intensively aerated. During the day, water flow between the ponds is restored and photosynthesis provides the oxygen for faunal respiration. These ponds have consistently produced over 10,000 kg/hr of catfish (calculated based on total area of the two ponds in the system). Because the fish are concentrated within a smaller area, aeration can be better targeted there. Also, with high-value marine fish as a subject of farming, placement of bird netting over the production pond may be economically practical. A good discussion of split-pond systems and a comparison to other production systems is presented in Kumar et al. (2018).

Effective management of effluent in coastal environments can be challenging, and solutions will be site specific. The best strategy is to limit the generation of effluent as much as possible. When split ponds are built, the openings between the ponds can be gated to allow lowering or draining of the small pond to permit harvesting without draining the larger pond. The use of settling ponds will allow solids to settle from the water column before effluent is discharged from the culture facility. In areas where nutrients need to be removed, constructed wetlands may be appropriate. Whatever the selected treatment of effluents, the costs of the process need to be included as a part of any business plan. Tucker (1999) provides a good introduction to effluent management.

The GoM has a well-developed commercial fishing industry (National Marine Fisheries Service, 2016). Finfish markets exist for red snapper, *Lutjanus campechanus*, cobia, *Rachycentron canadum*, red drum, *Sciaenops ocellatus*, spotted sea trout, *Cynoscion nebulosus*, southern flounder, *Paralichthys lethostigma*, and many more species. Many of these species are euryhaline which expands other possibilities for siting of inland farms. Estuarine organisms live in a range of dilute seawater salinities; therefore the pump station for the production facility does not need to be immediately located on the GoM—it can be on the shore of one of the many bays along the GoM. Red drum and spotted sea trout are widely produced for stock enhancement programs by state resources agencies. The technology for reproduction and fingerling production is well developed. Resource agencies are also developing expertise in the production of southern flounder fingerlings. If markets can be identified, then these species may be good starters for inland GoM culture. Indeed, commercial red drum farms have been operating near the GoM coast for several years with varying levels of success.

Production of native species on inland farms offers two advantages over non-native species. First, distribution channels already exist and may be available and useful for marketing of farmed products. Second, permitting and effluent management would be simplified because potential escapement of native species would not be an issue.

To this point, the focus has been on finfish; however, shrimp (several species of the family Penaeidae) and blue crabs (*Callinectes sapidus*) are also economically important products of the GoM. Estuarine shrimp culture in ponds is well developed. However, most shrimp culture occurs in tropical areas where multiple crops can be harvested each year. Blue crabs are in high demand. They are difficult to culture, but may offer an option for a second crop—perhaps in the water treatment pond of a split-pond system. This integrated aquaculture approach would provide a second crop with limited inputs. However, the possible implementation of such an approach will need to be studied carefully. There may be incidences at times during the evening, the water quality in the water treatment ponds may not support survival of invertebrates. Additionally, ways need to be developed to prevent invertebrates from entering the fish culture ponds, given that they will likely be stocked with carnivores.

Before any plan for building a production facility is executed, the species to be cultured needs to be identified. Species selection is determined by three critical aspects:

- 1 Species and production system compatibility: Some species do well in pond culture, while others flourish in raceways, tanks, or net pens.
- 2 Supportive infrastructure: Are fingerlings and feed that you need reliably available at a reasonable price? Are both engineering and fish health expertise available near your facility?
- 3 Marketing: This is the most important aspect. In the United States, probably the most common reason for failure of aquaculture businesses is the lack of identification of suitable and sufficient markets before investments are made and production initiated. Where are your markets, both geographically and demographically (who buys the fish from you) for the candidate species? Understanding the details of the presentation of the product (size of fish

demand, live or on ice, seasonal or year-round demand) is critical. Complementing this information must be a knowledge of the depth of the market (how much fish can it absorb). What will people who buy your fish pay for it, and what is the price elasticity as farmed fish hit the market?

The cost of production may commonly result in difficulty in competing with lower costs that characterize the imported, frozen product market. Fish and shellfish can usually be produced at lower costs in tropical, developing countries, and transportation is not a major cost factor. Developed, temperate countries are at a disadvantage with respect to cost of production, but do have the advantage of proximity to markets demanding live and fresh product.

In summary, aquaculture along the U.S. GoM coast has potential. Well-developed fisheries already exist, demonstrating the marketability of the products. Much of the technology described here is already in use elsewhere, and the scenario put forward helps address the two most overt shortcomings of successful sustainable GoM aquaculture—the high cost of competing for the multiple uses of coastal land and the fear of catastrophic weather events. Undoubtedly, the role of entrepreneurship will be as large as the production technology adopted in achieving successes.

10 | THE ROLE OF DOMESTICATION TO HELP ENHANCE SUSTAINABLE FISH AQUACULTURE PRODUCTION—FABRICE TELETCHÉA

Domestication is the process by which groups of different species of animals become progressively adapted to both humans and captivity. During domestication, captive animals are modified generations after generations and gradually diverge from their wild ancestors and, at some point, are considered domesticated (Teletchea, 2019a). Although the first domestication trials of fish actually started about 8,000 years ago with common carp *Cyprinus carpio* and later Nile tilapia *Oreochromis niloticus* (Balon, 2004; Nakajima, Hudson, Uchiyama, Makibayashi, & Zhang, 2019; Teletchea, 2019b), noteworthy efforts began during the early 1980s in response to both increasing demand of seafood coupled with a decrease in the contribution of global capture fisheries (Pauly & Zeller, 2016; Teletchea, 2019c). As a result, worldwide aquaculture production currently relies on the farming of species for which domestication has either just commenced or, for some species of fish, have occurred due to genetic and morphological modifications during numerous successive generations (Klinger et al., 2013; Teletchea, 2019b). To better describe this diverse array of production, Teletchea and Fontaine (2014) have proposed a new classification based on the human control of the life cycle of farmed species and the link between captive fish and their wild congeners. This classification consists of five levels of domestication. Level 1 corresponds to the first conducted trials of domestication (i.e., initial transfer of wild fish into a rearing system). Level 2 is reached when only a portion of the life cycle is controlled in captivity due to the existence of key bottlenecks (e.g., control of only larval rearing or spawning of breeders under farming conditions). Level 3 is achieved when the entire life cycle is closed in captivity, yet wild inputs are still used, principally to maintain genetic diversity. Level 4 is achieved when wild inputs are no longer used, a condition that occurs when a genetic barrier between wild and captive is established. The final level (5) involves the application of breeding programs focusing on specific goals (Teletchea & Fontaine, 2014). Based on the analysis of the FAO aquaculture production database from 1950 to 2009, among the 250 fish species listed in 2009, 70% appear to belong to the first three levels of domestication (Teletchea, 2019c). In addition, the farming of 67 species ceased after only a few years of production (Teletchea, 2019c). This analysis thus highlights the fact that trials of domesticating new fish species most commonly either rapidly failed or reached only low production levels (Bilio, 2008; Teletchea, 2019c). For example, Fontaine and Teletchea (2019) recently described the domestication of Eurasian perch *Perca fluviatilis* in Europe where farming started in the early 1980s and reached only a few hundreds of tons.

Thus, an analysis of the recent history of aquaculture reveals that successful development of the farming of a new species is highly problematic. Success is dependent on the interaction of numerous factors, principally in nature being biological (disposal of wild individuals, capacity to control the life cycle under artificial conditions), economical

(economic return, acceptability by consumers, competition with other animal products, particularly imports from developed countries), and environmental (availability of suitable sites and water, competition for use of other resources) (Jobling, 2016; Teletchea, 2019b). The 20 most-produced species that are globally responsible for more than 90% of aquaculture production by volume fall within Level 3 ($n = 2$), Level 4 ($n = 7$), or Level 5 ($n = 11$). Thus, even though controlling the entire life cycle of a fish species in captivity is not always a prerequisite to produce a large quantity (Ottolenghi, Silvestri, Giodano, Lovatelli, & New, 2004), levels of domestication and production are partially correlated (Teletchea & Fontaine, 2013). In other words, domestication contributes to increased production (Teletchea, 2019c). Half of the 20 most produced species are cyprinids ($n = 10$), followed by cichlids ($n = 2$), and salmonids ($n = 2$) (Teletchea, 2019c). Sixteen inhabit freshwaters, four are diadromous, and none is strictly marine (Teletchea, 2019c). In 2016, the proportional contribution to the total production for the first three species ranged between 32.8 and 89.2% in Asia and Oceania, respectively (Table 5). Atlantic salmon, *Salmo salar*, ranked first on three continents (it was introduced in both South America and Oceania), contributing from one-third up to two-thirds of the total finfish production (Table 5).

Atlantic salmon is certainly the fish species for which the domestication history is best known (Teletchea, 2019b) and was the first species to be subject to a systematic family-based breeding program. Currently, over 12 generations have been consecutively bred in captivity for the oldest breeding programs in Norway (Glover et al., 2017). Common carp, *Cyprinus carpio*, production held third place on three continents, varying between 2.0 to 9.1% of the total production. Rainbow trout, *Oncorhynchus mykiss*, ranked twice at the second place, with a contribution of 9.4 and 13.2%. Both common carp and rainbow trout have been introduced into numerous countries for farming (Teletchea, 2019b). Seven other species were ranked within the top three only once for each of the five continents (Table 5). For marine aquaculture only, the top three fish species, gilthead seabream, *Sparus aurata*, European sea bass, *Dicentrarchus labrax*, and Japanese amberjack, *Seriola quinqueradiata*, represent together nearly 40% of the global production in 2013, when excluding groups not identified at the species level (Teletchea, 2015). It is notably

TABLE 5 Top three fish species produced by continents in 2016, with the contribution of each species within the continent (based on the FAO database)

Continents	Top 3 species ^a	%
Africa	1. Nile tilapia, <i>Oreochromis niloticus</i>	56.9
	2. North African catfish, <i>Clarias gariepinus</i>	10.8
	3. Common carp, <i>Cyprinus carpio</i>	2.8
Americas	1. Atlantic salmon, <i>Salmo salar</i>	33.9
	2. Rainbow trout, <i>Oncorhynchus mykiss</i>	9.4
	3. Channel catfish, <i>Ictalurus punctatus</i>	7.4
Asia	1. Grass carp, <i>Ctenopharyngodon idella</i>	12.7
	2. Silver carp, <i>Hypophthalmichthys molitrix</i>	11.0
	3. Common carp, <i>Cyprinus carpio</i>	9.1
Europe	1. Atlantic salmon, <i>Salmo salar</i>	65.2
	2. Rainbow trout, <i>Oncorhynchus mykiss</i>	13.2
	3. Common carp, <i>Cyprinus carpio</i>	7.0
Oceania	1. Atlantic salmon, <i>Salmo salar</i>	64.2
	2. Chinook salmon, <i>Oncorhynchus tshawytscha</i>	14.8
	3. Southern bluefin tuna, <i>Thunnus maccoyii</i>	10.2

^aThe “not elsewhere included (nei) groups” were taken into account to calculate the percentage of the total production, but are not listed as one of the top three species.

obvious that despite the increasing number of farmed fish species in the past decades, global aquaculture production today continues to be heavily skewed toward the production of only a few species (Teletchea, 2019b, 2019c).

Through the course of domestication, species that reached Level 5 have been significantly modified from their wild congeners. Currently, about 10% of global aquaculture production is estimated to be based on genetically improved individuals (Gjedrem & Rye, 2018). In Europe, the proportion of aquaculture production that originates from selective breeding is much higher, with a market share that exceeds 80% (Janssen, Chavanne, Berentsen, & Komen, 2017). Atlantic salmon clearly appears as an outlier with 100% of production based on improved stocks (Teletchea, 2019b, 2019c).

Historically, selective breeding programs principally focused on growth performance, morphology, disease resistance, and meat quality (Gjedrem & Rye, 2018; Janssen et al., 2017). For instance, the average genetic gain in growth rate for 44 estimates of groups for the major farmed fish species, like Atlantic salmon or Tilapia, is 14.3% per generation (Gjedrem & Rye, 2018). New traits, such as age at sexual maturity or feed efficiency were progressively added to breeding programs (Gjedrem & Rye, 2018; Janssen et al., 2017). Improving feed efficiency, that is, either reducing feed consumption per kg of fish produced, or increasing fish production from the same amount of feed, is essential to achieve an enhancement of the sustainability of fish production, as feed is a major economic cost, accounting for 30–70% of total production costs (de Verdal et al., 2018), and a key environmental issue of fish production (Cashion, Le Manach, Zeller, & Pauly, 2017). A complementary solution to further reduce the reliance of aquaculture on marine fishery resources is to decrease the use of fishmeal and fish oils in feeds, with concomitant increases in the dietary amounts of plant protein and oil sources (Jobling, 2016). Several breeding programs are now specifically focusing on the selection of fish that are able to efficiently use novel dietary ingredients of feed, such as in rainbow trout (e.g., Lazzarotto, Médale, Larroquet, & Corraze, 2018). More recently, it has also become increasingly evident that climate change arising from global warming, may alter aquaculture production strategies due to the occurrence of saline water intrusion, water stress, and ocean acidification (D'Abramo & Slater, 2019; Sae-Lim, Kause, Mulder, & Olesen, 2017). Therefore, breeding programs should also focus on the production of robust animals not suffering from inbreeding depression that will have the physiological traits to be able to effectively cope with those anticipated changes and production systems that will have to evolve as well (D'Abramo & Slater, 2019). Importantly, the welfare of farmed fish is also becoming a key issue as for land farmed animals for which strong negative side effects for several reproduction, health and metabolic traits have become more apparent for some highly inbred breeds selected only for high production efficiency (Teletchea, 2016). Therefore, welfare of farmed fish should be addressed, and properly evaluated, by using, among others, the only exhaustive database on this topic: FishEthobase (Saraiva, Arechavala-Lopez, Castanheira, Volstorf, & Heinzptter Studer, 2019; Saraiva, Castanheira, Arechavala-Lopez, Volstorf, & Heinzptter Studer, 2019).

The sustainable future of aquaculture will rely first on the continuous improvement of already domesticated fish species, such as Atlantic salmon, Nile tilapia, or rainbow trout to become both more efficient and resilient to global changes. Sustainability will also depend on our will and capacity to diversify the number of farmed species and thereby avoid, as much as possible, introduction of the same species throughout the world (Teletchea, 2016, 2019a, 2019b). Such a strategy might also help to eliminate, or at least minimize, the adverse ecological and genetic impacts of either direct or indirect introduction of alien species (De Silva, Nguyen, Turchini, Amarasinghe, & Abery, 2009). In recent years, the resolve to promote native species for aquaculture enterprise has resulted in significant changes in various countries, particularly in South America (Ramos Valladão, Gallani, & Pilarski, 2016). For example, the production of pacu *Piaractus mesopotamicus* has increased substantially in recent years, and has exceeded the production of the alien rainbow trout in 2012 in Argentina (Ramos Valladão et al., 2016).

Domestication is a powerful tool to both continue improving the production of already domesticated species and farm new and exclusively native species. Maintenance of a balance between the two approaches will depend on our resolve to achieve a more even and diverse, and probably more resilient, aquaculture production during the coming decades.

11 | THE ROLE OF INTEGRATED PRODUCTION SYSTEMS FOR SUSTAINABLE AQUACULTURE—GEORGE S. LOCKWOOD, WAGNER C. VALENTI

The United Nations (United Nations, Department of Economic and Social Affairs, Population Division, 2019) has estimated that the world population will increase from the level of 7.7 billion in 2019 to 9.7 billion in 2050, and this estimate may actually be low. The rising middle classes in developing countries are resulting in a greater demand for meat protein as a substitute for plant protein. However, sufficient meat protein derived from terrestrial production systems will be unable to satisfy this new demand. In fact, to produce this additional meat, new tillable land equivalent to the area of South America would be required. Expansion of the required additional plant production would also require considerably more fresh water resources than are available to grow the plant protein needed to feed the animals (Rosenberg, 2017).

Conventional terrestrial production of meat would also generate dramatic increases in the amounts of greenhouse gas that contributes to climate change. World capture fisheries are not the solution as their sustainable limits have already been realized and cannot be significantly expanded. Thus, new sources of protein cannot be produced using conventional technologies and management practices or through commercial overfishing. Finding methods for the most efficient conversion of our limited amounts of plant protein into meat protein is critically important. If global food shortages develop, widespread malnutrition and human suffering are inevitable. Such conditions will most probably foment civil unrest and perhaps civil or international wars as people without food seek to forcibly obtain food from those who do have food.

Under sustainable aquaculture practices, meat protein production potentially offers the least environmental impact. Nonetheless, reliable methodology that will yield a compellingly comparative assessment of different food production sectors using environmental economics is needed (Knowler, 2007). In contrast to freshwater resources, marine water resource will not be a limitation for expanding the production of fish and shellfish (Gentry et al., 2017). The area of ocean surface required to produce sufficient amounts of farmed fish to meet the increasing protein demand is equivalent to the area of the Great Lakes in the United States. Therefore, marine aquaculture offers a feasible and efficient solution to increase the supply of protein necessary to feed the increasing global population. Focus on those animals with high protein retention allows for the use of less amounts of dietary plant protein per unit of animal protein.

11.1 | The concept of integrated aquaculture

The farming of a singular species, called monoculture, is largely practiced throughout the world at different levels of density. Some species, such as filtering mollusks and algae, derive their food from the environment and even at very high levels of density do not need to be fed. Others, such as most species of the fish and shrimp, need allochthonous (outside) sources of food and generally are farmed in Intensively Fed Monoculture (MIF) systems. In contrast, two or more species can be farmed as part of an aquaculture enterprise in which the sharing of the same pond, tank, cage, or pen, or nearby areas occurs. Under these conditions, some kind of relationship is maintained whereby some resources such as space, water, feed, or nutrients in general are shared among the different species, thereby offering the potential for increased efficiency. These systems may include terrestrial organisms such as plants, swine, and aquatic birds among others.

In the past, the production of more than one aquatic species in the same culture unit, such as ponds, tanks, net-cages, and pens, was termed polyculture, whereas when aquatic and terrestrial organisms were produced together, the culture was termed integrated aquaculture (IA) (Muir, 1995). Over time, these terms have evolved leading to a change in their meanings. According to the FAO Glossary (FAO, 2020), polyculture means the rearing of two or more noncompetitive species in the same culture unit, whereas IA is defined as the culture of aquatic organisms

based on the sharing of resources that originate from agricultural, agro-industrial, wastewater, power stations, and other activities. Neori et al. (2004) described IA as derived from traditional extensive polyculture, that is, the culture of fish or shrimp with microalgae, vegetables, shellfish, and/or seaweed, and emphasized use of biofiltration in marine systems. In integrated farming, the waste outputs from one subsystem generally become an input to another subsystem resulting in higher efficiency of producing aquatic organisms. According to the same glossary, this integrated farming, integrated multi-trophic aquaculture (IMTA), combines the cultivation of fed species (e.g., finfish/shrimp) with organic extractive species (e.g., shellfish/herbivorous fish) and inorganic extractive species (e.g., seaweed) in the appropriate proportions to create balanced systems for environmental and economic sustainability, and social acceptability (FAO, 2020). Research that investigated the potential of IMTA began during the early 1970s and included several different models that used fish, bivalves, and algae under both small- and pilot-scale conditions. Neori, Shpigiel, Guttman, and Israel (2017) and Neori, Guttman, Israel, and Shpigiel (2017) provide information about the investigative evolution of the IMTA models with combinations of directly fed and extractive species. In the early 1970s, seabream and mullet were grown in seawater containing earthen ponds that contained flowing water with large microalgal populations that recycled through bivalve and macroalgal populations. In the 1980s, this work included the quantification of nutrient budgets in these systems followed by investigations in the 1990s when additional species of interest were added, and the global relationship between sustainability and related economics of IMTA was the investigative focus.

Chopin, Cooper, Reid, Cross, and Moore (2012) stated that the term IMTA is very flexible and may comprise many variations of the traditional definition, which includes open-water, land-based, and aquaponics systems. The advantage of conversion of our limited amounts of plant protein into meat via production of aquatic animal production systems can be substantially improved through IMTA systems (Lockwood, 2018). In IMTA, nutrients (metabolic products) derived from one production system are complementarily used in another production system to produce more protein. Feed costs of IMTA systems are thereby distributed among two or more multi-niche commercial crops whereby carbon can be captured and sequestered, and loss of valuable soluble nutrients is avoided. Thus, this type of IMTA has the potential to produce more meat protein from a given amount of plant-derived ingredients in feed than achieved with other conventional production systems. For example, an integrated large-scale system consisting of abalone, sea urchins, salmon and oysters along with aquatic plants to feed them has been developed. Instead of being wasted, most of the metabolites produced by the group of organisms cultured serve as nutrients for others. Currently, IMTA is practiced where metabolites/uneaten food from salmon grown in floating net pen ocean culture are transferred from the pens by currents and used as nutrient sources by adjacently located large leafy macro-algae and filter-feeding mollusks (Buck et al., 2018; Chopin, 2013a, 2013b; Chopin et al., 2010). This is a unique approach to further increase the efficiency of aquatic plant and animal production to satisfy future global demand for meat.

The most important characteristic is the farming of a combination of species that show complementary ecosystem functions. A large and variable combination of species may be possible in IA whereby significant advantages for the use of natural resources, biomitigation, and improved sustainability are realized. Organisms that occupy the same trophic level can also be produced if they make use of different food webs. Organisms that occupy different spatial areas in the same culture unit, such as pond water column and bottom, may feed on components of the same trophic level, for example, phytoplankton (autotrophic) or detritus (heterotrophic), using the grazing and detritus food webs. Generally, the species that feed on the grazing food web provide detritus as food for detritivore species. Farmed species sharing the same space may have different feed habits, such as fishes that live in the water column, eating different organisms of the same trophic level, such as herbivorous copepods and cladocerans. Therefore, a broader definition of IA may be the culture of species that occupy different ecological niches in the same culture unit (or in the proximity where interactions occur), and in the more appropriate proportions maximize the use of natural resources and minimize the production of potential pollutants liberated into the environment by liquid or gaseous effluents. This integration may be called Integrated Multi-Niche Aquaculture (IMNA). Split-pond aquaculture (Brown & Tucker, 2013; Kumar et al., 2016; Tucker et al., 2014) is based on a high efficiency concept whereby very high production intensities of fish that are located in one area of a pond are separated from the remaining area where

algae absorb the nitrogenous metabolites produced by the fish and during the day release oxygen (photosynthesis) into the water that is then pumped to the side where fish are held. The area that does not contain fish may potentially serve for culture of another organism occupying a different niche.

11.2 | Levels of integration

Generally, in IA, one or more species are defined as the principal species and the others as secondary species. Different levels of IA can be conceived, according to the level of integration among the species farmed together:

- Level 1: The cultivated species occupy different spaces in the same production facility. All aquaculture systems that use pelagic and benthic species are in this category. However, very frequently, the level of integration is higher because more interactions occur.
- Level 2: The cultivated species occupy similar habitats but different ecological niches. The polyculture of silver carp, *Hypophthalmichthys molitrix*, which eat phytoplankton, with big-head carp, *Aristichthys nobilis*, which eat zooplankton and grass-carp, *Ctenopharyngodon idella*, which feed on plant material is an example.
- Level 3: The cultivation of one species improves the environmental conditions for the other species. For example, the culture of silver carp and big-head carp, in low density, with freshwater prawn brings significant improvements in phytoplankton stability, improving the water quality conditions for the prawns.
- Level 4: The cultivated species is a source of by-products that can be used as inputs for the cultivation of other species. Marine integrated farming of salmon, mussels, holothurians, and macroalgae is an example. Salmon generate particulate organic wastes which are ingested by benthic holothurians and filtering mollusks, as well as dissolved nutrients that are absorbed by macroalgae.
- Level 5: The cultivated species originates by-products, which are inputs for the other and vice versa, for example, in rice-fish IA, the leftover rice, after harvest, serves as food for fish, while their feces and excreta serve as fertilizers for the vegetables. In addition, fish and shrimp control plant competitors and insects, which are pests to rice culture. Another widespread example is freshwater prawn-fish farming. Freshwater prawns feed on the feces and leftover diet from the pelagic fish (e.g., tilapia, carps, tambaqui, lambari, etc.), while the bioturbation of prawns suspends the nutrients accumulated in the bottom, increasing the plankton available for fish grazing.

Integrated systems are very different from polycultures, which do not take into account most of the relationships among the farmed species. The IA is always complex, increasing from Levels 1 to 5. Generally, more than one level of integration can be recognized in most of the IA systems. In addition, biomitigation, reduction of environmental impacts and ecosystem services are frequent bonuses obtained in IA (see Song, Pang, Pingping, & Sun, 2020, for example). Appropriately configured, IA systems can sequester carbon rather than emit it. Global food production is responsible for about one third of all greenhouse gas (GHG) emissions (Wallace-Wells, 2019), and approximately 15% is derived from livestock emissions (Hawken, 2017). Reduced GHG emissions from IA are a very important factor in the effort to simultaneously combat global climate change and the challenge of establishing global food security. Higher levels of integration may involve terrestrial and aquatic animals and plants and most often its complexity increases. The use of terrestrial flora in aquaponics is an example of IA that is complex but flexible, whereby urban aquaculture can be realized with significant gains in sustainability.

11.3 | Advantages of IA for sustainable bioeconomy development

Bioeconomy has been noted as a major field for sustainable development in the current century. Aquaculture certainly is included in this field, and decision-makers have developed a high expectancy that the culture of aquatic

organisms will be essential to feed the billions added to the global human population in the next decades. The high efficiency in producing aquatic animal protein is evident when compared to the terrestrial ones (Table 6). Protein retention efficiencies of aquatic animals, such as salmon, are notably higher than those of terrestrial animals, such as beef and pork (Marine Harvest, 2017). Salmon produce twice the amount of protein as beef per unit of protein fed, therefore representing an attractive, alternative source of meat protein. In addition, each kilogram of salmon produced represents a reduction of 27 kg of CO₂ discharged into the environment relative to the production of beef, thereby reducing the production of GHG. Aquatic organisms are more effective in producing biomass because they are poikilothermic and have no energy requirements to maintain body temperature and produce ammonia rather than uric acid (birds) or urea (mammals) as a nitrogenous waste product. Comparatively higher fecundity permits the use of less space for maintenance of the needed broodstock (Tidwell, 2012). These contrasting biological characteristics also result in higher levels of productivity for aquaculture. One hectare of land can support the production of less than a ton of beef, whereas the same water area can support more than 100 ton of fish by year.

Monoculture intensively fed (MIF) has been stated as a very efficient and productive aquaculture model and much science-based knowledge has been generated to support these systems. The efficiency of production realized through MIFs is much higher than that of terrestrial animals. Generally, to produce 1 kg of cattle takes 7–8 kg of feed, 1 kg of swine 3–4 kg, and 1 kg of poultry 2–3 kg, whereas 1 kg of fish is produced using ~1.5 kg of feed (Tidwell, 2012). Nevertheless, MIF is still very inefficient in converting food in biomass. A feed conversion ratio of 1.5 means that 1.5 kg of diet, containing ~90% of dry matter, produce 1 kg of fish, containing 20–25% of dry matter. Thus, the efficiency is only ~18.5%. Therefore, more than 80% of the organic material contained within the feed is lost either as particulate matter or dissolved nutrients to the environment or incorporated into the biomass of aquatic biota with no economic value.

Like terrestrial production systems, MIFs use high-quality commercial diets that generally represent 50–80% of the production costs and high-value fishes and shrimps are the primary products. Considerable effort has been devoted to the reduction of the FCR in MIF. For this, a balanced diet of macronutrient and micronutrients is essential. The most efficient diet would ideally match the gene expression of the target species. However, aquaculture does not use domesticated species with homogeneous gene pools. On the contrary, different lots and strains of animals may have different genetic profiles which confer different nutrition requirements and this condition increases the difficulty of developing a specific-balanced diet for farmed fish or shrimp. Nutritional research allied with research on genetic improvements is a long term and costly endeavor. A dilemma may arise as the effort to reduce genetic variability and homogenize strains may lead to increased susceptibility to diseases and adverse environments. The resulting lack of range of response compromises farm sustainability.

The IA uses different species to explore the commercial diet and natural resources available in commercial aquaculture enterprise. Using different species allows the opportunity to decrease FCR without genetic and diet improvements because different species (genetic pools) have abilities to explore the different source of resources. Nutrients and energy resulting from metabolic products or wastes derived from one species farmed are recycled when used by another species resulting in higher efficiency to explore the available resources. Feed costs of IA systems are shared

TABLE 6 Environmental factors associated with meat production (farm gate) from different species (adopted from Marine Harvest (2017))

	Protein retention (%)	Edible meat per 100 kg feed	Carbon footprint kg CO ₂ /kg meat	Freshwater consumption L/kg edible meat
Beef	15	4–10	30	15,400
Pork	18	17	5.9	6,000
Chicken	21	21	2.7	4,300
Salmon	31	61	2.9	2,000

among two or more commercial crops whereby carbon can be captured and sequestered, and the loss of valuable nutrients is reduced. MIF systems do not have this benefit. Franchini, Costa, Pereira, Valenti, and Moraes-Valenti (2020) farmed three non-genetic improved species (*Colossoma macropomun*, *Macrobrachium amazonicum*, and *Prochilodus lineatus*), by supplying an unspecified fish diet, in experimental earthen ponds (0.01 ha) for 2 months. They showed that the FCR, which generally ranges from 1.1 to 3.0 for monoculture of these species (Dantas et al., 2020; Moraes-Valenti & Valenti, 2010), might decrease to 0.61–0.42 in a IA culture system when considering the total harvested biomass. This result indicates that a change in the paradigm from improving feed quality to introducing new species into the system may effectively improve feed use, thereby increasing the level of sustainability. Scientific literature provides plenty of examples like this, mainly for carps or fish-prawn IA systems (Marques et al., 2016; New & Valenti, 2017). Certainly, IA also benefits from genetic and diet improvements and such studies remain essential for aquaculture development. Efforts to reduce FCR will reach a limit. Thus, maximizing the use of diet and natural resources is essential toward moving to another paradigm. IA may be the foundation for achieving more competitive costs of aquatic animal production relative to terrestrial animal production. IA may be both an innovative and disruptive strategy to produce aquatic organisms.

The evident advantages of IA in comparison to MIF as supported by experimental results have not been observed under commercial aquaculture conditions. This lack of verification may exist because farmers practice IA in a rudimentary way and receive little or no scientific support. Technological development primarily addresses MIF systems and is readily available for technicians, decision-makers, and farmers. Compared to MIF systems, very little attention has been paid to IA systems by scientific researchers and stakeholders, perhaps because of their inherent complexity which discourages such actions. Investigations that focus on the content and flow of nutrients in each compartment (including the integrated species) and the carrying capacity of IA systems have been performed (David, Proença, & Valenti, 2017a, 2017b; Flickinger, Costa, Dantas, Moraes-Valenti, & Valenti, 2019; Flickinger, Dantas, Proença, David, & Valenti, 2020; Gao et al., 2019; Song et al., 2020). Such information is essential to the development of ecosystem engineering and establish a suitable proportion for each integrated species. However, the state of knowledge remains insufficient to plan balanced systems. Some analyses have demonstrated the profitability of coastal and inland IA systems (Boock et al., 2016; Fonseca, David, Ribeiro, Wainberg, & Valenti, 2017; Knowler et al., 2020; Rodrigues, Engle, Garcia, Amorim, & Valenti, 2019). Nevertheless, these preliminary results are insufficient to convince the more resistant stakeholders to change paradigms. Without additional knowledge, researchers, professors, technology-transfer persons, technicians, and farmers will consider an evolution to a disruptive model of production like the IAs to be too risky.

The challenge of attaining sustainable aquaculture is to develop innovative systems, environmentally, socially, and economically well balanced that optimize production efficiency and maintain the health of coastal and inland ecosystems (Valenti, Kimpara, Preto, & Moraes-Valenti, 2018). The aquaculture systems should produce food, using a comparatively lower amount of natural resources, energy, and recycled wastes while generating ecosystem services at the same time. The architecture of the IAs matches these requests. They are much more efficient than MIF to use resources and recycle wastes. It is possible to save space and water, optimize the use of nitrogen, phosphorous, carbon energy and decrease the emission of GHGs and pollutants in the effluents. The best results are attained by commercial farming of high value species from different trophic niches and with complementary ecosystem functions (IMNA), regardless of the trophic level or taxonomic position. Algae, holothurians, mollusks, crustaceans, and fishes can integrate the systems. Usually marine systems are currently cited in the literature although IAs are more developed in freshwater systems. The IA of different species of carps, tilapias and prawns, as well as the rice-fish and rice-prawn cultures, are relatively well developed worldwide (Marques et al., 2016). Some marine farms culture salmon integrated to macroalgae and filter-feeding mollusks, placed adjacently in a way that extractive organisms feed on the salmon wastes and metabolites (Buck et al., 2018; Chopin, 2013a, 2013b; Chopin et al., 2010). The mollusks and macro-algae are valuable additional commercial crops that utilize nutrients and carbon that would be lost to the environment in their absence.

The theoretical basis for implementation of IA is well established and should be effectively adopted by the production sector. Currently, freshwater IA has great social and economic importance in some Asian countries, but still needs to be commercially expanded worldwide. Commercial expansion seems to be limited by the complexity of management that resides in the balancing of the quantitative and qualitative flow of nutrients to the crops and the accompanying increase in costs. Another contributing constraint is the lack of interest of some scientists and decision-makers who do not believe in IA systems. In addition, some scientists have no desire to change to investigations with different species due to lack of seed production of extractive species as well as restrictive legislation in some countries.

11.4 | Perspectives for the future

Research effort is still required to establish the basis for marine IA, although a large number of articles have been published in recent years. The IA has the potential to produce more meat protein from a given amount of plant input than that of other production systems. The setup of IA in open-ocean areas and the introduction of fish and prawns in the millions of hectares of rice culture have a considerable potential in helping to meet the global animal protein demand in the near future. In contrast to IA, conventional aquaculture that is sustainable is poised to make a major contribution to satisfying the large increase in global demand for meat protein that is projected during the next 30 years. In the absence of the enhanced benefits of IA, salmon production still yields twice the amount of meat per unit of plant protein consumed. This feed efficiency, characteristic of aquatic animal production and enhanced through IMTA, can be further improved through advances in genetics (domestication) and nutrition, particularly through application of knowledge that is being gained about diet-dependent influence and control of the composition of gut microbiome. These combined management practices can be accomplished to yield retail costs that are competitive with those associated with terrestrial animal production. These comparative costs should also serve as a foundation to encourage more consumption of fish and shellfish to replace beef, pork and poultry products. Consumers would benefit from the recognized nutrient value of fish and shellfish. In addition, improved protein retention efficiencies with and without IMTA contribute to economic and environmental sustainability achieved through reduction of potentially harmful waste discharges and reduced amounts of GHG.

The bioeconomy (and other areas of economy) may be developed using a linear or circular economy approach. Linear economy, based on the principles of “take, make, use, dispose, and pollute,” is the traditional way to produce and has been almost exclusively followed during the past century. Circular economy is based on looping systems that are characterized as “take only a few times, make, use, reuse, remake, recycle, and make again.” This new concept is founded on the responsible use of resources to promote sustainable development (Moraga et al., 2019).

The MIF matches the concepts of the linear economy, whereas the IA clearly matches the concepts of the circular economy which is undoubtedly the best choice to develop the bioeconomy and support the implementation of the Sustainable Development Goals. An aquaculture 4.0 will be based on use of updated technologies and innovations designed to improve the efficiencies of management practices, product quality and the ability to compete successfully in the market. This upgrade of approach will most probably be based on highly technological processes and controls, such as the internet of things, artificial intelligence, machine learning, cybernetics, and the principles of the circular economy. For aquaculture 4.0, as with all industry 4.0, certification of sustainable production will be an essential component of marketing strategies.

As we confront the challenges of achieving global food security and all of the adverse environmental and societal costs that will be inflicted by global climate change, the obvious solution is efficient protein production systems that are dually founded on intensive and integrated aquatic animal farming. IAs will definitely play a vital role in developing sustainable aquaculture systems in the present century.

12 | SUMMARY

This collection of essays provides a foundation of knowledge that will undoubtedly be tested, applied and ultimately manifested in sustainable aquaculture systems. The essays represent an exciting blueprint for what aquatic animal production systems will look like in response efficiently producing protein to meet the demands of an estimated global population of approximately 9.4 billion by 2050. As a foundation, definitions and paths to sustainable aquaculture have been presented. It is evident that intensive aquaculture systems will have to predominate as they have been demonstrated to be the most efficient. These systems must operate using technology and management practices that are reliable, offer reduced risk of catastrophic loss, and adhere to regulatory policy. An aquaculture 4.0 will be based on the use of updated technologies and innovations designed to improve the efficiencies of management practices, product quality and the ability to compete successfully in the market.

For those management practices where the aquatic organisms will need to be fed, nutritionally complete sources of feed will be essential and must be efficiently digested to reduce waste. Novel feed ingredients that are readily available in sufficient quantity must be developed to serve as partial replacements or exclusive alternatives to reduce costs or eliminate the use of sources that are not sustainable. Two exciting areas of applied research are the use of ingredients characterized as pre- and probiotics. When supplied in an active form these ingredients positively alter both the qualitative and quantitative intestinal microbiome to yield improved growth efficiencies. More importantly, in the capacity of altering the microbiome, immunocompetence to pathogenic organisms is conferred, representing a significant contribution to sustainability whereby the use of sub-therapeutic levels of antibiotics as a common management practice in systems can be eliminated. If technological bottlenecks can be eliminated, another possibly significant contributor to economic and environmental sustainability may reside in the rise of IA systems to maximize efficiency via simultaneous production of more than one species.

While finite amounts of freshwater and land resources are limiting increases in freshwater aquaculture production due to competition with terrestrial animal production, the highly underutilized resources of marine coastal areas of the world remain very attractive as a solution to meeting protein demand. Coastal and offshore production systems are attractive because of the potential to meet global production demands dramatically while using comparatively less resources than those consumed on land. The application of needed technology can result in efficient management practices that can be applied to cage culture of fish. These efforts must be combined with an effort to diversify the number of domesticated farmed species by using species native to particular areas of the world. This goal would hopefully eliminate the farming of species that are good aquaculture candidates but are considered to be exotics relative to particular regions of the world. Climate change may become the greatest threat to continued and increasing levels of sustainable global aquaculture. Inevitable changes in physical and biological conditions will need to be confronted by the ability to make changes in management practices (site, species) including the use of more suitable organisms from selective breeding programs.

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How to cite this article: Boyd CE, D'Abramo LR, Glencross BD, et al. Achieving sustainable aquaculture: Historical and current perspectives and future needs and challenges. *J World Aquacult Soc.* 2020;51: 578–633. <https://doi.org/10.1111/jwas.12714>