PLOS SUSTAINABILITY AND TRANSFORMATION

RESEARCH ARTICLE

Maximising sustainable nutrient production from coupled fisheries-aquaculture systems

David F. Willer[1]*, **James P. W. Robinson**[2], **Grace T. Patterson**[3], **Karen Luyckx**[4]

1 Department of Zoology, University of Cambridge, The David Attenborough Building, Pembroke Street, Cambridge, United Kingdom, **2** Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom, **3** Department of Livestock and One Health, Institute of Infection, Veterinary and Ecological Sciences, University of Liverpool, Leahurst Campus, Neston, Cheshire, United Kingdom, **4** Feedback Global, Unit 413, The Archives, Unit 10 High Cross Centre, Fountayne Road, Tottenham, London, United Kingdom

* dw460@cam.ac.uk

Abstract

Aquaculture expansion is expected to meet growing demand for sustainable animal-source foods. Yet marine-fed species already require millions of tonnes of wild-caught fish for feed, over 90% of which are nutritious food-grade species. Allocating feed fish for human consumption could reduce pressure on marine resources while increasing seafood production. We examine micronutrient flows (the transfer of micronutrients from feed to fish) in Scotland's farmed salmon industry, which is particularly reliant on marine feeds, to show that 1–49% of essential dietary minerals and fatty acids available in wild fish are retained in farmed salmon. Using three alternative production scenarios we show that reducing marine feeds in salmon production and allocating wild-caught feed fish for human consumption could produce more nutritious seafood and leave 66–82% of feed fish in the sea. Using global data on marine-fed aquaculture production, we show that removing wild-caught fish from salmonid production could leave 3.7 Mt fish in the sea while increasing global seafood production by 6.1 Mt.

Author summary

In this paper we demonstrate that marine-fed farmed salmon is an inefficient way to produce nutritious seafood, and that directing wild-caught 'feed' fish towards human consumption could maximise nutrient production while also relieving pressure on fisheries stocks. Substantial growth in aquaculture is required to sustain growing global demand for animal-source foods, with potential for the sector to provide all 177 million tonnes of additional animal-source food needed worldwide by 2050. Currently, Atlantic salmon production uses 60% of global supplies of fish oil and 23% of fishmeal destined for aquaculture. Yet salmon production only makes up 4.5% of global aquaculture, and feed reduction processes result in lost potential production of food volume and essential micronutrients. We quantify the volume of micronutrients and wild fish retained by marine-fed farmed salmon, using data on Scotland's farmed salmon production and nutrient concentrations in wild-caught feed fish. We then develop alternative seafood

Citation: Willer DF, Robinson JPW, Patterson GT, Luyckx K (2022) Maximising sustainable nutrient production from coupled fisheries-aquaculture systems. PLOS Sustain Transform 1(3): e0000005. https://doi.org/10.1371/journal.pstr.0000005

Editor: Semra Benzer, Gazi Universitesi, TURKEY

Received: June 3, 2021

Accepted: January 11, 2022

Published: March 1, 2022

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pstr.0000005

Data Availability Statement: All data is available in the manuscript or supplementary materials.

Funding: D.F.W. was funded by the Department of Zoology and a Henslow Fellowship at Murray Edwards College, University of Cambridge. J.P.W. R. was funded by a Leverhulme Trust Early Career

Fellowship. K.L. was funded by the Waterloo Foundation. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

production scenarios that minimise marine feeds to assess the potential sustainability benefits of maximising micronutrient production in coupled fisheries-aquaculture systems, in the UK and worldwide.

1. Introduction

Growth in aquaculture is crucial to meet global animal-source food demands [1–3]. Our ability to increase production of land-derived foods is increasingly limited by scarce land and water resources [3], fish and seafood are rich in bioavailable nutrients not easily found in plant-based foods [2], and there are opportunities for aquaculture to provide all of the 177 Mt of additional animal-source food needed worldwide by 2050 [3]. Aquaculture can provide a low-carbon, sustainable, affordable substitute for terrestrial meat sources, and demand is expected to continue to grow quickly [4–6]. Yet with a large proportion of production—70% in 2018 [1]—reliant upon external sources of feed, further growth in fed aquaculture is unsustainable [7,8]. Fishmeal and fish oil are key components of fed aquaculture, comprising 76% and 71% of global resources used in aquafeeds, respectively [9]. Yet 90% of fishmeal and fish oil is derived from nutritious food-grade fish such as sardines and anchovies that could be fed directly to humans [10]. There is therefore an urgent need to optimise resource allocation in aquaculture [11,12].

The salmon industry, which from 1998 grew by 270% to become the most valuable sector in aquaculture at US$ 23 billion in 2018 [1], is particularly reliant on feed from wild-caught fish [13]. Over 72% of protein in feed is lost in salmon production [14], while feed accounts for over 90% of the detrimental environmental impacts of salmon aquaculture [15]. Marine feeds are also increasingly produced using forage fish caught off West Africa [16], likely impacting fish consumption in places with high levels of food insecurity [17]. Growth in salmon production is therefore expected to increase pressure on wild-caught fish populations globally [7,8], particularly impacting tropical nations by removing an irreplaceable source of nutrients [7,18]. Though these issues may be mitigated by uptake of alternative aquaculture feeds, including plant-based sources (soy, corn, wheat) and novel feeds (insects, bacteria), it remains unclear whether these products can be produced at sufficient scale [7]. Furthermore, evidence that plant-based feeds decrease the nutritional value of farmed fish [7,19] may disincentivize adoption of alternative feeds. Alternative approaches to fed aquaculture that reduce forage fish demand therefore also need to protect supply of nutritious seafood.

Farmed Atlantic salmon provide a rich source of protein and the omega-3 fatty acids EPA (eicosapentaenoic acid), DHA (docosahexaenoic acid), and DPA (docosapentaenoic acid) which are essential to neuro-development and highly cardioprotective [2]. However, compared to feed-fish species, salmon are less concentrated in other essential dietary micronutrients such as calcium, iron and zinc [20,21]. Wild-caught feed fish thus contain higher nutrient density than the farmed salmon they produce, suggesting that redirecting wild-caught feed fish for human consumption and limiting marine feed in farmed salmon would reduce pressure on wild fish stocks while increasing nutritious seafood production. Such optimisation of nutrient production from coupled fisheries-aquaculture systems has been proposed as a method of nutrition-sensitive aquaculture, maximising the contribution of aquatic food systems to human health [5].

Here, we examine potential for optimising nutrient production in marine-fed Scottish salmon, developing production scenarios that both improve nutrient output and reduce forage fish pressure. We focus on Scotland's salmon industry, the third largest worldwide valued at over £1 billion [1] and the UK's largest food export by value [22], as a case study. To improve over previous investigations which have centred on different approaches to fish in/fish out and forage fish dependency ratios [23,24], our approach focuses on maximising micronutrient retention. This is based upon the principle that the most nutritionally valuable output of salmon farming is omega-3 fatty acids and several other micronutrients [1], and that fed fish aquaculture performs poorly from a protein retention and greenhouse gas emission perspective compared to unfed seafood or plant crops [25]. Three different scenarios for fed aquaculture industry development are assessed, each enabling over 65% of wild-caught fish to remain in the sea while maintaining or increasing production of nutritious seafood. Scenarios are designed to identity trade-offs in nutrient production across seafood sectors, and do not consider economic and consumption factors. We demonstrate how the model could be applied globally in the context of all marine fed aquaculture to improve the sustainability and efficiency of nutrient utilisation across multiple sectors.

2. Results

2.1. Micronutrient retention in farmed salmon

Production of the 179,000 tonnes of Scottish Atlantic salmon in 2014 required fish oil derived from 460,000 t of wild-caught fish, 76% of which were species edible by humans. We compile the latest publicly available data on fishmeal and fish oil (FMFO) inputs from wild-caught fish used in farmed Scottish salmon production, taking the form of FMFO composition data from 2014 (Fig 1) (see Methods). In 2014 179,000 t of Scottish salmon were produced (Fig 1A), requiring 33,000 t of fish oil [26]. Based upon established rates of fish oil conversion (4.8% [27]) we estimate that 688,000 t of fish would be required to produce this quantity of fish oil. Fish oil production is comprised of 24–47% trimmings (i.e. by-products) leaving 53–76% of fish oil derived from wild-caught fish. Taking the global average of trimmings use (33%), we estimated that 460,000 t of wild-caught fish were required for Scottish salmon production in 2014 (range = 363,000 to 523,000 t) (Fig 1B). This volume would also produce 155,000 t of fishmeal, of which 55,000 t was used in salmon production [26], leaving 100,000 t spare for other

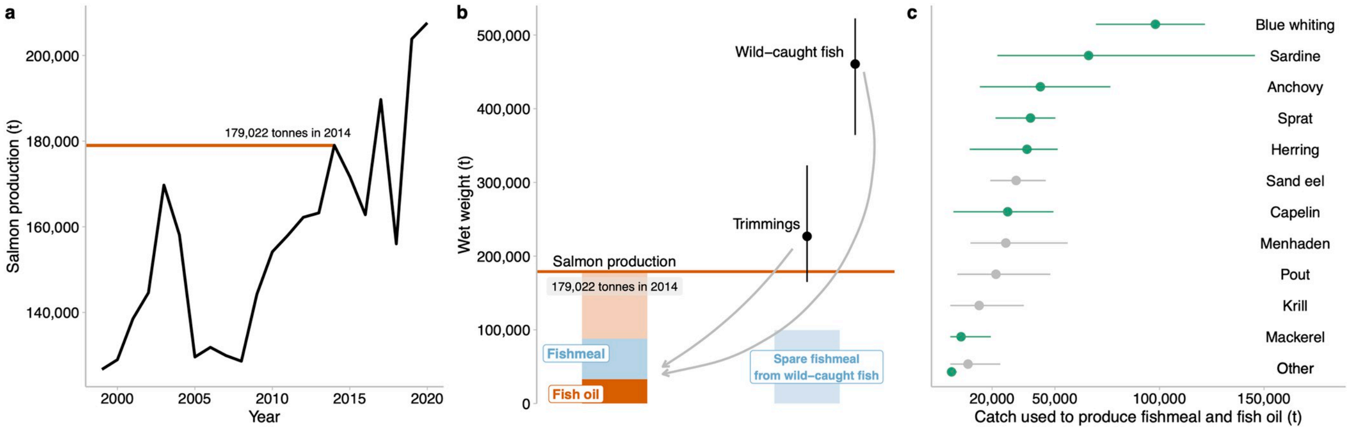

Fig 1. Fishmeal and fish oil inputs in Scottish farmed salmon production. Panel (a) shows salmon production from 1999–2020, highlighting 2014 when 179,022 tonnes were produced. Panel (b) demonstrates how 2014 production used 33,000 t of fish oil, which required 227,500 t of trimmings and 460,000 t of wild-caught fish. Points and uncertainty bars reflect variation in the composition of trimmings and wild-caught fish in fishmeal and fish oil (FMFO), showing the Scottish salmon estimate (lower), global average (point), and EU average (upper). Salmon production used 55,000 t of the fishmeal produced leaving 99,688 t spare. Panel (c) shows the contribution of food-grade (green) and non-food-grade (grey) species in the 460,000 t of wild-caught fish required for FMFO. Points and uncertainty bars represent the mean, minimum and maximum contribution of each species based on FMFO composition data of two major FMFO producers over 2016–2019 (see Methods).

https://doi.org/10.1371/journal.pstr.0000005.g001

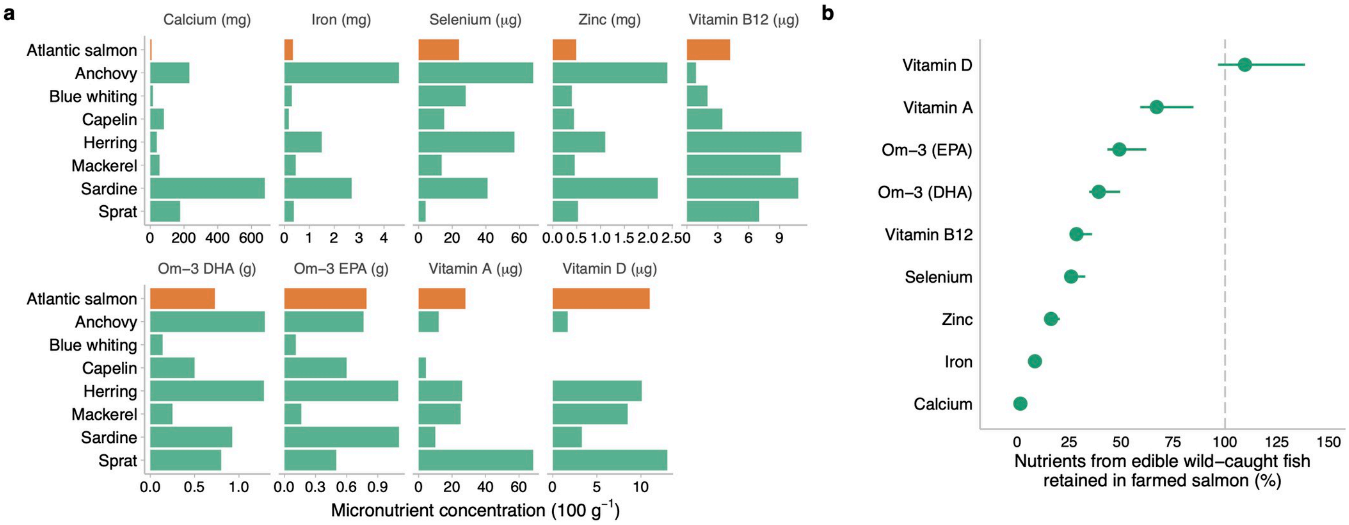

Fig 2. Retention of micronutrients from wild-caught fish in farmed salmon. Panel (a) shows the micronutrient composition of wild-caught fish in salmon feed relative to the farmed salmon produced. Panel (b) shows the proportion of these micronutrients from wild-caught fish included in feed that are retained in farmed salmon, based upon the mean volume of wild-caught fish in fish oil required to support Scottish salmon production in 2014. In (b) the error bars represent the uncertainty derived from the minimum and maximum contributions to fishmeal and oil among species.

https://doi.org/10.1371/journal.pstr.0000005.g002

purposes, such as feeds for other aquaculture species. Data on the species composition of FMFO from major feed producers used by Scottish salmon farms (S2 Table) shows that most FMFO is derived from food-grade fish species (as defined by Seafish [28]). Based on 2014 production values, this corresponds with ~315,000 t from seven food-grade species, or 76% of wild-caught fish (Fig 1C).

Most edible wild-caught fish species in FMFO have higher concentrations of key micronutrients than farmed salmon, and for some of these micronutrients as little as 1% is retained in farmed salmon (Fig 2A and 2B). For calcium, iron, selenium, and zinc, 1–28% is retained in farmed salmon (Fig 2B). Scottish salmon is often marketed as high in omega-3 fatty acids (EPA and DHA), yet omega-3 concentrations are similar in anchovy, herring, sardine, and sprat, and only 49% of EPA and 39% of DHA available from wild fish are retained in farmed salmon (Fig 2B). Vitamin D is the only micronutrient with a high level of retention by farmed salmon, showing a 10% increase compared to the wild-caught fish, owing to relatively lower vitamin D concentrations in the species that dominated FMFO production (blue whiting, anchovy and sardine) (Fig 2B). Full details on the micronutrient composition of the wild-fish species used in salmon feed, and the micronutrient composition of Scottish salmon, are provided in S4 Table. Retention rates depended on the relative nutrient content of feed fish species and farmed salmon, with nutrients high in feed species and low in salmon having low retention rates. Nutrient retention can also be impacted by dietary composition and the general health state of fish [29].

2.2. Scenarios to optimise micronutrient retention and resource usage in salmon production

We construct three alternative production scenarios to assess potential benefits in seafood production and nutritional quality from human consumption of fish used in salmon feeds, relative to a 'business-as-usual' scenario (Scenario I) in which farmed salmon is fed on FMFO from both wild-caught fish and fish trimmings (Fig 3). A recommended seafood portion of 140 g is used to standardise comparison (see Methods) [30].

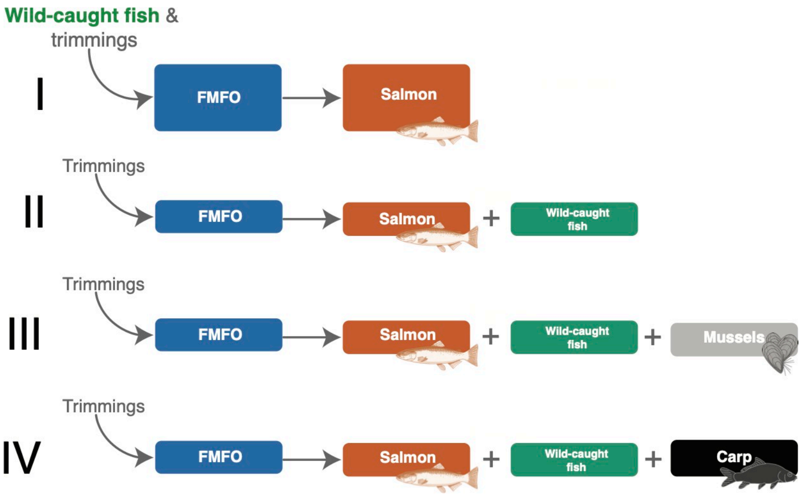

Fig 3. Overview of production scenarios. The panel outlines the business-as-usual scenario: (I) salmon fed on trimmings and wild-caught fish, alongside three alternative production scenarios: (II) trimmings-only salmon and wild-caught fish; (III) trimmings-only salmon and mussels; and (IV) trimmings-only salmon and carp.

https://doi.org/10.1371/journal.pstr.0000005.g003

In Scenario II, salmon are produced using only FMFO from fish trimmings ('trimmings-only salmon'), and these salmon are supplied directly to humans alongside a proportion of the wild-caught fish that would have been destined for FMFO. All of the edible edible species local to waters surrounding the UK are supplied directly to humans, alongside 44% of the anchovy and sardine catch, leaving 305,000 t of wild-caught fish in the ocean and 149,000 t edible seafood (Fig 4C). The result is that 101 g of edible wild-caught fish is supplied alongside 39 g salmon, providing equivalent or greater omega-3 fatty acids (EPA + 0.1%, DHA + 19.6%), substantially more minerals and vitamin B12, although less vitamin A (- 18%) and D (- 28%).

In Scenarios III and IV, trimmings-only salmon is supplied alongside wild-caught fish and an equal portion of mussels (III) or carp (IV) (Fig 3). Both Scenarios III and IV produce seafood portions with higher mineral concentrations (Fig 4B), whilst further reducing the use of wild-caught fish and producing the same total volume of seafood (Fig 4C). Both the mussel and carp scenarios provide 10–20% lower levels of omega-3 than the business-as-usual salmon-only scenario, but provide twice the amount of vitamin A (mussels) or a 20% increase in vitamin D (carp). Accounting for edible meat yields [3,31] we estimate that 132,000 t mussels or 98,000 t carp would be required to maintain seafood production levels, with ~1,200 t fishmeal needed for carp. All three alternative scenarios use at least 66% less fishmeal than business-as-usual salmon.

2.3. Reallocating seafood resources on a global scale

We next explore Scenario II in a global context to assess the potential food and sustainability benefits of limiting farmed salmonid production to FMFO from trimmings. Under business-as-usual conditions (based on 2016 data), 15 Mt of wild-caught fish were reduced to FMFO, and primarily used to grow salmonids (0.705 Mt fishmeal, 0.395 Mt fish oil), freshwater fishes (0.675 Mt fishmeal, 0.0860 Mt fish oil), crustaceans (0.951 Mt fishmeal, 0.04 Mt fish oil), and livestock (1.24 Mt fishmeal, pig and poultry) (Fig 5, S5 Table). Under business-as-usual salmonids accounted for 60% of fish oil and 23% of fishmeal usage in aquaculture. When applying Scenario II on a global scale, limiting marine feeds in salmonid production to trimmings, fish oil use by salmonids is reduced to 0.158 Mt, reducing total fish oil production by 27%, and

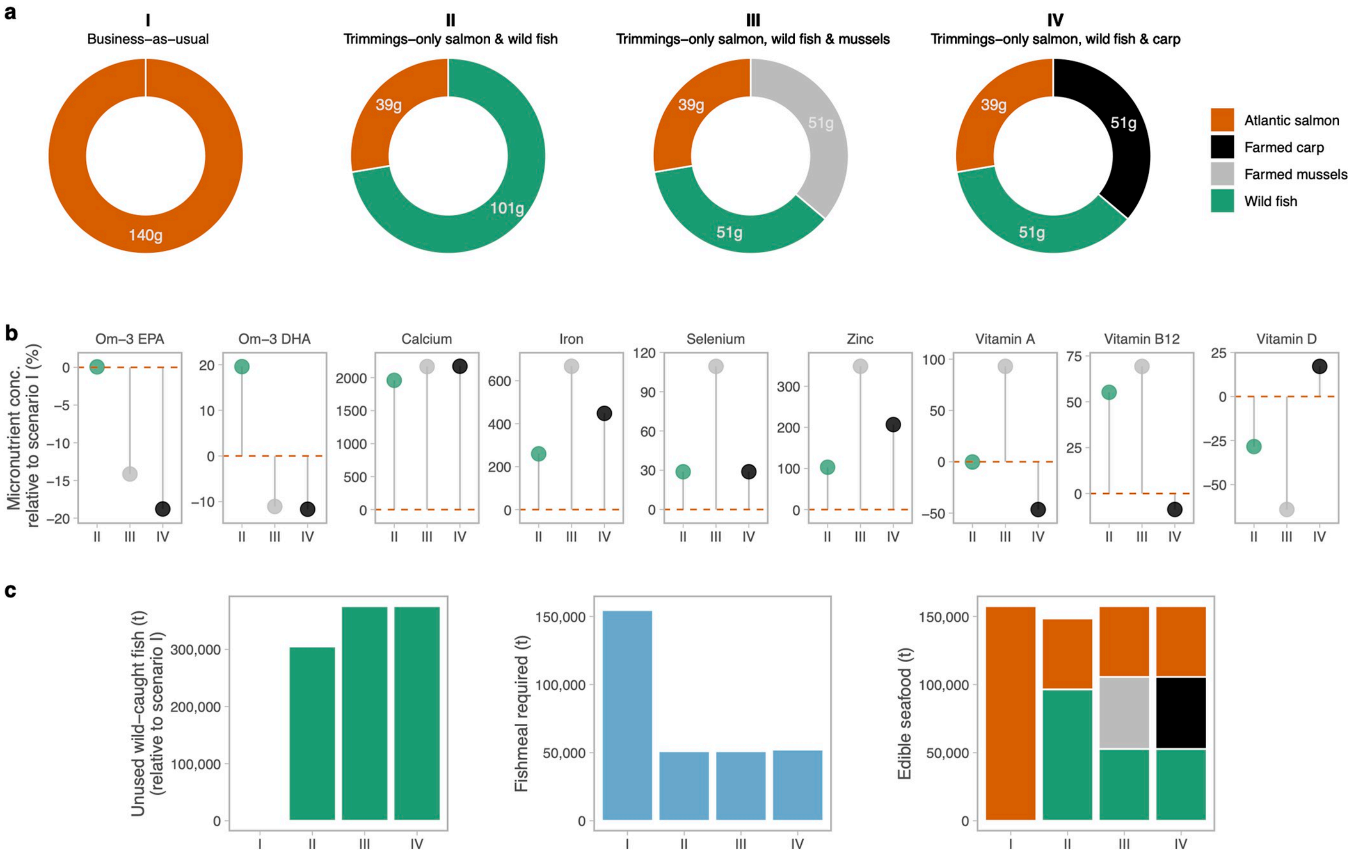

Fig 4. Micronutrient composition, feed requirements and food outputs of alternative production scenarios. Four production scenarios are presented in (a): I is farmed salmon fed on FMFO from wild-caught fish and trimmings (business-as-usual); II is salmon produced only from trimmings, with the spare edible wild-caught fish supplied directly to humans; III is trimmings-only salmon with equal portions of wild-caught fish and mussels; IV is trimmings-only salmon with equal portions of wild-caught fish and carp. In (b) the micronutrient concentration of Scenarios II—IV are shown relative to Scenario I (red dashed line). In (c) changes to seafood production required for each scenario are shown by the spare volume of wild-caught fish (relative to wild-caught fish in FMFO, Fig 1B), the fishmeal required for production, and the total volume of seafood produced corrected for edible portion sizes.

https://doi.org/10.1371/journal.pstr.0000005.g004

releasing 4.9 Mt wild-caught fish for other uses (Fig 5). If 24% of these wild-caught fish were supplied to humans directly, maintaining both seafood production volumes and DHA/EPA concentrations in a standard seafood portion (Fig 4, Scenario II), 3.7 Mt of wild-caught fish could remain unfished. Furthermore, by maintaining fish oil use in other species groups and re-allocating fishmeal towards carp, total seafood production in systems using commercial aquafeed could increase by 6.1 Mt (39%) relative to business-as-usual.

3. Discussion

3.1. The need for new approaches to salmon farming

Our analysis indicates that salmon aquaculture (Scenario I) is associated with the loss of large volumes of micronutrients which could otherwise be of great value to human health. In our case study of Scotland's salmon industry, 76% of the wild-caught fish included in salmon feed were edible to humans, and only 1–50% of most key micronutrients in these fish were retained in farmed salmon. Worldwide salmon production takes 60% of all fish oil and 23% of all fishmeal used in aquaculture [28], yet salmon only makes up 4.5% of global aquaculture production by volume [1]. In comparison cyprinids (carp) make up 35.3% of global aquaculture

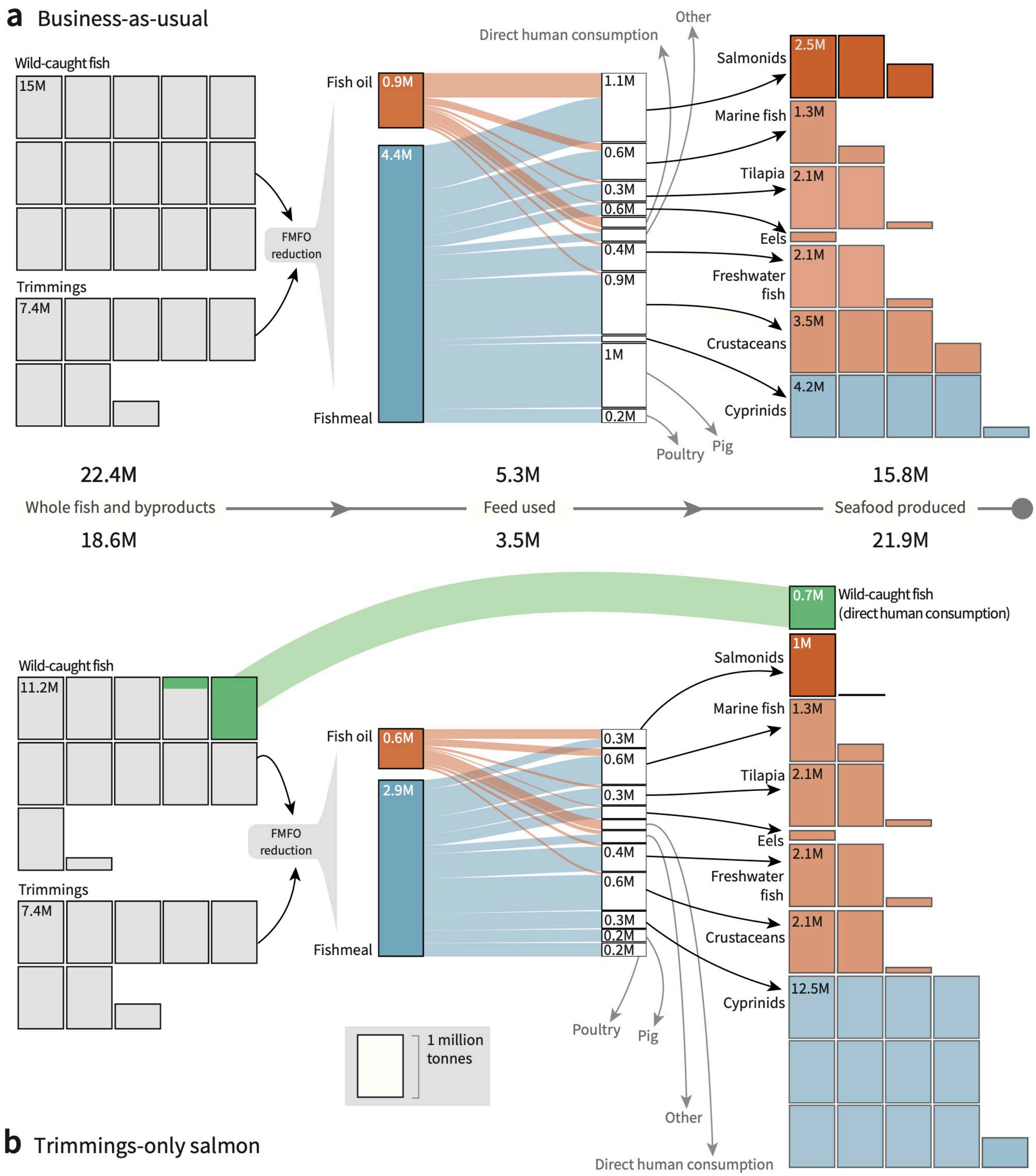

Fig 5. Limiting farmed salmonid FMFO usage to trimmings on a global scale. Panel (a) is the business-as-usual scenario in which salmonids are fed on FMFO from both wild-caught fish and trimmings. Panel (b) represents Scenario II applied on a global level, where farmed salmonid production is limited to FMFO from trimmings. The total wild fish capture, feed usage, and seafood production of the business-as-usual and Scenario II conditions are shown in-between panel (a) and (b). Box colours indicate species groups that require fish oil and fishmeal (red) or only fishmeal (blue). Each box represents 1 million tonnes. Seafood produced is corrected for species-specific edible yields (S6 Table).

https://doi.org/10.1371/journal.pstr.0000005.g005

production by volume [1], but use close to 0% of fish oil and 3% of fishmeal supplies [28]. Feed production now accounts for 90% of the environmental footprint of salmonid production [15]. Allowing salmonid production to expand further via its current approach will place exceptional stress on global fish stocks already at sustainable limits [1,11,32]. Salmon production could still expand without increasing its wild-fish footprint with use of plant-based feeds, but these products are not yet produced at scale [7], and alternative feeds may also reduce the nutrient composition of salmon [19]. Promoting human consumption of forage fish destined for feed is therefore possible using current wild-fish production levels, and delivers additional nutrient benefits.

Current approaches to marine-fed aquaculture could be further optimised for nutritious food production, if solutions are developed that continue to provide the high-quality nutritional benefits of fish and seafood to the human population, whilst also ensuring the aquaculture sector is able to maintain or increase its economic output. We considered three alternative production scenarios that direct only fish-trimmings towards salmon production. This would, at least initially, mean a drop in salmon production volumes, but would not prevent the salmon industry from becoming more profitable relative to production volumes. Integrated multitrophic aquaculture systems, for example salmon farming combined with mussels, could enable salmon farmers to diversify production and become more sustainable [25]. Alternative feeds for salmon farming are increasing in availability and effectiveness [33], although there are still hurdles to be overcome regarding their nutritional quality and sustainability [7]. Our case study used 2014 data to allow for sufficient information on FMFO composition, but dependence on marine feeds for salmon is decreasing, now at around 18% of total salmon feeds [34]. Continued reduction in marine dependency would improve nutrient efficiency, if wild-caught fish are directed for human consumption. In addition, with alternatives to fishmeal and fish oil such as insects (e.g. black soldier fly larvae), bacteria and yeasts, microalgae (e.g. chlorella) and macroalgae (e.g. schizochytrium sp.), the industry is now expanding further in a more sustainable manner, and our study highlights further benefits of allocating more forage fish for human consumption [7,35].

3.2. Alternative production scenarios

We considered three alternative production scenarios: (II) trimmings-only salmon and wild-caught fish; (III) trimmings-only salmon and mussels; and (IV) trimmings-only salmon and carp.

3.2.1. Scenario II: Trimmings-only salmon and wild-caught fish.

Scenario II offers potential to improve human dietary nutrient composition and reduce pressure on wild fish stocks. By reallocating the recommended 140 g portion of seafood to 39 g of trimmings-only salmon and 101 g of wild-caught fish, the omega-3 and mineral content of a standard seafood portion could improve substantially. The total amount of seafood available could increase, whilst leaving 66–79% of wild fish uncaught.

There are however significant challenges to encouraging increased human consumption of forage fish. 20 Mt of fish per year are directed towards feeding fish or livestock instead of humans and 90% of these fish are food-grade [10]. In Peru, the world's top producer of FMFO, only 1% of anchovy landings are directed to human consumption [32], and patterns are similar elsewhere, with only 3% of the Baltic herring catch used for human food [36]. Although some of these species are consumed by local markets, limited economic incentive is a barrier. Increasing demand for FMFO means fishermen will usually receive higher prices to sell fish for FMFO compared to selling fish for canning or freezing, for example for Peruvian anchovy profits are 19% higher when selling for FMFO [32]. Similar patterns of feed reduction are also developing in emerging markets such as West Africa, where forage fish are already an important source of protein [37] and micronutrients [18]. Other foods such as broiler chicken also displace forage fish from the cheap protein market, for example the average price of chicken breast is cheaper than that of canned anchovy (3.5 vs 4.1 US$ per kg) [32]. Poor demand at the consumer end is also a major issue, with fish such as sardines, herring and anchovies often cited as having poorer taste and appeal than species like salmon or tuna [32,36]. Furthermore if aquaculture demand for forage fish is reduced, there is uncertainty around whether rebound effects may increase or decrease the price of forage fish, impacting affordability for both consumers and feed producers.

Both industry management and marketing approaches could be used to overcome these challenges. Altering supply chain structures so that more bargaining power is given to food processors instead of industrial fishers could lower the relative price point for canned and frozen products and shift demand away from FMFO [10,32]. Improving cold storage facilities on ships could allow entire catches of forage fish to be classed as food-grade and avoid high allocation of sub-standard fish towards feed [32]. The development of new appealing and convenient consumer products would increase demand. In Finland, approaches including ecolabelling and the development of new products such as boneless heat-to-eat 'pulled herring' have been highly successful in increasing consumption of species that would otherwise go to FMFO [36].

3.2.2. Scenario III Trimmings-only salmon, wild-caught fish and mussels. Scenario III offers further potential nutritional and sustainability advantages over Scenarios I and II. By including 51 g of mussels within each 140 g seafood portion, levels of key micronutrients including iron, selenium, zinc and vitamin A are elevated an order of magnitude above salmon-only seafood portions. The need for wild-caught fish is further reduced, providing the option to potentially leave over 85% of wild fish uncaught. Major sustainability benefits could be realised; the CO_2 emissions to produce 1 t of edible mussel meat are just 127 kg [31] compared to 2400 kg for salmon [38], and eutrophication potential per t of meat is orders of magnitude lower at 0.06 kg PO_4 for mussels [31] compared to 26.7 kg PO_4 for salmon [38]. There is also ample space to expand production of bivalves such as mussels, and using just 1% of the potential production space globally could provide 1 billion people with all their protein requirements [25].

Mussel production already makes up a third of EU aquaculture [39] and worldwide mussel production was 2.1 Mt (live weight) in 2019 [1]. There are however significant challenges in industry expansion. Diseases such as *Vibrio sp*. are a problem in bivalve stocks and contributing to the low availability of high-quality bivalve seed which limits industry growth [39,40]. The atomised structure of the producer sector in the UK and Europe means that it is cheaper to import mussels from nations including Chile where production costs are lower, stifling domestic production and increasing environmental impacts in shipping [39]. In Chile, bivalves represent an affordable food choice, with frozen meat available to consumers at around $1.40 kg^{-1} [41]. However, in the UK coastal space is limited and there are potential conflicts with other coastline users [39], while there are concerns about mussel food safety due to perceived contamination with microplastics, pathogens, or heavy metals. [42]. There is also the major challenge of encouraging mass-market uptake of mussels, with lack of knowledge on food preparation and a limited availability of accessible, convenient, and appealing products important hurdles [42].

There are numerous options to overcome challenges in mussel production and consumption and enable Scenario III to become a reality in the UK and beyond, with bivalves as a species group recognised as one of the most promising candidates for the expansion of sustainable seafood [34]. New bivalve breeding technologies and innovations such as microencapsulated feeds can provide an efficient means to rear high quality bivalve seed [43]. Developing the value chain to include facilities which integrate mussel hatcheries, depuration, and processing could dramatically lower domestic production costs, and provide the opportunity to create added-value mussel foods [39], for example through nutritional fortification with vitamin D during depuration [44]. The development of offshore mussel farms, such as Offshore Shellfish (Devon, UK), can avoid conflicts with coastal activities and could be integrated with other green initiatives such as wind farms [25]. Major advantages have now been made which can improve the safety and appeal of mussels as a food. During depuration the use of chelating agents such as chitosan can remove 90% of heavy metals within 24 h and UV light can be combined with Fe^{3+} rich water to eliminate pathogens more efficiently [45], while a large 300g serving of mussel meat contains just 0.06% of the tolerable daily intake of PCBs (polychlorinated biphenyls) [46], and there are opportunities to develop fresh pre-shucked mussels with a doubled shelf life using high hydrostatic pressure processing [47].

3.2.3. Scenario IV: Trimmings-only salmon, wild-caught fish and carp. The inclusion of carp within seafood portions in Scenario IV provides further opportunity for nutritional benefits and less use of wild-caught fish. Including carp could deliver 20% more dietary vitamin D to the human population compared to the business-as-usual scenario, of particular merit given vitamin D deficiency prevalence in Western Europe is 30–60% [48]. Scenario IV would also deliver higher concentrations of calcium, iron, selenium and zinc in seafood produced, but decreased concentrations of omega-3 fatty acids and vitamins A and B12. By balancing consumption of vitamin D-rich carp with wild fish concentrated in vitamins A and B12 (kippers, mackerel, sardines, and sprats), consumers can maximise their micronutrient intake in this scenario. The environmental footprint of carp production is also smaller than farmed salmon, with outlet waters from carp ponds generally cleaner than inlet waters, and a eutrophication potential considerably lower than salmon (6.1 vs 26.7 kg PO_4 per t of meat) [38,49]. Carp require no fishmeal or fish oil, and can use cereal-based feeds [50]. CO_2 emissions are however higher than salmon or mussel production (4300 kg CO_2 per t meat), 55% of this due to the carbon released during pond dredging (50), and the construction of carp ponds themselves can lead to undesirable landscape changes.

Carp production has been rapidly expanding worldwide, growing 120% between 1997 and 2017 [34]. In Europe the scenario is less positive, with the European production share falling from 10.9 to 1.9% over the past 30 years [50]. Carp are also exclusively freshwater fish unlike salmon, and hence could not offer a direct local replacement to the sea loch salmon farming systems in Scotland. Increases in carp consumption in the UK and Europe are likely to be fuelled by overseas imports, and there is outstanding potential for the expansion of freshwater carp production worldwide [51], albeit with considerable hurdles regarding land and freshwater availability under climate change and disease constraints from intensification [51]. Consumer uptake may however be limited, as in Europe carp is perceived as a relatively unappealing option, is bony and can have a sludgy aftertaste. In nations such as Poland where carp is a seasonal delicacy, consumption is still less than 5% than that of salmon [50]. The development of convenience products such as boneless carp fillets, carp burgers, and carp sausage has already been shown as an effective means to increase consumption in German and Polish consumers, and wider application of this approach could help drive demand [52]. When developing convenience products, it will be important to ensure that the nutritional merits of carp are not overwhelmed by undesirable filler ingredients, and that any other ingredients included are of a sustainable nature.

3.3. Global application of trimmings-only salmonid production

Applying Scenario II on a global level demonstrates that major reductions in wild fish capture and increases in seafood supply for human consumption can be made by strategic resource reallocation. Over 3.7 Mt of wild-caught fish could remain unfished, 1.8 Mt less FMFO used, and total fed seafood production could increase by 39% to 21.9 Mt, providing benefits to both human nutrition and the marine environment. Our findings complement research demonstrating potential for novel feeds to replace forage fish demand [7], suggesting there are multiple pathways towards reducing aquaculture dependency on marine ecosystems. However, by re-allocating feed fish for human supply, our scenarios are aimed at promoting dietary nutrient intakes (e.g. Fig 4), and may deliver greatest human health benefits in places with high fish consumption and existing nutrient deficiencies. For example, forage fish are an irreplaceable and affordable source of nutrients in many tropical coastal regions, but are increasingly reduced into aquafeed [16], whereas salmon is primarily consumed in wealthier countries where other food products can contribute to nutritious diets [53].

3.4 Limitations of trimmings-only salmonid production

We discuss two key limitations of our alternative production scenarios. First, efforts to reduce salmonid production and allocate more forage fish for human consumption on a global level faces strong cultural, political and economic barriers, particularly with FMFO industries resistant to change [54]. Our global model only allocates a small proportion (0.9 Mt) of wild-caught fish for direct human consumption, but the same barriers exist (e.g. section 3.2.1). Developed economies still favour high-value carnivorous fish and crustaceans [1,12]. The focus of fisheries managers is primarily to maximise (sustainable) catch, rather than on post-harvest resource use [37,54,55] while growing demand for seafood is expected to place further pressure on wild fish populations [54]. Indeed, there is a lack of evidence that increasing direct human consumption of underutilised forage fish will reduce overall pressure on stocks [56], while management of these species is inherently difficult due to high inter-annual variation in abundances [54]. Reduction in fishing pressure on forage fish will therefore require coordinated fisheries governance across several regions where forage fish stocks are key contributors to aquafeeds [56]. Nevertheless, reducing demand for marine feeds sourced in regions such as West Africa can protect the availability of affordable and nutritious seafood in food-insecure regions [18].

4. Concluding remarks

To manage growing pressure on wild-fish populations while ensuring aquatic foods can contribute to micronutrient sufficiency in global diets, the aquaculture sector needs to consider alternative pathways for meeting seafood demand. Limiting production of major fed-aquaculture species such as salmon to volumes that can be produced from fish by-products alone, and creating new markets for wild-caught fish and aquaculture species requiring little or no feed (e.g. carp and mussels), can increase sustainable production of nutritious seafood. Applying this approach to Scotland alone could allow over 75% of wild-caught fish currently used in Scottish salmon production to be left in the sea, while increasing production of more nutritious seafood products. Globally, our results suggest that limiting the volume of wild-caught fish used to produce FMFO can help to relieve pressure on wild fish stocks while increasing supply of nutritious wild fish for human consumption. Combined with adoption of non-marine aquafeeds [7], reduced use of wild-caught fish in aquaculture can help to protect local fish supply from tropical marine systems while sustaining global growth in aquaculture production.

5. Methods

This study centres around salmon production systems in Scotland. Commercial farming of Atlantic salmon began in Scotland in 1969, and the industry is now primarily controlled by six large companies. Scotland is the third largest salmon producer globally, and salmon is the UK's largest seafood export product by value [57]. Salmon are reared in sea cages and fed on diets containing fishmeal and fish oil (FMFO) derived from wild-caught fish and fish by-products, alongside other dietary components derived from plant crops such as soya. Salmon represent an important source of protein, omega-3 fatty acids, vitamin D, and other key micronutrients to human diets.

The following approach was used to develop new models to improve micronutrient retention and sustainability in aquaculture. Datasets were compiled on Scottish salmon production, FMFO composition, whole fish to FMFO conversion rates, and the micronutrient composition of edible wild-caught fish species, mussels and carp. These data were used to quantify the volume of fish required to produce the fish oil needed in Scottish salmon production in 2014 and to estimate the micronutrient retention of essential dietary micronutrients (i.e. the ratio of micronutrients in to micronutrients out) [14,21,24]. We focus on 2014 as data on FMFO composition used in Scottish salmon were only available for this year, and on nine micronutrients that are essential in human diets and available in food composition tables. Unlike conventional fish in fish out, or forage fish dependency ratios, which represent average reliance on wild fish for both fish oil and fishmeal, in this paper we looked at the volume of wild-caught fish needed to produce fish oil specifically for two reasons. Firstly, salmon uses a disproportionate amount of fish oil compared to all other fed aquaculture species. Secondly, the nutrients most difficult to obtain in foods other than fish, omega-3 fatty acids (DHA and EPA) are concentrated into the fish oil not the fishmeal portion of the feed. Using the production values obtained, diet scenarios were then constructed that limit Scottish salmon production by the availability of fish oil from by-products (i.e. trimmings), and allocate spare wild-caught fish for human consumption. Finally, global aquaculture statistics were compiled to assess the potential nutrient gains from allocating wild-caught fish for human consumption, increasing consumption of lower trophic aquaculture species and reducing global salmon production.

5.1. Scottish farmed salmon production

Scottish farmed salmon volumes (Scottish Government) [57] and data on FMFO used in production [26] were extracted for 2014, and are the latest publicly available data. The total volume of wet fish (wild-caught + trimmings) required for production in 2014 was estimated as the volume of fish oil divided by the fish oil yield efficiency (4.8% [27]). The relative proportions of trimmings in this wet fish volume are estimated at 24% (Scotland [58–62]), 47% (EU [63]), and 33% (global [27]) (S1 Table). These three values were then used to estimate the volume of wild-caught fish in wet fish used in 2014 and to provide uncertainty on the volume of wild-caught fish in Scottish salmon production. All subsequent analyses used the wild-caught fish volume estimate based upon the global average proportion of trimmings in wet fish (33% [27]).

Data were then compiled on the wild-caught fish species composition of FMFO used by Scotland salmon farms (S2 Table) [28,58,60–62]. Across two major companies in 2016–2019 the contribution of 16 species groups and trimmings to FMFO were recorded. As different companies reported different taxonomic resolution or only common names, related species were grouped together (anchovy = four anchovy and anchoveta species, sardine = five sardine, sardinella and pilchard species, mackerel = five mackerel species). Cod, boarfish and silver smelt, which had negligible contributions to FMFO in most years, were combined with 'Other' species. With these data estimates were made of the minimum, mean and maximum contribution of each species to fish oil, weighted by the relative proportion of fish oil and fishmeal and total FMFO production by each producer in each year (S3 Table) [28,58,60–62]. Species contributions were multiplied by the estimated wild-caught fish used in salmon production in 2014, giving the catch weight of wild-caught fish species required to produce Scottish salmon. Uncertainty estimates were generated to represent the observed variation in species' contributions across several years in two major salmon feed producers.

5.2. Micronutrient composition

Using the estimated production volumes and species catch sizes the flow of micronutrients from wild-caught fish to farmed Scottish salmon was traced. The study focussed on nine micronutrients that are essential or important in human diets, including four minerals (calcium, iron, selenium, zinc), two forms of omega-3 fatty acids (EPA and DHA), and three vitamins (A, D and B12). Micronutrient concentrations per 100g were extracted for Atlantic salmon (smoked), all edible species used in farmed salmon production (seven wild-caught fish species [28]), alongside two common aquaculture species (blue mussel, *Mytulis edulis*; common carp, *Cyprinus carpio*). Data were extracted (S4 Table) [18,20,64–68] to represent the nutrient value of seafood in its most commonly consumed forms (e.g. smoked, canned). Species which were not found in food composition databases were extracted from a trait-based model of micronutrient concentrations in marine fish [18], or represented by closely related species (e.g. rainbow smelt for capelin). All micronutrient concentrations and data sources are indicated in S4 Table. Species' catch volumes were multiplied by their micronutrient concentration, giving the total volume of micronutrients in wild-caught fish. These values were compared with the total volume of micronutrients in farmed Scottish salmon in 2014 that were produced using food-grade wild-caught fish products; using the assumption that 33% of fish in FMFO is trimmings this is the volume of micronutrients in 66% of Scottish salmon production (119,945 t). These values enabled calculation of a unitless proportion of micronutrients from wild-caught fish retained by farmed salmon ($mn_{retained}$) using the formula below.

$$mn_{retained} = mn_{farmed} / \Sigma \, mn_{wild,\, i}$$

In the formula, mn_{wild} represents the micronutrient yield for each wild-caught fish species i in fish oil, and mn_{farmed} the micronutrient yield from fish-oil derived salmon production in 2014. Micronutrient yields for wild-caught species and for fish-oil derived salmon are represented in units of μg/100g, mg/100g, or g/100g of edible fish, dependent on conventional presentation of each micronutrient.

5.3. Alternative production scenarios

Four production scenarios were constructed to examine the impact of limiting salmon production to the volume of salmon that could be produced using fish oil only from trimmings (Fig 3). Impacts on nutrient availability for human diets, seafood production, and fisheries catches were examined. All scenarios are limited by the volume and composition of wild-caught fish used in 2014 Scottish salmon production, and thus represented alternative pathways of nutrient production in a coupled fisheries-aquaculture system. Scenario I (business-as-usual) is a production scenario of 100% Scottish salmon, using salmon production and our estimated wild-caught fish volumes for 2014, because for 2014 reliable data exist on FMFO usage in Scottish salmon production [26]. Scenario I was then used as a baseline against which to compare alternative production scenarios. Scenarios II-IV limit salmon production to the volume available if FMFO is entirely derived from trimmings, thereby making 420,000 t of wild-caught fish available for human consumption or left in the sea unfished. Scenarios II-IV represent alternative uses of trimmings, wild-caught species, and farmed species produced using systems that require no feed or plant-based feed (mussels and carp). Based on business-as-usual trimmings production (i.e. scenario I) we measure the total seafood produced, and the volume of wild-caught fish and fishmeal required to do this. We also examine nutrient potential of each supply scenario by expressing seafood volume as number of seafood portions (140g) and nutrient content in each portion, according to hypothetical proportions of each seafood type.

Scenario II prioritises consumption by humans of wild-caught fish from fisheries in European EEZs (blue whiting, capelin, herring, mackerel and sprat in Northeast Atlantic fishing areas), allocating these species for direct supply to humans according to their relative proportions in FMFO. Scenario II is then optimised to reach equivalent omega-3 DHA and EPA concentrations as Scenario I by adding 44% of the total anchovy and sardine catch that would have been directed to FMFO. This study optimised for omega-3 fatty acids and not other micronutrients because of the relatively greater difficulty in sourcing EPA and DHA in foods other than fish [2], and because Atlantic salmon is often marketed as a rich source of omega-3 [1]. The anchovy and sardine groups in FMFO used in Scottish salmon were broad groups that likely contained several species, often including high volumes from reduction fisheries in tropical countries [1]. Although data were not available on the areas or countries that provide wild-caught fish species for FMFO, this sustainability issue is addressed by maximising consumption of intensively managed and relatively local to the UK Atlantic fish species and minimizing consumption of tropical or subtropical species. All three alternative scenarios use 56% less anchovy and sardine than scenario I.

Scenarios III and IV examine the effect of incorporating two common aquaculture species that can be produced without marine-animal ingredients, mussel and carp. These scenarios further limit the consumption of wild-caught edible fish relative to scenario II. DHA and EPA in human diets were again prioritised by allocating omega-3 rich anchovy and sardine species for direct human supply but leaving all other wild-caught fish species not used for feed and food so potentially leaving this volume unfished. Scenarios III and IV have equal volumes of farmed salmon, wild fish, and mussels or carp.

In all scenarios the concentration of each micronutrient in a standard portion of seafood (140g) was measured, alongside the volume of wild-caught fish used and seafood produced. In Scenario II, the wild-caught fish volume is the sum of blue whiting, capelin, herring, mackerel and sprat catches, plus 44% of anchovy and sardine catches. In scenarios III and IV, the wild-caught fish volume is 44% of anchovy and sardine catches. These values were expressed relative to the volume of wild-caught fish used to produce fish oil in Scenario I, giving the volume of fish that are no longer used in salmon production. The fishmeal required for salmon production (Scenario I) was set to 2014 values (S1 Table), and the volume of fishmeal required to produce the carp was estimated from global production statistics [1]. Mussel were assumed unfed and did not require fishmeal. The total volume of seafood produced was calculated as the tonnes of edible food in each scenario, accounting for species-specific portions of wild-caught fish (anchovy, 62%; capelin, 60%; herring, 61%; sardines, 62%; sprat, 56%; whiting, 40%) [69,70], cultured finfish (S6 Table) and mussels (40% [31]). The edible portion for farmed salmon was set at the maximum edible portion size reported in Fry et al. 2018 (88%, range = 59–88%) [14]. The estimate of seafood produced in Scenarios II-IV is likely an underestimate, as many wild-caught species used in FMFO are often consumed whole, for example anchovy, sardine and whiting.

5.4. Optimising micronutrient retention on a global scale

Global aquaculture production data were analysed to assess whether reducing wild-caught fish in salmon production could enhance production across marine-fed food systems worldwide while also reducing pressure on marine capture fisheries. Using data from multiple governmental, non-governmental, and industry bodies (S5 Table) the current flow of wild-caught fish into FMFO and all FMFO-derived food products was traced [1,28,64–68]. This business-as-usual scenario was based on data from 2016, when production estimates for wild-caught fish and FMFO utilization percentages for FMFO-fed food were available (S1 Table). Of the fish in FMFO, 67% was from wild-caught whole fish and the remaining 33% was from trimmings and by-products [27]. This was applied to the FAO global volume of wild-caught fish destined for FMFO [71], to estimate the additional volume of trimmings and by-products used for FMFO in 2016. Data was then collated on the proportion of FMFO usage by seven aquaculture species groups (salmonids, eels, marine fish, tilapia, cyprinids, other freshwater fish, crustaceans), direct human supply, livestock (pig and poultry), and other industries [28]. The collated data was then combined with the total volume of fish oil (878,000 t) and fishmeal (4.4 Mt) in 2016 to estimate the volume of wild-caught fish required to support these 11 FMFO end users (S5 Table). For example, aquaculture used 75% of fish oil production, of which salmonids comprised 60% of all aquaculture species, which was 45% the fish oil used by all end users (395,000 t) [28]. Finally, for each FMFO end use, data was extracted on production volumes from 2016 [1] (S6 Table), and then all production volumes of each end user were estimated for the proportion of marine-fed species in each species group [1,55].

The model then limited salmonid production to the fish oil available in trimmings, following the approach used for Scenario II in the Scottish salmon case study. This ‘trimmings-only salmon’ scenario reduced global fish oil usage by salmonids to 158,000 t, 40% of 2016, as globally 40% of fish oil was derived from trimmings [1]. Fish oil volumes for all other species were maintained at business-as-usual levels, such that total fish oil usage across all marine-fed products and fish oil for direct human supply was 641,000 t. The volume of whole wild-caught fish no longer required for salmonid production was then estimated assuming a fish oil yield of 4.8% [27]. Using the estimate of wild-caught fish required to meet DHA and EPA levels of farmed salmon (Fig 4), 24% of the wild-caught fish previously used for fish oil in salmonid production were then allocated for direct human consumption. It was assumed that the nutrient composition of FMFO used in Scottish farmed Atlantic salmon is representative of feed used by other farmed Atlantic salmon producers, and that most FMFO species are edible.

The global availability of fishmeal was then re-estimated to account for the reduced wild-caught fish input into FMFO, and then allocated among fishmeal-fed species groups (S5 Table). The result was that 978,000 t fishmeal was available from trimmings and 1.91 Mt from wild-caught fish, giving 2.87 Mt total fishmeal. The fishmeal volume from wild-caught fish was the proportion of wild-caught fish in re-allocated fish oil (55%) multiplied by the volume of fishmeal from wild-caught fish in business-as-usual (3.5 Mt). This volume was reallocated among four species groups in proportions that would enhance total seafood production. Fishmeal used by commercially fed carp was increased by 300% relative to business-as-usual, and reduced for salmonids (20%), pigs (20%) and crustaceans (60%) (S7 Table). Salmonid fishmeal use was set at 20% to acknowledge the declining reliance on fishmeal in salmon feed formulation with industry research. In 2016 average fishmeal inclusion in global salmon diets stood at 16% [28]. However, recent studies by Egerton et al. in 2020 have found that salmon need a minimum of just 5% fishmeal in their diets [72]. Therefore, in the alternative scenario it was assumed that salmon diets could be feasible with 8% fishmeal inclusion, 8% being half of 2016 usage and slightly higher than the minimum found by Egerton et al. 2020. This assumption then allowed the fishmeal allocation to salmon in the trimmings-only salmon scenario to be halved, whilst keeping the volume of salmon production stable. Marine-fed carp systems were allocated more fishmeal, as these do not require fish oil and use low volumes of fishmeal per kg seafood produced [55]. This reduced fishmeal used by for crustaceans, which require high volumes of fishmeal per kg seafood produced [9]. Finally, fishmeal usage by pigs was determined by the Eat Lancet recommendations to reduce pork production by 80% to improve environmental sustainability and human health [2]. Overall, when applied on this global level, the trimmings-only salmon scenario used 2.87 Mt of fishmeal, 64% of the business-as-usual usage.

Production volumes were then re-estimated for salmonids, carp, crustaceans and pigs. As carp and pigs did not use fish oil, and crustaceans used the same volume of fish oil as in the business-as-usual scenario, total production volumes for these groups were corrected by the proportional change in fishmeal. For example, a 10% increase in fishmeal corresponded with a 10% increase in food production. For salmonids, production volumes were assumed to be proportional to the volume of fish oil used and therefore equal to 40% of business-as-usual production. The remaining five species groups (eels, tilapia, marine fish, freshwater fish, poultry, other) did not change FMFO usage and were allocated business-as-usual production volumes. In both scenarios, production volumes were corrected for edible portion size (S6 Table) [1,14,55,69,70,73–76]. Average edible portions per species group were calculated using reported statistics on the edible portions of the major species of cultivated salmonids, eels, carp, tilapia, freshwater fish, crustaceans, alongside marine fish (S6 Table), and the groups of wild-caught fish used for FMFO (S2 Table) [55]. For cultivated fish, averages were weighted according to the production tonnage within the species group (S7 Table). Finally, the resulting global production volumes, alongside FMFO allocations, were visualised in Fig 5.

Supporting information

S1 Table. Data sources and key statistics.
(XLSX)

S2 Table. Species composition of FMFO of major feed producers used by Scottish salmon farms.
(XLSX)

S3 Table. FMFO production volumes of major feed producers used by Scottish salmon farms.
(XLSX)

S4 Table. Micronutrient composition of wild-fish species and Atlantic salmon.
(XLSX)

S5 Table. Global allocation of FMFO in aquaculture and non-fish products.
(XLSX)

S6 Table. Global production volumes of FMFO-derived products.
(XLSX)

S7 Table. Re-allocation of global FMFO in trimmings-only salmon scenario.
(XLSX)

Author Contributions

Conceptualization: Karen Luyckx.

Data curation: David F. Willer, James P. W. Robinson, Grace T. Patterson, Karen Luyckx.

Formal analysis: David F. Willer, James P. W. Robinson, Grace T. Patterson, Karen Luyckx.

Funding acquisition: David F. Willer, James P. W. Robinson, Grace T. Patterson, Karen Luyckx.

Investigation: David F. Willer, Karen Luyckx.

Methodology: David F. Willer, James P. W. Robinson, Grace T. Patterson, Karen Luyckx.

Project administration: David F. Willer.

Resources: David F. Willer.

Software: David F. Willer, James P. W. Robinson.

Supervision: David F. Willer, Karen Luyckx.

Validation: David F. Willer, James P. W. Robinson, Grace T. Patterson, Karen Luyckx.

Visualization: David F. Willer, James P. W. Robinson, Karen Luyckx.

Writing – original draft: David F. Willer, James P. W. Robinson, Grace T. Patterson, Karen Luyckx.

Writing – review & editing: David F. Willer, James P. W. Robinson, Grace T. Patterson, Karen Luyckx.

References

1. FAO. The State of World Fisheries and Aquaculture 2020 [Internet]. Rome: FAO; 2020. Available from: http://www.fao.org/documents/card/en/c/ca9229en
2. Willett W, Rockström J, Loken B, Springmann M, Lang T, Vermeulen S, et al. Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. The Lancet [Internet]. 2019 Feb; 393(10170):447–92. Available from: https://linkinghub.elsevier.com/retrieve/pii/S0140673618317884 https://doi.org/10.1016/S0140-6736(18)31788-4 PMID: 30660336
3. Costello C, Cao L, Gelcich S, Cisneros-Mata MÁ, Free CM, Froehlich HE, et al. The future of food from the sea. Nature [Internet]. 2020 Aug 19; Available from: https://doi.org/10.1038/s41586-020-2616-y
4. Golden CD, Koehn JZ, Shepon A, Passarelli S, Free CM, Viana DF, et al. Aquatic foods to nourish nations. Nature. 2021; 598(7880).
5. Shepon A, Gephart JA, Henriksson PJG, Jones R, Murshed-e-Jahan K, Eshel G, et al. Reorientation of aquaculture production systems can reduce environmental impacts and improve nutrition security in Bangladesh. Nature Food. 2020; 1(10).
6. Hamilton HA, Newton R, Auchterlonie NA, Müller DB. Systems approach to quantify the global omega-3 fatty acid cycle. Nature Food. 2020; 1(1).
7. Cottrell RS, Blanchard JL, Halpern BS, Metian M, Froehlich HE. Global adoption of novel aquaculture feeds could substantially reduce forage fish demand by 2030. Nature Food. 2020; 1(5).
8. Froehlich HE, Gentry RR, Halpern BS. Global change in marine aquaculture production potential under climate change. Nature Ecology & Evolution [Internet]. 2018; 2(11):1745–50. Available from: https://doi.org/10.1038/s41559-018-0669-1 PMID: 30201967
9. Malcorps W, Kok B, van't Land M, Fritz M, van Doren D, Servin K, et al. The Sustainability Conundrum of Fishmeal Substitution by Plant Ingredients in Shrimp Feeds. Sustainability [Internet]. 2019 Feb 25 [cited 2020 Oct 26]; 11(4):1212. Available from: https://www.mdpi.com/2071-1050/11/4/1212
10. Cashion T, le Manach F, Zeller D, Pauly D. Most fish destined for fishmeal production are food-grade fish. Fish and Fisheries. 2017; 18(5):837–44.
11. Attenborough D. A Life on Our Planet: My Witness Statement and a Vision for the Future [Internet]. Random House; 2020. Available from: https://books.google.co.uk/books?id=DRjcDwAAQBAJ
12. Tacon AGJ, Metian M. Fish Matters: Importance of Aquatic Foods in Human Nutrition and Global Food Supply. Reviews in Fisheries Science [Internet]. 2013 Jan; 21(1):22–38. Available from: http://www.tandfonline.com/doi/abs/10.1080/10641262.2012.753405
13. Tacon AGJ, Metian M, McNevin AA. Future Feeds: Suggested Guidelines for Sustainable Development. Reviews in Fisheries Science and Aquaculture. 2021. https://doi.org/10.1016/j.aquaculture.2021.736783 PMID: 33883784
14. Fry JP, Mailloux NA, Love DC, Milli MC, Cao L. Feed conversion efficiency in aquaculture: Do we measure it correctly? Environmental Research Letters. 2018; 13(2).

15. Newton RW, Little DC. Mapping the impacts of farmed Scottish salmon from a life cycle perspective. International Journal of Life Cycle Assessment. 2018 May 1; 23(5):1018–29.

16. Corten A, Braham CB, Sadegh AS. The development of a fishmeal industry in Mauritania and its impact on the regional stocks of sardinella and other small pelagics in Northwest Africa. Fisheries Research. 2017;186.

17. FAO, IFAD, UNICEF, WFP W. The State of Food Security and Nutrition in the World 2020 [Internet]. Vol. R ome. FAO, IFAD, UNICEF, WFP and WHO; 2020. Available from: http://www.fao.org/documents/card/en/c/ca9692en

18. Hicks CC, Cohen PJ, Graham NAJJ, Nash KL, Allison EH, D'Lima C, et al. Harnessing global fisheries to tackle micronutrient deficiencies. Nature [Internet]. 2019; 574(7776):95–8. Available from: https://doi.org/10.1038/s41586-019-1592-6 PMID: 31554969

19. Moxness Reksten A, Ho QT, Nøstbakken OJ, Wik Markhus M, Kjellevold M, Bøkevoll A, et al. Temporal variations in the nutrient content of Norwegian farmed Atlantic salmon (Salmo salar), 2005–2020. Food Chemistry. 2022;373. https://doi.org/10.1016/j.foodchem.2021.131445 PMID: 34731805

20. United States Department of Agriculture Agricultural Research Service. USDA Food Composition Databases. [Internet]. 2020 [cited 2020 Jul 14]. Available from: https://fdc.nal.usda.gov

21. Aas TS, Ytrestøyl T, Åsgård T. Utilization of feed resources in the production of Atlantic salmon (Salmo salar) in Norway: An update for 2016. Aquaculture Reports. 2019 Nov 1;15.

22. Food and Drink Federation. Export Statistics [Internet]. 2020 [cited 2020 Oct 27]. Available from: https://www.fdf.org.uk/

23. Ytrestøyl T, Aas TS, Åsgård T. Utilisation of feed resources in production of Atlantic salmon (Salmo salar) in Norway. Aquaculture. 2015;448.

24. Kok B, Malcorps W, Tlusty MF, Eltholth MM, Auchterlonie NA, Little DC, et al. Fish as feed: Using economic allocation to quantify the Fish In: Fish Out ratio of major fed aquaculture species. Aquaculture [Internet]. 2020; 528:735474. Available from: http://www.sciencedirect.com/science/article/pii/S0044848620309741

25. Willer DF, Aldridge DC. Sustainable bivalve farming can deliver food security in the tropics. Nature Food [Internet]. 2020 Jul 9; 1(7):384–8. Available from: http://www.nature.com/articles/s43016-020-0116-8

26. Shepherd CJ, Monroig O, Tocher DR. Future availability of raw materials for salmon feeds and supply chain implications: The case of Scottish farmed salmon. Aquaculture. 2017;467.

27. IFFO. Fish in: Fish Out (FIFO) ratios for the conversion of wild feed to farmed fish, including salmon [Internet]. Fish in: Fish Out (FIFO) ratios. 2017 [cited 2020 Dec 11]. Available from: https://www.iffo.com/fish-fish-out-fifo-ratios-conversion-wild-feed

28. Seafish. Fishmeal and fish oil facts and figures. Seafish [Internet]. 2018 [cited 2020 Dec 11];March:1–35. Available from: https://www.seafish.org/document/?id=1b08b6d5-75d9-4179-9094-840195ceee4b

29. Vera LM, Hamre K, Espe M, Hemre GI, Skjærven K, Lock EJ, et al. Higher dietary micronutrients are required to maintain optimal performance of Atlantic salmon (Salmo salar) fed a high plant material diet during the full production cycle. Aquaculture. 2020;528.

30. UK National Health Service. Fish and Shellfish—Eat Well Guidelines [Internet]. Live Well Guidelines. 2020 [cited 2020 Dec 14]. Available from: https://www.nhs.uk/live-well/eat-well/fish-and-shellfish-nutrition/

31. Frösell M. Mussel farming using various techniques evaluated using Life Cycle Assessment (LCA). SLU Dept of Energy and Technology [Internet]. 2019 [cited 2020 Oct 27];7. Available from: https://stud.epsilon.slu.se/14639/

32. Fréon P, Sueiro JC, Iriarte F, Miro Evar OF, Landa Y, Mittaine JF, et al. Harvesting for food versus feed: A review of Peruvian fisheries in a global context. Vol. 24, Reviews in Fish Biology and Fisheries. 2014. p. 381–98.

33. Cottrell RS, Metian M, Froehlich HE, Blanchard JL, Sand Jacobsen N, McIntyre PB, et al. Time to rethink trophic levels in aquaculture policy. Reviews in Aquaculture. 2021;

34. Naylor RL, Hardy RW, Buschmann AH, Bush SR, Cao L, Klinger DH, et al. A 20-year retrospective review of global aquaculture. Vol. 591, Nature. 2021.

35. Cadillo-Benalcazar JJ, Giampietro M, Bukkens SGF, Strand R. Multi-scale integrated evaluation of the sustainability of large-scale use of alternative feeds in salmon aquaculture. Journal of Cleaner Production. 2020 Mar 1;248.

36. Pihlajamäki M, Asikainen A, Ignatius S, Haapasaari P, Tuomisto JT. Forage fish as food: Consumer perceptions on baltic herring. Sustainability (Switzerland). 2019 Aug 1; 11(16).

37. Tacon AGJ, Metian M. Fishing for feed or fishing for food: Increasing global competition for small pelagic forage fish. Ambio. 2009; 38(6). https://doi.org/10.1579/08-a-574.1 PMID: 19860152

38. Philis G, Ziegler F, Gansel LC, Jansen MD, Gracey EO, Stene A. Comparing life cycle assessment (LCA) of salmonid aquaculture production systems: Status and perspectives. Vol. 11, Sustainability (Switzerland). MDPI AG; 2019.

39. Avdelas L, Avdic-Mravlje E, Borges Marques AC, Cano S, Capelle JJ, Carvalho N, et al. The decline of mussel aquaculture in the European Union: causes, economic impacts and opportunities. Reviews in Aquaculture. 2020. https://doi.org/10.1111/raq.12367 PMID: 32612676

40. Willer DF, Aldridge DC. Microencapsulated diets to improve bivalve shellfish aquaculture for global food security. Global Food Security [Internet]. 2019; 23(May 2018):64–73. Available from: https://doi.org/10.1016/j.gfs.2019.04.007

41. Instituto Nacional de Estadísticas. Chile National Statistics Database [Internet]. 2021 [cited 2021 Sep 24]. Available from: www.ine.cl

42. Wright AC, Fan Y, Baker GL. Nutritional Value and Food Safety of Bivalve Molluscan Shellfish. Vol. 37, Journal of Shellfish Research. 2018.

43. Willer DF, Aldridge DC. Microencapsulated diets to improve growth and survivorship in juvenile European flat oysters (Ostrea edulis). Aquaculture. 2019; 505:256–62. https://doi.org/10.1016/j.aquaculture.2019.02.072 PMID: 30890854

44. Willer DF, Aldridge DC. Vitamin Bullets. Microencapsulated Feeds to Fortify Shellfish and Tackle Human Nutrient Deficiencies. Frontiers in Nutrition [Internet]. 2020 Jul 20; 7(102). Available from: https://www.frontiersin.org/article/10.3389/fnut.2020.00102/full PMID: 32766272

45. Martinez-Albores A, Lopez-Santamarina A, Rodriguez JA, Ibarra IS, Mondragón A del C, Miranda JM, et al. Complementary Methods to Improve the Depuration of Bivalves: A Review. Foods [Internet]. 2020 Jan 24; 9(2):129. Available from: https://www.mdpi.com/2304-8158/9/2/129

46. Garrido Gamarro E, Ryder J, Elvevoll EO, Olsen RL. Microplastics in Fish and Shellfish–A Threat to Seafood Safety? Vol. 29, Journal of Aquatic Food Product Technology. Taylor and Francis Inc.; 2020. p. 417–25. https://doi.org/10.1016/j.toxicon.2020.05.001 PMID: 32387348

47. Bonfim RC, de Oliveira FA, Godoy RL de O, Rosenthal A. A review on high hydrostatic pressure for bivalve mollusk processing: Relevant aspects concerning safety and quality. Food Science and Technology. 2019; 39(3):515–23.

48. Lips P, Cashman KD, Lamberg-Allardt C, Bischoff-Ferrari HA, Obermayer-Pietsch B, Bianchi ML, et al. Current Vitamin D status in European and Middle East countries and strategies to prevent Vitamin D deficiency: A position statement of the European Calcified Tissue Society. European Journal of Endocrinology. 2019 Apr 1; 180(4):P23–54. https://doi.org/10.1530/EJE-18-0736 PMID: 30721133

49. Biermann G, Geist J. Life cycle assessment of common carp (Cyprinus carpio L.)–A comparison of the environmental impacts of conventional and organic carp aquaculture in Germany. Aquaculture. 2019 Feb 25; 501:404–15.

50. Karnai L, Szucs I. Outlooks and perspectives of the common carp production. Annals of the Polish Association of Agricultural and Agribusiness Economists. 2018 Apr 4; XX(1):64–72.

51. Belton B, Little DC, Zhang W, Edwards P, Skladany M, Thilsted SH. Farming fish in the sea will not nourish the world. Nature Communications [Internet]. 2020; 11(1):5804. Available from: https://doi.org/10.1038/s41467-020-19679-9 PMID: 33199697

52. Zander K, Feucht Y. How to increase demand for carp? Consumer attitudes and preferences in Germany and Poland. British Food Journal. 2020 Jun 30; 122(11):3267–82.

53. Gephart JA, Golden CD, Asche F, Belton B, Brugere C, Froehlich HE, et al. Scenarios for Global Aquaculture and Its Role in Human Nutrition. Reviews in Fisheries Science & Aquaculture [Internet]. 2020 Jul 9;1–17. Available from: https://doi.org/10.1080/23308249.2020.1782342

54. Froehlich HE, Jacobsen NS, Essington TE, Clavelle T, Halpern BS. Avoiding the ecological limits of forage fish for fed aquaculture. Nature Sustainability. 2018; 1(6).

55. Tacon AGJ, Hasan MR, Metian M. Demand and supply of feed ingredients for farmed fish and crustaceans: Trends and prospects. FAO Fisheries and Aquaculture Technical Paper [Internet]. 2011;564. Available from: http://www.fao.org/docrep/015/ba0002e/ba0002e.pdf

56. Farmery AK, van Putten IE, Phillipov M, McIlgorm A. Are media messages to consume more under-utilized seafood species reliable? Fish and Fisheries. 2020; 21(4).

57. Government Scottish. Scottish Fish Farm Production Survey 2019 [Internet]. Edinburgh; 2019 Oct [cited 2021 Mar 17]. Available from: https://www.gov.scot/publications/scottish-fish-farm-production-survey-2019/pages/5/

58. BioMar. Integrated Sustainability Report [Internet]. Aarhus; 2019 [cited 2021 Jan 17]. Available from: https://www.biomar.com/en/global/sustainability/sustainability-report/#refid-42178

59. Cargill. Aqua Nutrition Sustainability Report [Internet]. Minneapolis; 2019 [cited 2021 Jan 17]. Available from: https://www.cargill.com/doc/1432142322239/cargill-aqua-nutrition-sustainability-report.pdf

60. Mowi. Integrated Annual Report [Internet]. Bergen; 2019 [cited 2021 Jan 17]. Available from: https://mowi.com/blog/mowis-2019-annual-report/

61. BioMar. Integrated Sustainability Report [Internet]. Aarhus; 2018 [cited 2021 Jan 17]. Available from: https://www.biomar.com/en/global/sustainability/sustainability-report/#refid-42178

62. Mowi. Integrated Annual Report [Internet]. Bergen; 2018 [cited 2021 Jan 17]. Available from: https://mowi.com/blog/mowis-2018-annual-report/

63. European Commission. European Market Observatory for Fisheries and Aquaculture Products (EUMOFA) Monthly Highlights No. 1 [Internet]. 2020 Jan [cited 2021 Jan 17]. Available from: https://newacceptance.eumofa.eu/documents/20178/339391/MH1+2020.pdf

64. Swedish Food Agency. The Swedish Food Composition Database [Internet]. 2021 [cited 2021 Jan 17]. Available from: http://www7.slv.se/SokNaringsinnehall/

65. Nettleton JA. Introduction to Fatty Acids. In: Omega-3 Fatty Acids and Health. Boston: Springer; 1995.

66. Public Health England. McCance and Widdowson's The Composition of Foods Integrated Dataset 2019 [Internet]. London; 2019 [cited 2021 Jan 17]. Available from: https://www.gov.uk/government/publications/composition-of-foods-integrated-dataset-cofid

67. Agencia Española de Seguridad Alimentaris. Spanish Food Composition Database [Internet]. BEDCA. 2021 [cited 2021 Jan 17]. Available from: https://www.bedca.net/bdpub/index_en.php

68. UK Department of Health. Nutrient analysis of fish and fish products [Internet]. London; 2013 [cited 2021 Jan 17]. Available from: https://www.gov.uk/government/publications/nutrient-analysis-of-fish

69. FAO. Yield and nutritional value of the commercially more important fish species. FAO Fisheries Technical Paper 309 [Internet]. 1989 [cited 2021 Jan 20]; 309:1–187. Available from: http://www.fao.org/3/T0219E/T0219E00.htm

70. Seafish. The Seafood Guide [Internet]. 2009 Mar [cited 2021 Jan 20]. Available from: https://seafoodacademy.org/pdfs/seafood-guide.pdf

71. FAO. The State of World Fisheries and Aquaculture 2018 [Internet]. Rome: FAO; 2018 [cited 2021 Jan 17]. Available from: http://www.fao.org/state-of-fisheries-aquaculture/2018/en/

72. Egerton S, Wan A, Murphy K, Collins F, Ahern G, Sugrue I, et al. Replacing fishmeal with plant protein in Atlantic salmon (Salmo salar) diets by supplementation with fish protein hydrolysate. Scientific Reports. 2020; 10(1). https://doi.org/10.1038/s41598-020-60325-7 PMID: 32144276

73. Smith TIJ, Waltz W, Sandifer PA. PROCESSING YIELDS FOR MALAYSIAN PRAWNS AND THE IMPLICATIONS. Proceedings of the World Mariculture Society. 1980; 11(1–4).

74. Chen DW, Zhang M, Shrestha S. Compositional characteristics and nutritional quality of Chinese mitten crab (Eriocheir sinensis). Food Chemistry. 2007; 103(4).

75. Hung D, Nguyen NH. Modeling meat yield based on measurements of body traits in genetically improved giant freshwater prawn (GFP) Macrobrachium rosenbergii. Aquaculture International. 2014; 22(2).

76. Otwell WS, Rickards WL. Cultured and wild American eels, Anguilla rostrata: Fat content and fatty acid composition. Aquaculture. 1981; 26(1–2).