CellPress

Gold Standard
for the Global Goals
1 ton of
CO_2 offset

One Earth

Perspective

Interventions for improving the productivity and environmental performance of global aquaculture for future food security

Patrik John Gustav Henriksson,[1,2,3,*] Max Troell,[1,3] Lauren Katherine Banks,[2,4] Ben Belton,[2,5] Malcolm Charles Macrae Beveridge,[6] Dane Harold Klinger,[7,8] Nathan Pelletier,[9] Michael John Phillips,[2] and Nhuong Tran[2]
[1]Stockholm Resilience Centre, Kräftriket 2B, Stockholm, Sweden
[2]WorldFish, Jalan Batu Maung, Penang, Malaysia
[3]Beijer Institute of Ecological Economics, The Royal Swedish Academy of Science, Stockholm, Sweden
[4]Department of Biology, University of Waterloo & Canadian Rivers Institute, Waterloo, ON, Canada
[5]Department of Agricultural, Food, and Resource Economics, Michigan State University, East Lansing, MI, USA
[6]Faskally, Dollerie, Crieff, Perthshire, Scotland, UK
[7]Center for Oceans, Conservation International, Arlington, VA, USA
[8]Department of Nutrition, Harvard T.H. Chan School of Public Health, Boston, MA, USA
[9]Food Systems PRISM Lab, 340 Charles Fipke Centre for Innovative Research, University of British Columbia, Kelowna, BC V1V 1V7, Canada
*Correspondence: patrik.henriksson@su.se
https://doi.org/10.1016/j.oneear.2021.08.009

SUMMARY

Aquatic foods are increasingly being recognized as having an important role to play in an environmentally sustainable and nutritionally sufficient food system. Proposals for increasing aquatic food production often center around species, environments, and ambitious hi-tech solutions that mainly will benefit the 16% of the global population living in high-income countries. Meanwhile, most aquaculture species and systems suffer from large performance gaps, meaning that targeted interventions and investments could significantly boost aquatic food supply and access to nutritious foods without a concomitant increase in environmental footprints. Here we contend that the dialogue around aquatic foods should pay greater attention to identifying and implementing interventions to improve the productivity and environmental performance of low-value commodity species that have been relatively overlooked in this regard to date. We detail a range of available technical and institutional intervention options and evaluate their potential for increasing the output and environmental performance of global aquaculture.

INTRODUCTION

Sustainable food provisioning is increasingly recognized as one of the most pressing environmental challenges of our time, as food production contributes substantially to the risks of disrupting the Earth system.[1,2] Food production is estimated to account for 25% of greenhouse gas emissions, 75% of all deforestation, 70% of freshwater withdrawals, and largely all nitrogen, phosphorus, and pesticide emissions.[1] These environmental challenges are often attributed to our focus on enhancing productivity over resilience, through monocultures dependent on anthropogenic input, such as inorganic fertilizers, fuels, pesticides, and feed.[1,3] Terrestrial-animal-source foods, dominated by a handful of species, have disproportionately high impacts on the environment.[2,4,5]

Farmed fish add to these impacts, but have been estimated to have 87% smaller carbon footprints than beef, use 49% less land than poultry, and require 84% less stress-weighted fresh water than pigs.[4] It has also been projected that the production of aquatic foods (defined here broadly as fish and other aquatic animals) will increase by 32% between 2018 and 2030.[6] As only marginal increases (optimistic maximum $\approx$15%) in aquatic food production can be expected to result from improved fisheries management,[7,8] aquaculture's contribution to global aquatic food production is expected to increase from 46% in 2018 to 53% in 2030.[6] Aquaculture is highly diverse, comprising numerous species and systems with varied environmental impacts and nutritional values,[5,9–11] ranging from marine bivalves, which require minimal input during grow-out, to filter-feeding freshwater finfish species (e.g., silver and bighead carps), to omnivorous finfish and crustaceans that commonly rely on plant-based feed with partial inclusion of fishmeal and fish oil, to carnivorous finfish, including tuna, which can consume up to 20 times their weight in wild fish.[5,12–14]

Historically dominated by extensive and improved-extensive pond-based farming systems sometimes supplemented with agricultural by-products, the aquaculture sector has, over the past few decades, been increasingly steered toward intensification through the use of pelleted feed in marine, brackish-water, and freshwater environments.[15,16] These pelleted feeds are generally produced from a mix of fishmeal and fish oil, agricultural products, animal by-products, and micronutrients, often tailored to support the nutritional needs of individual species. Each of these ingredients is associated with its own set of environmental concerns, making feed the major driver behind many environmental life-cycle impacts caused by fed aquaculture.[17]

Intensification of fed aquaculture has consequently shifted resource needs from on-farm to: (1) other agricultural land, often in locations remote from the farm, for production of crop-based feed ingredients; (2) open waters for fish-based feed ingredients (fishmeal and fish oil); and (3) additional exogenous energy inputs (infrastructure, pumps, aeration, etc.) and/or land that may be used to maintain water quality (i.e., settling ponds).[17–21] Overall, intensification may aggravate some environmental concerns, such as acidification, eutrophication, and freshwater ecotoxicity, but reduce others, such as freshwater consumption.[18]

Fulfilling the potential of aquaculture to contribute positively to food system transformation will require better accounting of the environmental performance of different types of production systems, and interventions that facilitate upscaling of aquatic farming to support sustainable diets.[4,22] Some recent literature on this subject proposes that most of aquaculture's potential for environmentally sustainable growth lies in one of three domains: (1) marine finfish aquaculture (i.e., in offshore systems), (2) recirculating aquaculture systems (RASs), and/or (3) bivalve production.[7,23,24] The first two domains are expensive to operate and intensive, with a high reliance on off-farm resources. The third, bivalve production, is challenged by low edible yields, limited consumer demand, and more demanding processing and logistics.[25,26] We contend that the existing literature overlooks large "performance gaps" in existing conventional aquaculture systems, especially freshwater pond systems, that could be rapidly narrowed to meet future global demand for more sustainable aquatic foods. This approach would particularly benefit those most in need of the essential nutrients offered by aquatic foods.

In this perspective we reflect on the evolution and performance gains of different aquaculture farming systems in relation to terrestrial animal production. Given the great diversity of aquaculture species and production systems, we group production into four categories of aquatic food species: accessible commodity, accessible niche, luxury commodity, and luxury niche. Among these, we find that, while Atlantic salmon may have experienced gains comparable to those of broilers, most aquatic foods still suffer from substantial performance gaps (the gap between attainable and actual yields). We subsequently explore a variety of interventions that could close the performance gap in aquaculture, and thereby improve the environmental profile of global aquaculture. Nine intervention areas are identified for improving the productivity and environmental performance of global aquaculture: species choice, genetic improvements, farm technologies and practices, spatial planning and access, disease reduction, feed, regulations and trade, post-harvest processing and distribution, and financial tools. We argue that these could have the most impact if geared toward boosting accessible-commodity aquatic food species, as they play a vital role in food security and providing nutrients for low-income consumers. At the same time, they have experienced relatively limited advancements in farming to date, due to diverse farming practices, limited access to capital investments, and small profit margins.

CHALLENGE: THE PERFORMANCE GAP IN AQUACULTURE

In agriculture, reducing "yield gaps" (here defined as the difference between observed and attainable yield in a given region)[27] is often promoted as a way of meeting food security and sustainability challenges. Narrowing or closing of yield gaps in terrestrial crop production is generally achieved through better nutrient, chemical, or freshwater management.[28] In animal production systems, including aquaculture, attainable yields are also greatly influenced by feed availability and quality, access to genetically improved strains, sound biosecurity, and access to therapeutants and vaccines. Although competition among different uses of land and water can limit scope for spatial expansion of aquaculture in some locations, the availability of feed resources, technological capacity, and socioeconomic factors, such as demand, generally pose greater constraints to increasing fed aquaculture production.[29–32] Fish have metabolic advantages over terrestrial animals, as they are cold blooded and neutrally buoyant in water and thus do not need to expend energy maintaining body temperature, building supportive structures, or fighting gravity. Some forms of aquaculture do not compete for land (e.g., cages or suspended bivalves), and in forms that do (e.g., ponds), farmed aquatic animals utilize all three spatial dimensions (length, breadth, and depth) for production. Aquatic animals subsequently have biological advantages over terrestrial livestock in terms of their resource-use profiles.[8,33] However, given the short history of farming for most aquaculture species, few have reached the levels of efficiency seen in the highly homogenized terrestrial-animal production systems, such as poultry farming.

Benchmarking the environmental performance of aquatic foods

Feed conversion ratio (FCR) is commonly used as an efficiency indicator in aquaculture, since it, at least in theory, accounts for feed utilization, conversion of feed to body mass, and the survival of stocked organisms. FCR meanwhile disregards differences in feed ingredient components, feed quality, moisture content of feed and farmed aquatic products, and information about co-produced species and edible yields.[33,34] For example, some marine fish species are still fed whole wild fish, while carps often are fed agricultural by-products. Other species, such as salmon, have been partially weaned off carnivorous diets and are today raised using diets composed predominantly of agricultural feed resources.[5,35,36] Agricultural feed resources used to produce carnivorous fish species are generally of higher quality than those fed to omnivorous fish, but also allow for higher retention of nutrients.[34,36] The simplicity of FCR, however, allows farmers to easily benchmark their performance and recognize farming improvements. FCR can also serve as an indicator of environmental performance, as feed production remains the primary driver behind most environmental impacts related to fed aquaculture systems.[37]

Where more comprehensive efficiency measures are needed, life cycle assessment (LCA) enables evaluation of environmental performance and trade-offs on a multi-criteria basis.[18,33] LCA is a quantitative environmental assessment framework used to assess the environmental performance of a product or service throughout its life-cycle stages. The environmental impact assessment results produced by an LCA commonly detail impacts such as global warming, eutrophication, land use, and freshwater use, but may also include more aquatic-food-specific impacts, such as biotic resource use.[38] Most dietary comparisons based upon LCA results tend to generalize aquaculture into one or a few broad groups (e.g., circulating and non-circulating; fish and other "seafood"; freshwater finfish, farmed freshwater finfish, tuna, crustaceans, mollusks, etc.).[39,40] Relative LCA results are, moreover, heavily influenced by how the authors derive environmental footprint estimates for food categories. For example, David et al.[41] report 0.59 kg CO_2-equiv kg^{-1} seafood, while Shewmake et al.[42] report 8.94 kg CO_2-equiv kg^{-1} on average for "fish and seafood," with a minimum of 0.08 and a maximum of 15.06. Such discrepancies can result from differences among species and production system, but also reflect limited availability of LCA studies from which impact estimates are derived, as well as the differences in the methodological choices that condition them.[38] Moreover, such results are rarely weighted to represent actual production volumes and systems. This means that, in the literature on sustainable diets, aquatic foods are generally overrepresented by Atlantic salmon, which is the most researched aquaculture species.[38] Atlantic salmon farming constitutes one of the most homogeneous and intensive aquaculture practices, while the omnivorous species and freshwater finfish (especially carps [Cyprinidae]) that represent the majority of aquaculture production globally are underrepresented in LCA literature.[38]

Hilborn et al.[43] benchmark carp but present it as environmentally unfavorable compared with both Atlantic salmon and pork, based upon estimates from a report by Hall et al.[44] Hall et al.,[44] in turn, detail extensive, semi-intensive, and intensive carp production systems, but unfortunately mix up on-farm electricity consumption with embodied industrial energy,[45] resulting in the suggestion that electricity generation contributes more than half of the global warming and acidification impacts of carp production. MacLeod et al.,[46] in turn, assume all carp to be fed at an FCR of 1.7–1.8, despite the fact that global carp production comprises, by roughly one-third, filter-feeding silver and bighead carps,[47] and an estimated quarter of all carps are produced in extensive systems without external feed input.[15,44] These examples illustrate that, to date, no LCA-based comparison of global aquaculture has been able to capture the diversity of farming systems for cyprinids, nor has any LCA utilizing empirical data from China (where 71% of all cyprinids are farmed) been published. Henriksson et al.[18] show that the environmental performance of carps from Bangladesh can differ by two orders of magnitude, depending on farming system and the individual farms. This suggests that there is a large potential for efficiency improvement in carp farming, which makes up 54% of global finfish production or 36% of global aquaculture production (excluding aquatic plants).[47]

Comparing the evolution of animal farming sectors

Farming of aquatic organisms dates back millennia, but it was only in the 1980s that shrimp and salmon became the first mass-produced and widely traded farmed aquatic foods. Profitability and, to some extent, environmental sustainability concerns motivated large investments in R&D for improving Atlantic salmon production systems, genotypes, and feed.[35] Today's Atlantic salmon is the 12th selectively bred generation from Norway, which, together with better feed and farming practices, has reduced the FCR from 2.2 to 1.3, while nearly eliminating antimicrobial use (i.e., in Norway), reducing fishmeal and fish oil in feed, increasing growth rates, and achieving higher fillet yields (Figure 1).[35,48,49,50] This trend is similar to that of poultry, which is currently the most resource-efficient large-scale terrestrial-animal production system.[4,50,51] Tilapia was domesticated (cultivated for food) by humans before Atlantic salmon and has similar genetic potential with regard to improved growth rates and feed-use efficiency,[52] but has yet to show the same FCR gains. This is most likely explained by more limited R&D in breeding and feed, poorer dissemination of improved strains, less access to quality feed, higher metabolic rates of tropical finfish, and more heterogeneous farming systems.[53] Carps constitute a group of species with the longest history of farming, but have undergone more limited R&D. Development and adoption of improved genetic strains suited to individual farming systems and commercial tailored feed has been especially slow.[15,54]

Feed efficiency is only one of many breeding objectives in selective breeding programs. For example, the rate of egg laying for hens in the United States has increased by 46% between 1960 and 2010,[58] and the inclusion of animal products in Atlantic salmon feed decreased from 89% to 25% between 1980 and 2016 due to market considerations.[35] All of these promote net gains in edible protein and other nutrient output per input and have the potential to lower environmental impacts.[58]

While the salmon industry rapidly became a hyperefficient animal production system,[50] carps, tilapia, shrimp, and most other aquaculture species continue to be farmed in a diversity of systems and fed variable diets, resulting in more modest performance gains. Few of these systems have benefited from other improvements in the sector, such as genetic improvements and disease reduction, that could benefit all scales of production. They also have limited market access, which makes private investment less attractive. Hence, we argue that large potential remains to move the efficiency needle and consequently improve environmental performance and land-use efficiency in this important part of the aquaculture sector. A supporting economic and policy environment is, however, needed to ensure that small-scale aquaculture farmers are not excluded from technological advancements.[59]

IMPROVING AQUACULTURE'S ENVIRONMENTAL PERFORMANCE

Closing the performance gap in aquaculture appears to hold considerable potential for both productivity and environmental performance gains. Interventions can help to reduce the performance gap in global aquaculture and thereby improve resource-use efficiency, profitability, and overall environmental performance. Interventions that are financially feasible for most farmers are sufficiently scalable to contribute to global change, and importance to food security should be prioritized. As illustrated in Figure 2, and elaborated below, we identify and explore potential effects on farm environmental performance of key interventions in the areas of species choice, genetic improvements, farm technologies and practices, spatial planning and access, disease reduction, feed, regulations and trade, post-harvest processing and distribution, and financial tools.

Figure 1. Improvements in feed composition and efficiency over time for poultry, salmon, tilapia, Chinese carps, and marine shrimp
Improvements are the results of better genotypes, feeds, and farming practices based on data that present the best estimates for average sector performance. It is noteworthy that salmon has undergone a radical decline in both FCR and fishmeal/oil inclusion, but with an increase in micronutrients from 1% to 3%. Historical benchmarks on sector performance for Chinese carps, tilapia, and marine shrimp are, however, limited in terms of the systems and countries they represent. Trendline is a two-period moving average.[15,19,35,46,48,55–57]

Species choice

Different aquaculture species have different physiologies and metabolic characteristics, and consequently have diverse efficiencies and environmental impact profiles under different culture conditions.[5,12] Many species are filter feeders, while the nutritional needs of fed species range from largely herbivorous to almost exclusively carnivorous. Meanwhile, optimal farming conditions depend on appropriate temperature and oxygen and salinity levels. For example, some catfishes (Siluriformes) have evolved the ability to gulp air to help meet oxygen needs and can thrive in water containing low levels of dissolved oxygen, making them tolerant of a wide range of growing conditions. In contrast, production of organisms that perform optimally in brackish water (e.g., shrimp) is limited mainly to estuarine zones. The social behavior of the animals also determines what kind of farming environment is needed. For example, solitary animals such as lobsters and some crabs need to be grown separately from one another to avoid cannibalism. Understanding the biology of species, alongside technical solutions, is also key for reproduction in captivity, a prerequisite for selective breeding.

Apart from a capacity for reproducing in farm systems, aquaculture species have historically been chosen based upon their temperature tolerance, resource-use efficiency, feed preferences, and ease of farming. This allowed for low production costs and *accessible* aquatic foods (defined here as those costing less than half the global production weighted average) (Figure 3). Recently, however, there has been a growing trend toward farming *luxury* aquatic foods (those costing more than the global weighted average), driven by larger profits, changing consumer preferences, and reduced wild fish supplies.[6,60] Between these categories, 41 *commodity* species make up 90% of global production, while another 526 *niche* species comprise the remaining 10%.[47] We subsequently distinguish four categories of aquatic food species based on market value and production volumes: *accessible commodity*, *accessible niche*, *luxury commodity*, and *luxury niche*.

Production volumes are dominated by filter-feeding and omnivorous carps, bivalves, tilapia, milkfish, and catfishes, all *accessible commodities* important for food security and nutrition (lower right quadrant of Figure 3). For fed fish, these are dominated by species that are tolerant to low water quality and can be grown using naturally occurring primary production, agricultural by-products, or food waste as feed. They are primarily sold whole for local or regional markets and, in many cases, destined for household consumption. Bivalves make up a large volume of this group in terms of live wet weight (including shells), but are less important in terms of edible yield.[61] Among these accessible seafood commodities, there is a shift toward farming more non-indigenous species (e.g., tilapia and Clarias catfish), especially in Asia,[47] something that may pose both ecological (introduction of invasive species) and biosecurity (spread of disease) risks.[24,62,63] In contrast, there are a number of *accessible niche* species, predominantly other bivalves and omnivorous finfish species, that are more frequently farmed and consumed regionally (lower left quadrant of Figure 3), including mullets, gourami, and green and blue mussels. These also tend to be relatively inexpensive and can therefore make important

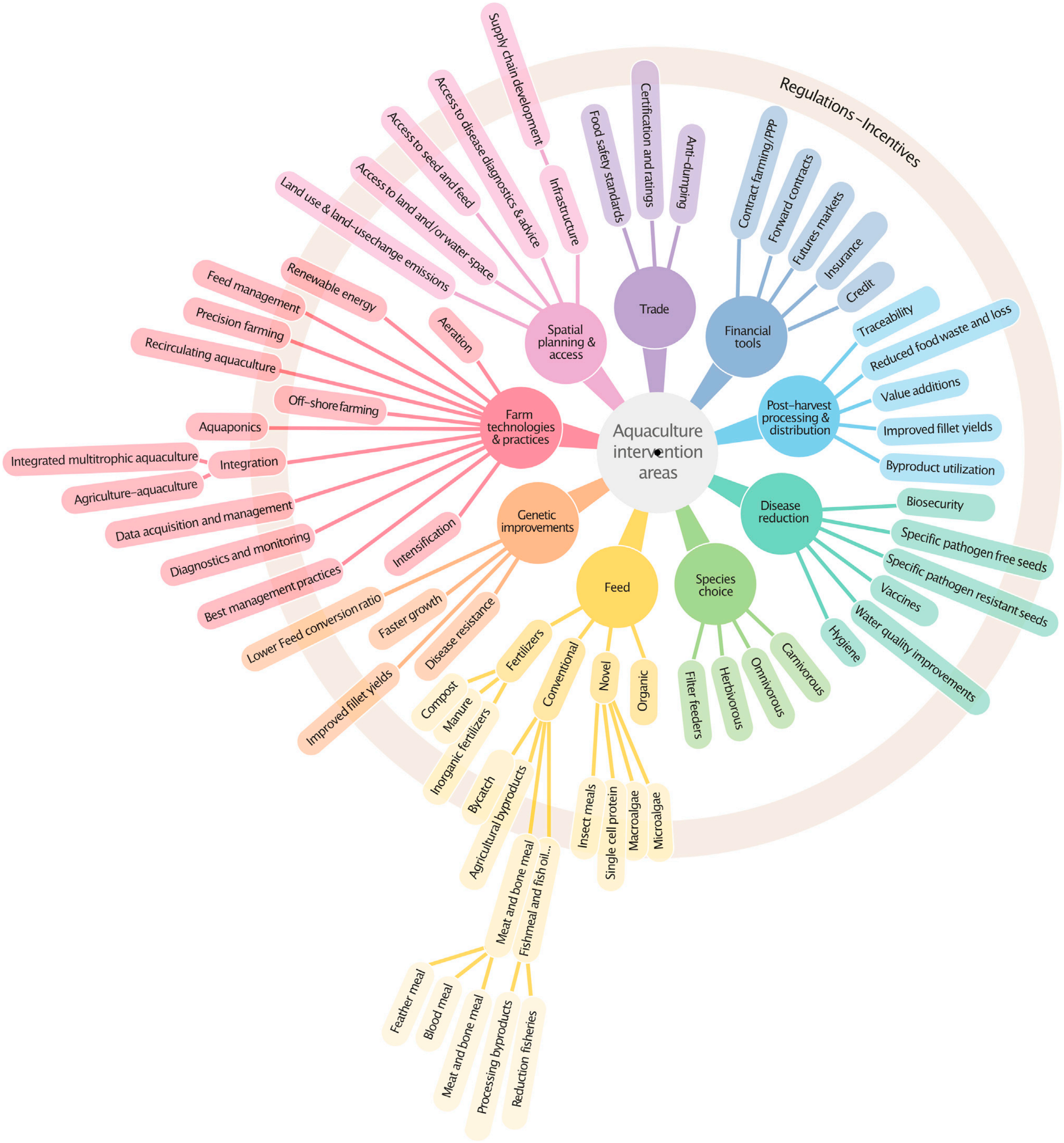

Figure 2. Mind map of the most promising aquaculture intervention areas

The interventions were identified in 2018 during a workshop in Penang, Malaysia, and a special session at the World Aquaculture Society's AQUA 2018 conference. Among these are improved farming practices that are already available to be implemented; improved farming systems, strains, and feeds that could be implemented within the year; and more overarching financial and value-chain reforms that would take years to implement.

contributions to regional animal-source food accessibility and food security. Meanwhile, the production of 11 *luxury commodity* species has been increasing over the past decade. This group consists mainly of naturally carnivorous and omnivorous finfish and crustaceans (upper right quadrant of Figure 3), including shrimp, crayfish, Chinese mitten crab, Atlantic salmon, and rainbow trout.[47,64] These species are often traded nationally or internationally and are primarily consumed by mid- or high-income consumers. Last, *luxury niche* species (upper left quadrant of Figure 3) constitute a diverse cluster of species, including

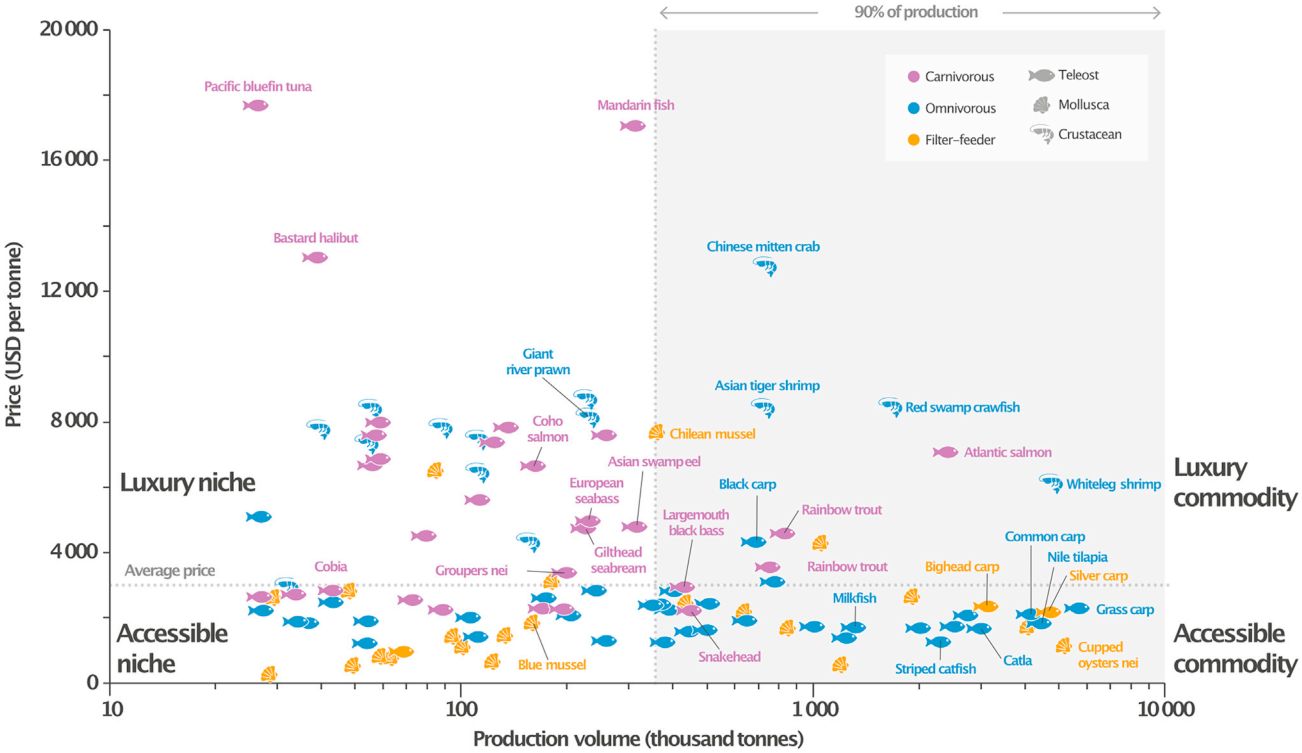

Figure 3. Production volumes and value per tonne of whole aquatic animal

The graph details the 69 top produced species, covering 97% of global aquaculture production by volume in 2017 (excluding snails and turtles) as reported by FAO FishStat.[47] Upper left corner is luxury niche species; upper right corner is luxury commodity species; lower right corner is accessible commodity species; lower left corner is accessible niche species.

abalones, groupers, and Pacific bluefin tuna, among others, that are usually traded internationally and primarily target high-income consumers. These tend to carry disproportionately large environmental footprints, as they are generally resource demanding without benefiting from the efficiency improvements brought by economies of scale.[65,66] Moreover, luxury species are most likely to be air freighted, which exacerbates greenhouse gas intensity.[67] Notably, while only 16% of the global population lives in high-income countries, they consume over 20% of all aquatic foods produced by capture fisheries and aquaculture.[6,68]

Selecting more tolerant and less resource-demanding species is therefore a precursor for lowering environmental impacts, but this is inevitably challenged by market demands. This could, to some extent, be overcome by nudging consumer behavior and value-added products (e.g., through deboning).

Genetic improvements

There are relatively few distinct strains domesticated for aquaculture, and only around 10% of global production is based upon species that have been improved via selective breeding programs.[53,69] Meanwhile, there are already commercially available transgenic Atlantic salmon, in which growth-hormone-regulating genes have been replaced by those from Pacific Chinook salmon. Other transgenic aquatic animals are in development.[70,71] The main long-term objectives of selective breeding are body conformation, physiological tolerance, edible yield, appearance, disease resistance, reproductivity (age of spawning, sex ratio, and fecundity), resistance to pollution, feed efficiency, and growth rate.[53,69] Increased growth rate is typically prioritized, and the average genetic growth gain has been estimated at 13% per generation (Table 1), with somewhat lower gains for multi-trait selection.[69] For traditional breeding, the regeneration rate of a species is the major determinant for the selection rate. This has triggered interest in non-traditional genetics techniques, such as CRISPR (clustered regularly interspaced short palindromic repeats).[72] While these techniques could rapidly increase and diversify the selection rate for certain traits, concerns about food safety and ecological risks have resulted in various regulatory frameworks across the world that restrict their implementation.[70,71]

Despite the facts that genetic gain per generation is generally higher for aquatic species (Table 1) than terrestrial livestock (reported growth rates of 2.5% for sheep and 4.5% for pig), and regeneration rates are shorter, there are fewer genetically improved strains farmed in aquatic environments than in land-based agriculture and livestock production systems.[69] This can be explained in part by a shorter history of farming for most of the aquatic species, higher species diversity, smaller market sizes, and more complex life cycles, but also that genetic improvement of most farmed aquatic species has relied on public financing for research and development rather than being industry driven.[53] For example, while there are commercially developed strains of Atlantic salmon and shrimp, most tilapia and carp strains have been developed and maintained by government institutions, academic institutions, or non-profit

Table 1. Potential genetic gains from selective breeding of a selection of aquatic species

Trait	Genetic gain per generation	Order, family, genus, or genus and species
Appearance[69]	4%–46%	*Mytilus galloprovincialis*
Growth rate[69]	12.7% (2.3%–42%)	*Oreochromis*, Cyprinidae, Salmonidae, Perciformes, Siluriformes, Penaeidae, Palaemonidae, Astacoidea, Bivalvia
Disease resistance[69]	6.3%–19%	*Oreochromis*, Salmonidae, *Litopenaeus vannamei*, Palaemonidae,
Reproductivity[69]	3.3%–11.7%	*Oreochromis*, Siluriformes, Salmonidae
Edible yield[69,73]	0.15%–1.7%	*Oreochromis*, Bivalvia

organizations (e.g., WorldFish), although there is increasing private sector interest in tilapia genetics. This approach to funding has likely resulted in fewer available strains, which limits the adaptive capacity of farmed aquatic animals to different farming environments.[53] Allocating more resources toward genetic breeding programs for a more diverse set of aquatic foods could therefore drastically boost production.

Farm technologies and practices

Traditionally, aquatic animal farming has been dominated by ponds, floating cages, fixed cages, and reservoirs for freshwater finfish and crustaceans; brackish water ponds for euryhaline crustaceans and finfish; and coastal marine floating cages, rafts, and longlines for finfish, crustaceans, and bivalves. In some locations, increasing competition with other users, stringent regulation, negative public perception, and/or rising global temperatures are limiting expansion of aquaculture.[29,62,63,74,75] Improved profitability is, however, driving most aquaculture systems toward intensification.[15,16]

Intensified production implies increasing reliance on formulated feeds and can involve higher costs related to maintaining water quality.[16] Intensification also often increases environmental impacts such as eutrophication and risks of diseases and pests, motivating promotion of recirculating land-based systems (RASs) and offshore ocean farming.[16,67] These systems are, however, generally costly to acquire and operate, and therefore mainly promote luxury species. High electricity and fuel dependency for operating these farms will also necessitate renewable sources of energy to avoid environmental life-cycle trade-offs.[67]

Unless there are paradigm shifts toward clean energy generation, the bulk of future finfish and crustacean farming will most likely continue to rely on farming in ponds, with a continued trend toward intensification.[15,26] These systems could, however, be greatly improved through better management practices, improved system design, and efficiency.[76] Better record keeping, ideally supported by water quality sensors, diagnostics, and monitoring, could be key here, allowing farmers to optimize production and improve feed and chemical use. Integration with additional species and/or agriculture may further improve sustainability outcomes and help maximize production through better utilization of feed and by-products, which could mitigate nutrient emissions per unit of farmed output.[77,78] Constructing efficient settlement ponds that allow for the reuse of nutrients could further reduce eutrophication impacts, but might require additional land. As for all fed aquaculture systems, access to quality feed from sustainably produced resources will be key for profitability and environmental performance.[17,30,36]

Spatial planning and access

Access to affordable land and/or water for farming is critical for profitable aquaculture,[79] which is why many previously unclaimed areas, such as lakes and mangrove forests, have historically been exploited. When left unregulated, such exploitation easily results in environmental degradation (including mangrove deforestation and eutrophication) and disease outbreaks.[49,80] It may also lead to privatization of public lands and/or raise public criticism.[62,63] Developing well-designed spatial plans would help protect essential ecosystems, respect ecosystem carrying capacities, and increase overall farm profitability.[24,81] These plans need to account for the right set of indicators and stakeholders and ensure enforcement.[81]

Disease reduction

Disease is identified as a major obstacle for future expansion of aquaculture, with potentially serious environmental, economic, and social impacts worldwide.[82] Global losses from infectious disease have been estimated to cost the global aquaculture industry US$6 billion annually, with mortality in some families of species, such as shrimp, sometimes exceeding 40%.[24,82] It is also a major driver of excessive antibiotic use and poor animal welfare.[24,49] Apart from choosing tolerant species and spatial planning, disease risks can be reduced through a range of interventions, from simple biosecurity measures and better hygiene to development of vaccines and the use of specific-pathogen-free and resistant seeds. These interventions are especially important for intensive systems, as the risks of disease ultimately are determined by stocking and/or farm density.

Feed

Fish resources from reduction fisheries and processing (i.e., transformed into fishmeal and oil) are nutritionally and palatably optimal for most fed aquatic species.[83,84] Fisheries targeting such small pelagic fish also tend to have low carbon footprints.[17] However, maximizing direct human consumption of this large fish resource (approximately 22% of global catches) should be prioritized where demand exists or can be cultivated, given that this would be a more efficient use of nutrients.[85] Fish and other aquatic species used for feed may also come from overexploited stocks, be harvested using destructive fishing methods, and/or risk undermining marine food webs.[14,86,87] For this reason, feed resources should be sourced only from sustainably certified sources. There is an increasing move to certify feed resources, such as the IFFO marine ingredients responsible sourcing standard and Aquaculture Stewardship Council (ASC) Feed Standard—something that may promote improved stock management but does not necessarily lead to more efficient use of these resources.

Fish proteins have been challenging to replace in the diets of higher-trophic-level species, but several alternatives have been developed, including livestock by-product meals, insect meals, terrestrial plant-based ingredients, macro- and microalgae, and precision formulations using synthetic amino acids.[5,20,21,88] Many of these have, however, raised sustainability concerns, with livestock by-product meals transferring burdens associated with livestock production, agronomy being associated with land use and land-use change, and micronutrient supplements often having proportionately large carbon footprints.[17,89]

In addition to being environmentally sustainable, alternative novel feed ingredients need to be cost effective, available in sufficient quantities year round, nutritious, free from contaminants and other undesirable compounds, able to endure a range of forms of processing, palatable to farmed aquatic organisms, and able to support the desired nutritional traits of seafood such as omega-3.[90–92] Moreover, from a broader ethical perspective, these resources should not compete with demand for direct human consumption and nutrition, i.e., being food-grade resources.[83,85] Terrestrial feed components (i.e., crop-based ingredients) are now being considered in certification schemes such as those operated by the ASC. In Table 2 we summarize the three most promising novel protein sources for aquafeed, their strengths, and their shortcomings. These were shortlisted based upon their potential for upscaling, economic viability, and sustainability.

Macroalgae have also been suggested as suitable aquafeed ingredients,[88] but variable nutritional content and digestibility problems for fish suggest that only a small fraction of feed ingredients can be substituted at the scale needed.[20] Energy requirements for desiccating macroalgae and by-product meals can also be high.[99,100]

Ultimately, the formulation of compound feed changes on a day-to-day basis, where the final product will be a combination of complementary raw materials sourced based upon nutritional profile and market price.[90] Feed ingredients must therefore be considered through the interacting nutritional effects of the feed as a whole.[20,79] Interactions with other markets also need to be factored into this equation, as the same set of feed resources is used in terrestrial animal production, and sometimes feed resources compete with direct human consumption or for agricultural land. In other cases, prices might be driven up by demand from more profitable commodities, such as omega-3 food supplements or biofuels. Thus, interactions in the feed-food system need to be considered in their entirety, but the environmental impacts related to individual feed resources need to be considered (using, e.g., fao.org/gleam) and communicated when formulating feed, accompanied by a continued drive toward reducing FCRs.

Regulations and trade

Various public and private regulatory frameworks have been initiated by governments and non-government actors to regulate some of the social and environmental problems of aquaculture development. Driven by non-governmental organizations (NGOs) and media campaigns, third-party certification schemes have been widespread among seafood commodities and potentially have the power to push industries toward more sustainable practices.[101] However, the role of certification remains limited, and the standards of the two largest certification groups—ASC and the Global Aquaculture Alliance Best Aquaculture Practices (GAA-BAP)—cover only 3% of global aquaculture production.[31] Many of the best established private certification schemes, however, mainly cover luxury aquatic food species, fail to consider interspecies differences, and mainly address the concerns of Western consumers.[101] Certification standards consequently need to become more comprehensive and consider a broader set of life-cycle impacts, as certifying common practices or targeting certain traits (e.g., organic) may not push production toward overall better practices.[102]

A prerequisite for changing the seafood industry through certification and consumer choices is value-chain upgrading and alignment to ensure product traceability. Based on DNA barcoding, it has been reported that as much as 30% of all traded seafood is incorrectly labeled as other species.[103,104] Mislabeling can be unintentional, through misidentification and confusion over common names, but most is probably deliberate, with the ambition to achieve higher market prices or to market unsustainably or illegally harvested species.[104,105] Given such widespread mislabeling for a characteristic as fundamental as "species," it will be difficult to assign trustworthy environmental profiles to aquatic foods. Better documented trace-back systems are an effective countermeasure here,[105] and there are currently several initiatives for tracking seafood using blockchain technology (e.g., fishcoin.co and traceability-dialogue.org). Traceability schemes are, however, only as effective as the initial data entered.

Regulations can address more comprehensive sets of farms and farming practices, but have also been seen as a barrier for potential grow-out sites, therapeutics, access to fresh water, effluent discharge, and the use of genetically modified organisms (GMOs), non-indigenous species, and novel feed ingredients.[106] Too stringent and/or inflexible regulations are also often blamed for impeding aquaculture in Europe and the United States, and newly introduced environmental regulations in China and elsewhere have resulted in the closure of farming systems in lakes and reservoirs.[106,107] Regulations should thus be drafted to discourage detrimental farming practices, without hampering otherwise effective interventions.[108]

Post-harvest processing and distribution

Aquatic foods vary widely in terms of edible yields, nutritional content, processing techniques, distribution, consumption, and food loss and waste.[109–112] These factors vary widely with geographical and cultural context and strongly influence environmental performance.[109] Alongside species selection, increasing edible yields and reducing food loss and waste are arguably the most efficient short-term interventions for improving the environmental performance of aquatic foods, as less needs to be produced in the first place.[12] Overall, edible yields and what actually is being eaten can range from 10% for some bivalves to 100% for some small-sized fish and sea cucumbers.[109,110]

Table 2. Strengths and shortcomings of three promising novel protein sources for aquafeed

Protein source	Strengths and shortcomings
Fish processing by-product meals	While already partially utilized, an estimated 8 million tonnes of fishmeal could potentially be available at an affordable price if more fish by-products from processing were utilized in fishmeal production globally.[14,93] Environmental impacts are, however, dependent on the supporting fishing, farming, and processing activities from where the resources derive and from which environmental burdens need to allocated.[19,94] There are also potential risks of bioaccumulation of toxins and spread of disease.[92]
Insect meals	Insect production represents a promising way to recycle slaughter- and plant-derived waste streams into feed resources with good nutritional profiles. The organic rearing substrate, however, along with the energy required to produce and process the insects, largely determines the environmental performance of the insect meals. Many are not yet financially competitive, and global production output potentials are questionable, but efficiency gains from scale and new innovations could still be realized.[17,94–96]
Single-cell organisms	These comprise a diverse group of bacteria, microalgae, and yeasts that are autotrophic or can be grown on a variety of organic materials, including fiber sludge from the forest industry or methane.[97,98] Production costs remain well above those of fishmeal and fish oil, but economies of scale and improved production practices are steadily being realized.[98] In addition, their potential to support maintenance of omega-3 profiles while replacing proteins and fish oil makes them attractive.[20]

The FAO (2011) estimates that 35% of all seafood is lost or wasted worldwide. While this estimate might be excessive,[113] it has been suggested that in North America almost half of all edible seafood supply is discarded, primarily as food waste at the consumer stage.[112] In Africa and Asia most discards are at the production stage or during processing and distribution,[114] often with accompanying losses in nutritional quality.[111] There is, however, an ongoing shift in low-income countries from subsistence production toward sourcing food from markets, and from home cooking to consumption of processed food and food eaten away from home, which implies longer supply chains that will influence utilization rates.[113,115] Other reduction strategies for food loss and waste range from simple changes in practices, such as handling fish with care, avoiding contamination, using insect nets, improved drying techniques, better hygiene and public awareness, to refrigeration, improved infrastructure, clean water, improved packaging material, food safety legislation, and promotion of value-added products from low-value fish species.[111]

Large-scale processing can improve possibilities for utilizing by-products for food, feed, or industrial uses. It has been estimated that better by-product utilization could increase food output from the Scottish salmon industry by 60%[85] and could satisfy 65% of China's fishmeal demand.[14] By utilizing these resources, larger volumes could be produced with a similar overall environmental footprint, resulting in lower impacts per volume and better resource efficiency. Product forms determine amounts being wasted and lost, but can also considerably influence the market demand for, and environmental impacts of, seafood production. Long transport of live animals should be avoided, as it can more than double environmental impacts through energy used for distribution and cooling, especially if the animals are airfreighted.[67,109] Canning minimizes food waste and allows for slower modes of transport, but packaging and using oil for preservation may instead become environmental hotspots.[116] Freezing is an efficient way of preserving food, but needs to be supported by efficient cooling methods as it otherwise might result in high energy use and the release of refrigerants.[19,109] Ultimately, sun-drying, where possible, may be promoted as one of the most sustainable forms of preservation if loss/waste levels are kept low.[111]

Financial tools

Many smallholder farmers cannot benefit from farm improvements, such as quality feed, seed, and disease diagnostics, due to limited access to credit. Neither are they likely to explore new farming methods, as they are vulnerable to risk. Enabling insurance providers and cooperatives could here play important roles in alleviating risk and gaining access to credit and markets among smallholder aquaculture farmers.[117] Cooperatives may also improve the utilization of infrastructure, and thereby reduce overall environmental impacts.[118] Access to shared infrastructure, improved fry, cheaper feeds, and markets could be improved by upscaling production of a limited selection of species.[119] This tendency is present in aquaculture, similar to what has been seen in terrestrial livestock farming. However, scaling may also counteract the resilience and resource efficiency that diversity can bring to aquaculture.[5,120] Striking a balance between industrial and smallholder farming, and implementing interventions appropriately, is key here for accommodating benefits associated with diversity and economies of scale simultaneously.

DISCUSSION

Aquaculture holds potential to improve the sustainability of animal-based foods and the overall food system, but additional efforts are urgently needed for it to reach its full potential. In agriculture, much research has focused on "closing the yield gap" (the mismatch between possible and realized maximum yields) and, more recently, on "sustainable intensification," which refers to achieving higher yields while using fewer resources per production output.[2,27] These strategies are aimed at increasing food supply while reducing food production's relative environmental footprint.[1,2] In aquaculture, it is harder to establish maximum potential yields per area, as there are more tradeoffs with life-cycle inputs, such as feed, water, and energy. Nonetheless, we argue that a huge performance gap persists for most accessible commodity and accessible niche seafood, including carps, tilapia, and milkfish. Much of this gap could be closed through simple interventions that are readily available, including better management practices, better hygiene and biosecurity, and post-harvest handling and processing.

In some cases, simple improvements have not been realized yet due to limited know-how among aquaculture farmers and other supply chain actors. Financial barriers and perceived risks are also important constraints. This scenario suggests scope for gains through efforts to strengthen and expand producer groups, extension services, training, and financial support. Other interventions would require longer-term resource commitments. These include upgrading farm infrastructure, establishing genetic improvement programs, and development of vaccines and novel feeds. A third group of interventions could provide incentives for farmers and industry to adopt more environmentally sustainable practices. These include spatial planning, stricter environmental regulations, and financial incentives encouraging better production practices. This last set of interventions is central for going beyond business as usual, as profitability is the most fundamental driver of the industry, which is in turn mediated by price premiums or cost reductions.

Even though many aquaculture systems perform environmentally favorably compared with most terrestrial animal production systems,[4] their continued expansion will lead to additional stress on resource systems and planetary health.[31] In response, innovations with plant-based and *in vitro*-cultured aquatic food alternatives are accelerating quickly. The extent to which these technologies will outperform traditional farming, both environmentally and economically, is uncertain, and at present such alternative products mainly target replacements for luxury aquatic foods and consumers in high-income countries. The bulk of accessible and affordable aquatic foods will continue to be produced by small- and medium-scale farmers that struggle with limited financial means and capacity to optimize the environmental performance of their production independently. Strengthening R&D together with widespread training programs and extension services for these farmers could offer a more efficient way forward for making aquatic foods more accessible.

The aquaculture sector has been slow to deploy financial tools (e.g., insurance, forward contracts, and futures markets) that can help farmers manage economic risks, often due to uncertainty about the risks themselves and volatility in production.[121] The improvements listed in the sections above can help make the business case for the use of financial tools by optimizing and stabilizing production and, in doing so, de-risk external investments in farm and sectoral improvements.

Adding all these together, we can expect that global aquaculture yields could increase substantially over the next decade, while reducing the environmental impact per unit of output. Improving production systems, management practices, and genetic strains could reduce FCR and environmental impacts by roughly 25%.[12,76] Achieving these gains will require access to tailored commercial feed for the most important species (e.g., carps) and novel feed ingredients. Market access and consumer acceptance will also be essential for promoting fish relying on lower-trophic level diets. Improvements in post-harvest processing and distribution could help improve utilization and profitability, while reducing food waste and loss with overall positive effects on global resource use.[12,111] Promoting value-added products would also encourage centralized processing and better utilization of by-products.

LCA, our most commonly used environmental framework for benchmarking food production systems, remains insufficient with respect to the availability of methods for assessing all sustainability aspects relevant to the growth of aquatic foods.[122] Some supplemental methodologies have been proposed to capture aquatic impacts in LCAs, including biotic resource use and seafloor disturbance.[109] However, the net gains in human food resources are rarely addressed.

In aquaculture, and particularly for luxury commodity and niche species, fish and crops that potentially could be consumed by humans are also used as ingredients in aquafeed. Agricultural feed substitutes may, moreover, compromise the nutritional quality of aquatic products[91,92,123] and aggravate impacts related to biodiversity loss, global warming, biogeochemical flows, and freshwater availability.[1,5,17,83] This applies to fed aquaculture systems in freshwater and marine environments alike, as feed often is responsible for >90% of farmed finfish environmental life-cycle impacts.[17,18] In these systems, FCR remains an important indicator of environmental performance. Meanwhile, further horizontal expansion of coastal and inland pond aquaculture risks increasing competition for freshwater resources, deforestation, and methane emissions, making a strong case for responsible intensification of already existing systems, with increased reliance on feed as a consequence.[74,124] Thus, just like for biofuels, the second and third generations of aquafeed need to focus on resources that do not compete with food for human consumption or for available land.

CONCLUSIONS

Aquaculture holds great potential to contribute to more sustainable diets, but many farming systems still suffer from large performance gaps and unsustainable practices. Many of the most impactful interventions for resolving these challenges are already available and would need to target accessible aquatic food species, a high proportion of which are produced on small- and medium-scale farms. These interventions require a mix of both short- and long-term actions, but many could be implemented at low monetary costs. However, tailoring the most efficient interventions to the diverse set of farming systems and incentivizing their implementation remains the greatest challenge and requires government support.

We contend that financial incentives and regulatory efforts, alongside investment in genetics, feed, and farm management, including better record keeping and data management by individual farmers, are needed to boost aquaculture production, improve resource-use efficiency, and reduce environmental impacts. Meanwhile, luxury aquatic foods from offshore systems and RASs have the potential to reduce environmental impacts on the scale of the global food system if they replace red meat in diets, but their contribution to feeding the global population will be limited.

Sustainable intensification of existing systems for increasing accessibility of aquatic foods, based on scaling of proven but infrequently adopted interventions, could contribute substantially to realizing sustainability goals in aquaculture. However, these systems and improvements also need to be better benchmarked using LCA and complementary frameworks, to identify overall potential sustainability gains. Aquatic foods alone cannot ensure future food security but, if developed thoughtfully, they can play a greater role in alleviating the current food system's environmental pressures on the planet.

ACKNOWLEDGMENTS

We thank the Kjell and Märta Beijer Foundation for supporting this work through the Beijer Institute's Aquaculture and Sustainable Seafood program. This work was undertaken as part of the CGIAR Research Programs on Fish Agri-Food Systems (FISH) led by WorldFish and on Climate Change, Agriculture and Food Security (CCAFS) led by CIAT. These programs are supported by contributors to the CGIAR Trust Fund. P.J.G.H. and M.T. are partially funded by the FORMAS SeaWin project (2016-00227), and P.J.G.H. is also partially funded by the FORMAS Inequality and the Biosphere project (2020-00454). We also thank Albert Tacon for supplementing data and Nathalie Bax for her continuous support. Azote AB designed the figures.

AUTHOR CONTRIBUTIONS

P.J.G.H., M.T., and M.J.P. initiated the study. P.J.G.H., M.T., L.K.B., B.B., M.C.M.B., N.P., M.J.P., and N.T. attended the initial workshop in Penang, Malaysia. All authors identified interventions and developed the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Gordon, L.J., Bignet, V., Crona, B., Henriksson, P.J., Holt, T. Van, Jonell, M., Lindahl, T., Troell, M., Barthel, S., Deutsch, L., et al. (2017). Rewiring food systems to enhance human health and biosphere stewardship. Environ. Res. Lett. *12*, 100201.
2. Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., Garnett, T., Tilman, D., DeClerck, F., Wood, A., et al. (2019). Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. Lancet *393*, 447–492.
3. Rockström, J., Edenhofer, O., Gaertner, J., and DeClerck, F. (2020). Planet-proofing the global food system. Nat. Food *1*, 3–5.
4. Poore, J., and Nemecek, T. (2018). Reducing food's environmental impacts through producers and consumers. Science *992*, 987–992.
5. Troell, M., Naylor, R.L., Metian, M., Beveridge, M., Tyedmers, P.H., Folke, C., Arrow, K.J., Barrett, S., Crépin, A.-S., Ehrlich, P.R., et al. (2014). Does aquaculture add resilience to the global food system? Proc. Natl. Acad. Sci. U S A *111*, 13257–13263.
6. FAO (2020). The State of World Fisheries and Aquaculture 2020 (United Nations Food and Agricultural Organization).
7. Costello, C., Cao, L., Gelcich, S., Cisneros-Mata, M.Á., Free, C.M., Froehlich, H.E., Golden, C.D., Ishimura, G., Maier, J., Macadam-Somer, I., et al. (2020). The future of food from the sea. Nature *588*, 95–100.
8. van der Meer, J. (2020). Limits to food production from the sea. Nat. Food *1*, 762–764.
9. Hicks, C.C., Cohen, P.J., Graham, N.A.J., Nash, K.L., Allison, E.H., D'Lima, C., Mills, D.J., Roscher, M., Thilsted, S.H., Thorne-Lyman, A.L., et al. (2019). Harnessing global fisheries to tackle micronutrient deficiencies. Nature *574*, 95–98.
10. Hallström, E., Bergman, K., Mifflin, K., Parker, R., Tyedmers, P., Troell, M., and Ziegler, F. (2019). Combined climate and nutritional performance of seafoods. J. Clean. Prod. *230*, 402–411.
11. Tlusty, M.F., Tyedmers, P., Bailey, M., Ziegler, F., Henriksson, P.J.G., Béné, C., Bush, S., Newton, R., Asche, F., Little, D.C., et al. (2019). Reframing the sustainable seafood narrative. Glob. Environ. Chang. *59*, 101991.
12. Henriksson, P.J., Banks, L.K., Suri, S.K., Pratiwi, T.Y., Fatan, N.A., and Troell, M. (2019). Indonesian aquaculture futures — identifying interventions for reducing environmental impacts. Environ. Res. Lett. *14*, 124062.
13. Metian, M., Pouil, S., Boustany, A., and Troell, M. (2014). Farming of bluefin tuna-reconsidering global estimates and sustainability concerns. Rev. Fish. Sci. Aquac. *22*, 184–192.
14. Cao, L., Naylor, R., Henriksson, P., Leadbitter, D., Metian, M., Troell, M., and Zhang, W. (2015). China's aquaculture and the world's wild fisheries. Science *80*, 347.
15. Tacon, A.G.J. (2019). Trends in global aquaculture and aquafeed production: 2000–2017. Rev. Fish. Sci. Aquac. *0*, 1–14.
16. Edwards, P. (2015). Aquaculture environment interactions: past, present and likely future trends. Aquaculture *447*, 2–14.
17. Pelletier, N., Klinger, D.H., Sims, N.A., Yoshioka, J.R., and Kittinger, J.N. (2018). Nutritional attributes, substitutability, scalability, and environmental intensity of an illustrative subset of current and future protein sources for aquaculture feeds: joint consideration of potential synergies and trade-offs. Environ. Sci. Technol. *52*, 5532–5544.
18. Henriksson, P.J., Belton, B., Jahan, K.M.-, and Rico, A. (2018). Measuring the potential for sustainable intensification of aquaculture in Bangladesh using life cycle assessment. Proc. Natl. Acad. Sci. U S A *115*, 2958–2963.
19. Henriksson, P.J.G., Rico, A., Zhang, W., Nahid, S.A.A., Newton, R., Phan, L.T., Zhang, Z., Jaithiang, J., Dao, H.M., Phu, T.M., et al. (2015). Comparison of asian aquaculture products by use of statistically supported life cycle assessment. Environ. Sci. Technol. *49*, 14176–14183.
20. Cottrell, R.S., Blanchard, J.L., Halpern, B.S., Metian, M., and Froehlich, H.E. (2020). Global adoption of novel aquaculture feeds could substantially reduce forage fish demand by 2030. Nat. Food *1*, 301–308.
21. Klinger, D., and Naylor, R. (2012). Searching for solutions in aquaculture: charting a sustainable course. Annu. Rev. Environ. Resour. *37*, 247–276.
22. Béné, C., Oosterveer, P., Lamotte, L., Brouwer, I.D., de Haan, S., Prager, S.D., Talsma, E.F., and Khoury, C.K. (2019). When food systems meet sustainability – current narratives and implications for actions. World Dev. *113*, 116–130.
23. Gentry, R.R., Froehlich, H.E., Grimm, D., Kareiva, P., Parke, M., Rust, M., Gaines, S.D., and Halpern, B.S. (2017). Mapping the global potential for marine aquaculture. Nat. Ecol. Evol. 1–8.
24. Stentiford, G.D., Bateman, I.J., Hinchliffe, S.J., Bass, D., Hartnell, R., Santos, E.M., Devlin, M.J., Feist, S.W., Taylor, N.G.H.H., Verner-Jeffreys, D.W., et al. (2020). Sustainable aquaculture through the one health lens. Nat. Food *1*, 468–474.
25. Ziegler, F., Winther, U., Hognes, E.S., Emanuelsson, A., Sund, V., and Ellingsen, H. (2013). The carbon footprint of Norwegian seafood products on the global seafood market. J. Ind. Ecol. *17*, 103–116.
26. Belton, B., Little, D.C., Zhang, W., Edwards, P., Skladany, M., and Thilsted, S.H. (2020). Farming fish in the sea will not nourish the world. Nat. Commun. *11*, 1–8.
27. Mueller, N.D., Gerber, J.S., Johnston, M., Ray, D.K., Ramankutty, N., and Foley, J.a. (2012). Closing yield gaps through nutrient and water management. Nature *490*, 254–257.
28. Licker, R., Johnston, M., Foley, J.A., Barford, C., Kucharik, C.J., Monfreda, C., and Ramankutty, N. (2010). Mind the gap: how do climate and agricultural management explain the "yield gap" of croplands around the world? Glob. Ecol. Biogeogr. *19*, 769–782.
29. Oyinlola, M.A., Reygondeau, G., Wabnitz, C.C.C., Troell, M., and Cheung, W.W.L. (2018). Global estimation of areas with suitable environmental conditions for mariculture species. PLoS One *13*, e0191086.
30. Troell, M., Jonell, M., and Henriksson, P.J.G. (2017). Ocean space for seafood. Nat. Ecol. Evol. *1*, 1224–1225.
31. Naylor, R.L., Hardy, R.W., Buschmann, A.H., Bush, S.R., Cao, L., Klinger, D.H., Little, D.C., Lubchenco, J., Shumway, S.E., and Troell, M. (2021). A 20-year retrospective review of global aquaculture. Nature *591*, 551–563.
32. Farmery, A.K., Alexander, K., Anderson, K., Blanchard, J.L., Carter, C.G., Evans, K., Fischer, M., Fleming, A., Frusher, S., Fulton, E.A., et al. (2021). Food for all: designing sustainable and secure future seafood systems. Rev. Fish Biol. Fish. 0123456789. https://doi.org/10.1007/s11160-021-09663-x.
33. Tlusty, M., Tyedmers, P., Ziegler, F., Jonell, M., Henriksson, P.J., Newton, R., Little, D., Fry, J., Love, D., and Cao, L. (2018). Commentary: comparing efficiency in aquatic and terrestrial animal production systems. Environ. Res. Lett. *13*, 128001.

34. Fry, J.P., Mailloux, N.A., Love, D.C., Milli, M.C., and Cao, L. (2018). Feed conversion efficiency in aquaculture: do we measure it correctly? Environ. Res. Lett. *13*, 024017.
35. Aas, T.S., Ytrestøyl, T., and Åsgård, T. (2019). Utilization of feed resources in the production of Atlantic salmon (Salmo salar) in Norway: an update for 2016. Aquac. Rep. *15*, 100216.
36. Cottrell, R.S., Metian, M., Froehlich, H.E., Blanchard, J.L., Sand Jacobsen, N., McIntyre, P.B., Nash, K.L., Williams, D.R., Bouwman, L., Gephart, J.A., et al. (2021). Time to rethink trophic levels in aquaculture policy. Rev. Aquac. *13*, 1583–1593.
37. Bohnes, F.A., Hauschild, M.Z., Schlundt, J., and Laurent, A. (2019). Life cycle assessments of aquaculture systems: a critical review of reported findings with recommendations for policy and system development. Rev. Aquac. *11*, 1061–1079.
38. Bohnes, F.A., and Laurent, A. (2019). LCA of aquaculture systems: methodological issues and potential improvements. Int. J. Life Cycle Assess. *24*, 324–337.
39. Clark, M., and Tilman, D. (2017). Comparative analysis of environmental impacts of agricultural production systems, agricultural input efficiency, and food choice. Environ. Res. Lett. *12*, 064016.
40. Heller, M.C., Willits-Smith, A., Meyer, R., Keoleian, G.A., and Rose, D. (2018). Greenhouse gas emissions and energy use associated with production of individual self-selected US diets. Environ. Res. Lett. *13*, 044004.
41. Davis, K.F., Gephart, J.A., Emery, K.A., Leach, A.M., Galloway, J.N., and D'Odorico, P. (2016). Meeting future food demand with current agricultural resources. Glob. Environ. Chang. *39*, 125–132.
42. Shewmake, S., Okrent, A., Thabrew, L., and Vandenbergh, M. (2015). Predicting consumer demand responses to carbon labels. Ecol. Econ. *119*, 168–180.
43. Hilborn, R., Banobi, J., Hall, S.J., Pucylowski, T., and Walsworth, T.E. (2018). The environmental cost of animal source foods. Front. Ecol. Environ. *16*, 329–335.
44. Hall, S.J., Delaporte, A., Phillips, M.J., Beveridge, M.C.M., and O'Keefe, M. (2011). Blue Frontiers: Managing the Environmental Costs of Aquaculture (The WorldFish Center).
45. Muir, J. (2005). Managing to harvest? Perspectives on the potential of aquaculture. Philos. Trans. R. Soc. Lond. B. Biol. Sci. *360*, 191–218.
46. MacLeod, M.J., Hasan, M.R., Robb, D.H.F., and Mamun-Ur-Rashid, M. (2020). Quantifying greenhouse gas emissions from global aquaculture. Sci. Rep. *10*, 1–8.
47. FAO (2020). FishStatJ (Fisheries and Aquaculture Department).
48. Tveterås, S. (2002). Norwegian salmon aquaculture and sustainability: the relationship between environmental quality and industry growth. Mar. Resour. Econ. *17*, 121–132.
49. Henriksson, P.J.G., Rico, A., Troell, M., Klinger, D.H., Buschmann, A.H., Saksida, S., Chadag, M.V., and Zhang, W. (2018). Unpacking factors influencing antimicrobial use in global aquaculture and their implication for management: a review from a systems perspective. Sustain. Sci. *13*, 1105–1120.
50. Asche, F., Cojocaru, A.L., and Roth, B. (2018). The development of large scale aquaculture production: a comparison of the supply chains for chicken and salmon. Aquaculture *493*, 446–455.
51. Pelletier, N., Doyon, M., Muirhead, B., Widowski, T., Nurse-Gupta, J., and Hunniford, M. (2018). Sustainability in the Canadian egg industry—learning from the past, navigating the present, planning for the future. Sustainability *10*, 3524.
52. de Verdal, H., Komen, H., Quillet, E., Chatain, B., Allal, F., Benzie, J.A.H., and Vandeputte, M. (2018). Improving feed efficiency in fish using selective breeding: a review. Rev. Aquac. *10*, 833–851.
53. FAO (2019). The State of the World's Aquatic Genetic Resources for Food and Agriculture (United Nations Food and Agricultural Organization).
54. Nguyen, N.H. (2016). Genetic improvement for important farmed aquaculture species with a reference to carp, tilapia and prawns in Asia: achievements, lessons and challenges. Fish Fish *17*, 483–506.
55. Tacon, A.G.J. (2018). Global Trends in Aquaculture and Compound Aquafeed Production (World Aquac), pp. 33–46.
56. Tacon, A.G.J., and Metian, M. (2008). Global overview on the use of fish meal and fish oil in industrially compounded aquafeeds: trends and future prospects. Aquaculture *285*, 146–158.
57. National Chicken Council. (2020). U.S. Broiler Performance. https://www.nationalchickencouncil.org/about-the-industry/statistics/u-s-broiler-performance/.
58. Pelletier, N., Ibarburu, M., and Xin, H. (2014). Comparison of the environmental footprint of the egg industry in the United States in 1960 and 2010. Poult. Sci. *93*, 241–255.
59. Hazell, P.B.R. (2009). The Asian Green Revolution.
60. Natale, F., Hofherr, J., Fiore, G., and Virtanen, J. (2013). Interactions between aquaculture and fisheries. Mar. Policy *38*, 205–213.
61. Edwards, P., Zhang, W., Belton, B., and Little, D.C. (2019). Misunderstandings, myths and mantras in aquaculture: its contribution to world food supplies has been systematically over reported. Mar. Policy *106*, 103547.
62. Pomeroy, R., Dey, M.M., and Plesha, N. (2014). The social and economic impacts of semi-intensive aquaculture on biodiversity. Aquac. Econ. Manag. *18*, 303–324.
63. Froehlich, H.E., Gentry, R.R., Rust, M.B., Grimm, D., and Halpern, B.S. (2017). Public perceptions of aquaculture: evaluating spatiotemporal patterns of sentiment around the world. PLoS One *12*, e0169281.
64. Tacon, A.G.J., Metian, M., Turchini, G.M., and De Silva, S.S. (2009). Responsible aquaculture and trophic level implications to global fish supply. Rev. Fish. Sci. *18*, 94–105.
65. Aubin, J., Papatryphon, E., Vanderwerf, H., and Chatzifotis, S. (2009). Assessment of the environmental impact of carnivorous finfish production systems using life cycle assessment. J. Clean. Prod. *17*, 354–361.
66. Aguado-Gimenez, F., and Garcia-Garcia, B. (2005). Growth, food intake and feed conversion rates in captive Atlantic bluefin tuna (Thunnus thynnus Linnaeus, 1758) under fattening conditions. Aquac. Res. *36*, 610–614.
67. Liu, Y., Rosten, T.W., Henriksen, K., Hognes, E.S., Summerfelt, S., and Vinci, B. (2016). Comparative economic performance and carbon footprint of two farming models for producing Atlantic salmon (Salmo salar): land-based closed containment system in freshwater and open net pen in seawater. Aquac. Eng. *71*, 1–12.
68. World Bank (2020). The World Bank Open Data. https://data.worldbank.org/.
69. Gjedrem, T., and Rye, M. (2018). Selection response in fish and shellfish: a review. Rev. Aquac. *10*, 168–179.
70. Wargelius, A. (2019). Application of genome editing in aquatic farm animals: Atlantic salmon. Transgenic Res. *28*, 101–105.
71. Wang, Y., Hamid, N., Jia, P., and Pei, D. (2021). A comprehensive review on genetically modified fish: key techniques, applications and future prospects. Rev. Aquac. Raq. *13*, 1635–1660.
72. Gratacap, R.L., Wargelius, A., Edvardsen, R.B., and Houston, R.D. (2019). Potential of genome editing to improve aquaculture breeding and production. Trends Genet. *35*, 672–684.
73. Fraslin, C., Dupont-Nivet, M., Haffray, P., Bestin, A., and Vandeputte, M. (2018). How to genetically increase fillet yield in fish: new insights from simulations based on field data. Aquaculture *486*, 175–183.
74. Klinger, D.H., Levin, S.A., and Watson, J.R. (2017). The growth of finfish in global open-ocean aquaculture under climate change. Proc. R. Soc. B Biol. Sci. *284*, 20170834.
75. Wang, Q., Li, Z., Gui, J.-F., Liu, J., Ye, S., Yuan, J., and De Silva, S.S. (2017). Paradigm changes in freshwater aquaculture practices in China: moving towards achieving environmental integrity and sustainability. Ambio *47*, 410–426.
76. Henriksson, P.J.G., Dickson, M., Allah, A.N., Al-Kenawy, D., and Phillips, M. (2017). Benchmarking the environmental performance of best management practice and genetic improvements in Egyptian aquaculture using life cycle assessment. Aquaculture *468*, 53–59.
77. Beveridge, M.C.M., and Brummett, R.E. (2015). Aquaculture and the environment. In Freshwater Fisheries Ecology, J.F. Craig, ed. (Wiley), pp. 794–803.
78. Neori, A., Troell, M., Chopin, T., Yarish, C., Critchley, A., and Buschmann, A.H. (2007). The need for a balanced ecosystem Approach to blue revolution aquaculture. Environ. Sci. Policy Sustain. Dev. *49*, 36–43.
79. Little, D.C., Newton, R.W., and Beveridge, M.C.M.M. (2016). Aquaculture: a rapidly growing and significant source of sustainable food? Status, transitions and potential. Proc. Nutr. Soc. *75*, 274–286.
80. Richards, D.R., and Friess, D.A. (2016). Rates and drivers of mangrove deforestation in Southeast Asia, 2000–2012. Proc. Natl. Acad. Sci. U S A. *113*, 344–349.
81. Bailey, J.L., and Eggereide, S.S. (2020). Indicating sustainable salmon farming: the case of the new Norwegian aquaculture management scheme. Mar. Policy *117*, 103925.
82. Stentiford, G.D., Sritunyalucksana, K., Flegel, T.W., Williams, B.A.P., Withyachumnarnkul, B., Itsathitphaisarn, O., and Bass, D. (2017). New

paradigms to help solve the global aquaculture disease crisis. PLoS Pathog. *13*, 1–6.

83. Malcorps, W., Kok, B., van‘t Land, M., Fritz, M., van Doren, D., Servin, K., van der Heijden, P., Palmer, R., Auchterlonie, N., Rietkerk, M., et al. (2019). The sustainability conundrum of fishmeal substitution by plant ingredients in shrimp feeds. Sustainability *11*, 1212.
84. Turchini, G.M., Torstensen, B.E., and Ng, W.K. (2009). Fish oil replacement in finfish nutrition. Rev. Aquac. *1*, 10–57.
85. Stevens, J.R., Newton, R.W., Tlusty, M., and Little, D.C. (2018). The rise of aquaculture by-products: increasing food production, value, and sustainability through strategic utilisation. Mar. Policy.
86. Deutsch, L., Gräslund, S., Folke, C., Troell, M., Huitric, M., Kautsky, N., and Lebel, L. (2007). Feeding aquaculture growth through globalization: exploitation of marine ecosystems for fishmeal. Glob. Environ. Chang. *17*, 238–249.
87. Zhang, W., Liu, M., Sadovy de Mitcheson, Y., Cao, L., Leadbitter, D., Newton, R., Little, D.C., Li, S., Yang, Y., Chen, X., et al. (2020). Fishing for feed in China: facts, impacts and implications. Fish Fish *21*, 47–62.
88. Hua, K., Cobcroft, J.M., Cole, A., Condon, K., Jerry, D.R., Mangott, A., Praeger, C., Vucko, M.J., Zeng, C., Zenger, K., et al. (2019). The future of aquatic protein: implications for protein sources in aquaculture diets. One Earth *1*, 316–329.
89. Winther, U., Hognes, E.S., Jafarzadeh, S., and Ziegler, F. (2020). Greenhouse Gas Emissions of Norwegian Seafood Products in 2017 (SINTEF Ocean AS).
90. Turchini, G.M., Trushenski, J.T., and Glencross, B.D. (2019). Thoughts for the future of aquaculture nutrition: realigning perspectives to reflect contemporary issues related to judicious use of marine resources in aquafeeds. N. Am. J. Aquac. *81*, 13–39.
91. Kwasek, K., Thorne-Lyman, A.L., and Phillips, M. (2020). Can human nutrition be improved through better fish feeding practices? a review paper. Crit. Rev. Food Sci. Nutr. 1–14.
92. Glencross, B.D., Baily, J., Berntssen, M.H.G., Hardy, R., MacKenzie, S., and Tocher, D.R. (2020). Risk assessment of the use of alternative animal and plant raw material resources in aquaculture feeds. Rev. Aquac. *12*, 703–758.
93. Roberts, C.A., Newton, R.W., Bostock, J., Prescott, S., Honey, D., Telfer, T.C., Walmsley, S., Little, D.C., and Hull, S. (2015). A Risk Benefit Analysis of Mariculture as a Means to Reduce the Impacts of Terrestrial Production of Food and Energy (Scottish Aquaculture Research Forum). http://hdl.handle.net/1893/23422.
94. Bohnes, F.A., and Laurent, A. (2021). Environmental impacts of existing and future aquaculture production: comparison of technologies and feed options in Singapore. Aquaculture *532*, 736001.
95. Arru, B., Furesi, R., Gasco, L., Madau, F.A., and Pulina, P. (2019). The introduction of insect meal into fish diet: the first economic analysis on European sea bass farming. Sustain *11*, 1–16.
96. Bava, L., Jucker, C., Gislon, G., Lupi, D., Savoldelli, S., Zucali, M., and Colombini, S. (2019). Rearing of hermetia illucens on different organic by-products: influence on growth, waste reduction, and environmental impact. Animals *9*, 289.
97. Smárason, B.Ö., Alriksson, B., and Jóhannsson, R. (2019). Safe and sustainable protein sources from the forest industry – the case of fish feed. Trends Food Sci. Technol. *84*, 12–14.
98. Gamboa-Delgado, J., and Márquez-Reyes, J.M. (2018). Potential of microbial-derived nutrients for aquaculture development. Rev. Aquac. *10*, 224–246.
99. Halfdanarson, J., Koesling, M., Kvadsheim, N.P., Emblemsvåg, J., and Rebours, C. (2019). Configuring the future Norwegian macroalgae industry using life cycle analysis. In Advances in Production Management Systems towards Smart Production Management Systems, F. Ameri, K.E. Stecke, G. von Cieminski, and D. Kiritsis, eds. (Springer), pp. 127–134.
100. Ramirez, A.D., Humphries, A.C., Woodgate, S.L., and Wilkinson, R.G. (2012). Greenhouse gas life cycle assessment of products arising from the rendering of mammalian animal byproducts in the UK. Environ. Sci. Technol. *46*, 447–453.
101. Jonell, M., Phillips, M., Rönnbäck, P., and Troell, M. (2013). Eco-certification of farmed seafood: will it make a difference? Ambio *42*, 659–674.
102. Jonell, M., Tlusty, M., Troell, M., and Rönnbäck, P. (2019). Certifying farmed seafood - a drop in the ocean or a śtepping stoné to increased sustainability. In Sustainability Certification Schemes in the Agricultural and Natural Resource Sectors, M. Vogt, ed. (Routledge), pp. 157–178.
103. Pardo, M.Á., Jiménez, E., and Pérez-Villarreal, B. (2016). Misdescription incidents in seafood sector. Food Control *62*, 277–283.
104. Kroetz, K., Luque, G.M., Gephart, J.A., Jardine, S.L., Lee, P., Chicojay Moore, K., Cole, C., Steinkruger, A., and Donlan, C.J. (2020). Consequences of seafood mislabeling for marine populations and fisheries management. Proc. Natl. Acad. Sci. U S A *117*, 30318–30323.
105. Barendse, J., Roel, A., Longo, C., Andriessen, L., Webster, L.M.I., Ogden, R., and Neat, F. (2019). DNA barcoding validates species labelling of certified seafood. Curr. Biol. *29*, R198–R199.
106. Anderson, J.L., Asche, F., and Garlock, T. (2019). Economics of aquaculture policy and regulation. Annu. Rev. Resour. Econ. *11*, 101–123.
107. Wang, Q., Cheng, L., Liu, J., Li, Z., Xie, S., and De Silva, S.S. (2015). Freshwater aquaculture in PR China: trends and prospects. Rev. Aquac. *7*, 283–302.
108. Belton, B., Reardon, T., and Zilberman, D. (2020). Sustainable commoditization of seafood. Nat. Sustain. *3*, 677–684.
109. Ziegler, F., Hornborg, S., Green, B.S., Eigaard, O.R., Farmery, A.K., Hammar, L., Hartmann, K., Molander, S., Parker, R.W.R., Skontorp Hognes, E., et al. (2016). Expanding the concept of sustainable seafood using Life Cycle Assessment. Fish Fish *17*, 1073–1093.
110. Belton, B., van Asseldonk, I.J.M., and Thilsted, S.H. (2014). Faltering fisheries and ascendant aquaculture: implications for food and nutrition security in Bangladesh. Food Policy *44*, 77–87.
111. Kruijssen, F., Tedesco, I., Ward, A., Pincus, L., Love, D., and Thorne-Lyman, A.L. (2020). Loss and waste in fish value chains: a review of the evidence from low and middle-income countries. Glob. Food Sec. *26*, 100434.
112. Love, D.C., Fry, J.P., Milli, M.C., and Neff, R.A. (2015). Wasted seafood in the United States: quantifying loss from production to consumption and moving toward solutions. Glob. Environ. Chang. *35*, 116–124.
113. Reardon, T., Echeverria, R., Berdegué, J., Minten, B., Liverpool-Tasie, S., Tschirley, D., and Zilberman, D. (2019). Rapid transformation of food systems in developing regions: highlighting the role of agricultural research & innovations. Agric. Syst. *172*, 47–59.
114. FAO (2011). Global Food Losses and Food Waste – Extent, Causes and Prevention (United Nations Food and Agricultural Organization).
115. Hernandez, R., Belton, B., Reardon, T., Hu, C., Zhang, X., and Ahmed, A. (2017). The “quiet revolution” in the aquaculture value chain in Bangladesh. Aquaculture *493*, 456–468.
116. Almeida, C., Vaz, S., and Ziegler, F. (2015). Environmental life cycle assessment of a canned sardine product from Portugal. J. Ind. Ecol. *19*, 607–617.
117. Watson, J.R., Armerin, F., Klinger, D.H., and Belton, B. (2018). Resilience through risk management: cooperative insurance in small-holder aquaculture systems. Heliyon *4*, e00799.
118. Lourguioui, H., Brigolin, D., Boulahdid, M., and Pastres, R. (2017). A perspective for reducing environmental impacts of mussel culture in Algeria. Int. J. Life Cycle Assess. *22*, 1266–1277.
119. Gephart, J.A., Golden, C.D., Asche, F., Belton, B., Brugere, C., Froehlich, H.E., Fry, J.P., Halpern, B.S., Hicks, C.C., Jones, R.C., et al. (2020). Scenarios for global aquaculture and its role in human nutrition. Rev. Fish. Sci. Aquac. *0*, 1–17.
120. Metian, M., Troell, M., Christensen, V., Steenbeek, J., and Pouil, S. (2020). Mapping diversity of species in global aquaculture. Rev. Aquac. *12*, 1090–1100.
121. Tisdell, C., Hishamunda, N., van Anrooy, R., Pongthanapanich, T., and Upare, M. (2012). Investment, insurance and risk management for aquaculture development. In Proceedings of the Global Conference on Aquaculture 2010, R.P. Subasinghe, J.R. Arthur, D.M. Bartley, S.S. De Silva, M. Halwart, N. Hishamunda, C.V. Mohan, and P. Sorgeloos, eds. (FAO and NACA), pp. 303–335.
122. Nash, K.L., Cvitanovic, C., Fulton, E.A., Halpern, B.S., Milner-Gulland, E.J., Watson, R.A., and Blanchard, J.L. (2017). Planetary boundaries for a blue planet. Nat. Ecol. Evol. *1*, 1625–1634.
123. Beveridge, M.C.M., Thilsted, S.H., Phillips, M.J., Metian, M., Troell, M., and Hall, S.J. (2013). Meeting the food and nutrition needs of the poor: the role of fish and the opportunities and challenges emerging from the rise of aquaculture. J. Fish Biol. *83*, 1067–1084.
124. Yuan, J., Xiang, J., Liu, D., Kang, H., He, T., Kim, S., Lin, Y., Freeman, C., and Ding, W. (2019). Rapid growth in greenhouse gas emissions from the adoption of industrial-scale aquaculture. Nat. Clim. Chang. *9*, 318–322.