



Full length article

Sustainable optimization of global aquatic omega-3 supply chain could substantially narrow the nutrient gap

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ABSTRACT

Omega-3 EPA and DHA fatty acids are vital for human health, but current human nutritional requirements are greater than supply. This nutrient gap is poised to increase as demand increases and the abundance of aquatic foods and the amount of omega-3 they contain may dwindle due to climate change and overfishing. Identifying and mitigating loss and inefficiencies across the global aquatic supply chain has great potential for narrowing this nutrient gap. Here, using an optimization model, we show that omega-3 supply to humans could potentially increase by as much as 50% (reaching 630 kt y⁻¹) compared to present baseline by shifting feed inputs to produce species that have the highest omega-3 content per feed input (i.e. carp and crustaceans), diverting other production flows towards direct wild fish consumption, improving byproduct utilization, and reducing waste at the retail and consumer level. We then discuss the implications of our findings by prioritizing policies and identifying demand- and supply-side interventions to realize these ambitious changes. This work emphasizes the urgency needed in managing aquatic resources towards greater utilization of resources and highlights the extent to which even partial adaptation of the measures we propose can have on narrowing the present and future nutrient gap as novel alternative sources of omega-3 become available on a larger scale.

1. Introduction

Polyunsaturated fatty acids are essential to human health, but humans are incapable of fully synthesizing omega-3 themselves and therefore must source this essential nutrient through food (Anderson and Ma, 2009; FAO, 2008; Gerster, 1998; Tocher et al., 2019). In particular, the long chain polyunsaturated fatty acids eicosapentaenoic (EPA) and docosahexaenoic (DHA) acids – also known as long chain omega-3 fatty acids – have a positive effect on early neurodevelopment (Jiao et al., 2014), and are associated with reduced risk of premature

death (Jayedi and Shab-Bidar, 2020; Wang et al., 2016), cognitive and behavioral disorders (Kirby and Derbyshire, 2018), and cardiovascular disease (Jayedi and Shab-Bidar, 2020; Rimm et al., 2018). The health benefits of the “shorter chain” omega-3 alpha-linolenic acid (ALA), a precursor to EPA and DHA but with low conversion efficiency in mammals, are less clear (Anderson and Ma, 2009). Omega ALA is derived from terrestrial food sources. However, EPA and DHA omega-3 (referred to hereafter as ‘omega-3’ for short throughout the manuscript unless explicitly stated differently) originate primarily at the base of aquatic ecosystems (e.g., in phytoplankton or heterotrophic unicellular

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organisms) and flow through food webs, bioaccumulating at higher trophic levels (Gladyshev et al., 2009; Hamilton et al., 2020). As a result, aquatic foods typically have high concentrations of omega-3 and serve as the primary source of omega-3 for humans, but concentrations vary among species and between farmed versus wild caught fish. Though critical for supplying omega-3 from direct human consumption, fish – and consequently omega-3 – can be used as feed to aquaculture or terrestrial animal production, either whole or as fishmeal and fish oil (FM&O) (Cao et al., 2015; Hamilton et al., 2020; Kwasek et al., 2020; Tacon and Metian, 2009; Tocher, 2015), often creating indirect and potentially inefficient pathways to human consumption.

While human intake of omega-3 varies by region, consumption falls short of health recommendations in many parts of the world (Micha et al., 2014). Globally, an estimated 1.5 million deaths are attributed to low intake of omega-3 each year, and omega-3 deficiency accounts for almost 10% of all diet-related health burdens (≈ 30 million Disability Adjusted Life Years, DALYs) (Afshin et al., 2019). Most work to date points to a gap between ecological supply and human requirements of omega-3 (hereafter nutrient gap for short) with mounting consequences to human health (Colombo et al., 2019; Hamilton et al., 2020; Salem and Eggersdorfer, 2015; Tocher, 2015). With few exceptions (e.g. Hamilton et al. (2020)), most estimates do not account for omega-3 losses across the supply chain and specifically at the retail and household levels, and thus likely underestimate the full scope of the nutrient gap.

The nutrient gap is poised to further widen in the future as demand increases while supply potentially decreases due to compounded climate change impacts (Cheung et al., 2016; Colombo et al., 2019; Lotze et al., 2019) and overfishing.

As the majority of wild caught stocks are already fished at maximal sustainable or unsustainable levels (FAO, 2020), there are limited opportunities to expand omega-3 supply from wild fisheries. Several novel solutions to alleviate the omega-3 nutrient gap have been proposed. These include increasing supply by utilizing additional marine sources such as krill or copepods, farmed micro and macro algae (Cottrell et al., 2020), and de novo synthesis of omega-3 via oilseed crops (Tocher, 2015). Novel production sources are, however, currently limited by costs, technological innovations (Tocher, 2015), competition for land resources, or public acceptance (in the case of genetically modified crops). Such barriers make sustainable management of aquatic resources of critical importance. Given its importance to human health, a critical question is whether improvements in the existing omega-3 supply chain can potentially supply enough omega-3 to meet present and future requirements. More specifically, to what extent are current omega-3 supply chain efficiently providing omega-3 for human consumption and how much additional omega-3 can be sourced without placing further pressure on wild fish stocks?

To identify opportunities to improve human health without expanding wild aquatic food harvest, we quantitatively assess the potential to increase omega-3 for human consumption ('final supply' in short) from aquatic environments by reducing losses and inefficiencies in the existing omega-3 supply chain. Building on Hamilton et al. (2020) we developed an optimization model for final supply of omega-3 using flux balance analysis (Orth et al., 2010). Flux balance analysis is particularly well suited for modeling nutrient flows through complex networks and examining how their production can be maximized under various predefined constraints because it identifies inefficiencies and amplifies efficient pathways. Our model explores the potential to increase final supply by shifting aquaculture production to species that have the highest omega-3 content per feed input, reducing food loss across the supply chain and recycling byproducts. We then examine the potential steps and policies required to narrow the global omega-3 nutrient gap and discuss the implications of our results to future supply and demand.

2. Material and methods

2.1. Omega-3 supply chain

Building on a recent material flow analysis (Hamilton et al., 2020), we first constructed a model of omega-3 supply chain (EPA and DHA) including all major flows and the circulation of omega-3 from natural and anthropogenic aquatic food webs (e.g. aquaculture) all the way to retail and actual human consumption (including supplements), which we refer to as final supply (Fig. 1). To facilitate comparisons between our work and the 'business-as-usual' baseline presented in Hamilton et al. (2020) we used the same compartments, names, and acronyms as well as the detailed breakdown into aquaculture stocks and flows by major species groups. We also used those flows to derive omega-out-omega-in conversion ratios (ω CR) for all aquaculture compartments of the model by comparing their feed and food omega-3 values (see below for further details).

As our goal was to explore options to maximize supply of omega-3 without further compromising natural systems, we held the amount of omega-3 sourced from the environment (wild catch; left side of Fig. 1) constant in our model. Thus, the system boundaries (see dashed gray line in Fig. 1) include all anthropogenic-controlled omega-3 flows, as well as internal recycling of by-products, systems losses (e.g., food waste), and exogenous losses to non-food uses.

2.2. The optimization model

We used flux balance analysis to optimize final supply under various constraints. Flux balance analysis is a mathematical method for analyzing cellular metabolic topology and design optimal processes within interactive networks (Orth et al., 2010). Originating in the field of biology, flux balance analysis has been used extensively in metabolic network analysis to explain and interpret experimental data, understand the topology of the system (e.g., interactions, redundancies, and competing pathways and dependencies), offer insight into optimizing processes, and devise novel pathways for meeting desired targets under specified constraints. Recently, the method was adapted from genome scale models to the study of industrial and biological processes at the ecosystem level (McCloskey et al., 2013).

Flux balance analysis assumes that systems (i.e. networks) are in a steady state and that material mass is preserved across flows meaning that the sum of inputs into a stock (i.e. node) is equal to the sum of its outputs (Orth et al., 2010). Although natural reservoirs and processes are typically dynamic, we assumed a steady state in our model for several reasons. First, the omega-3 stocks in the ocean are large, and therefore unlikely to change over short time periods (Gregg and Rousseaux, 2019). Since our model describes average flows over the course of a single year (Hamilton et al., 2020) and does not include future forecasting, it is reasonable to assume that omega-3 stocks are constant. Second, aquaculture's omega-3 stocks (nodes) are quite small compared to their flows (edges), and therefore changes in aquaculture stocks are unlikely to affect their omega-3 flows in significant ways.

2.3. Model constraints and specifications

Each flow in our model is constrained by a uniquely defined set of upper and lower mass bounds which collectively define the possible solution space (Edwards et al., 2002). As with any optimization scheme, the model is then set up to optimize a specific predefined objective function and derive a single "best" solution which accounts for all flows and their respective constraints. In the current analysis, we set the objective function to maximize final supply of omega-3 (r_{41}). Consequently, the model selected optimal values for each of the flows ($r_{11} - r_{40}$) such that final supply is maximized. Table 1 lists major flows, their present estimated values (Hamilton et al., 2020) and the permissible values the model can assign to them. Supplementary information

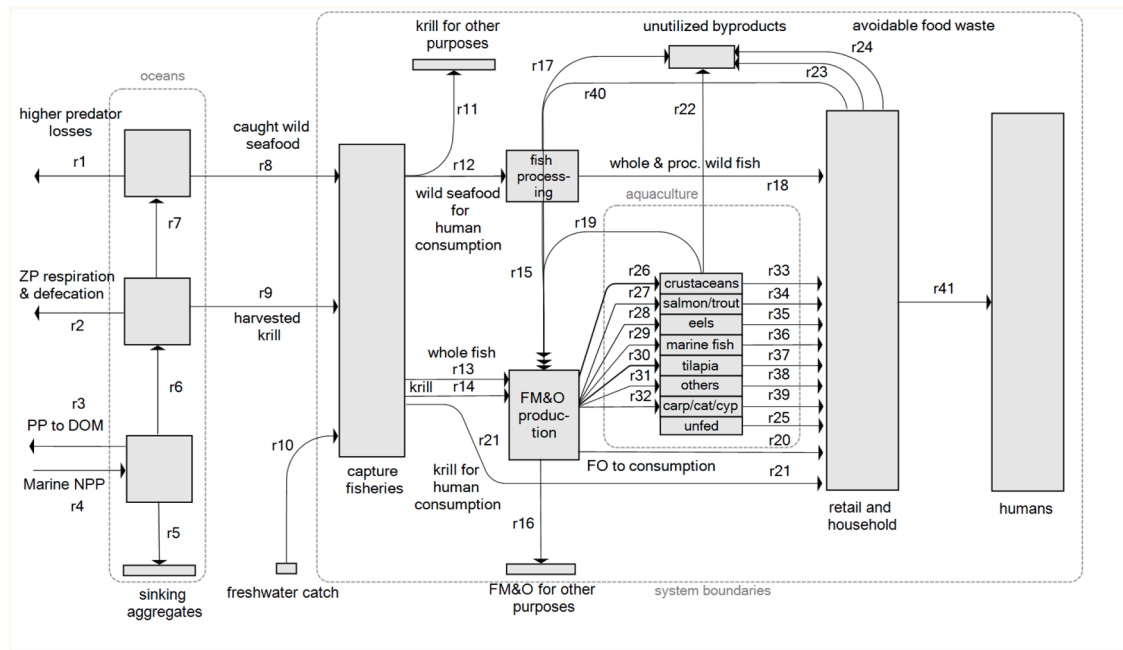


Fig. 1. Global aquatic omega-3 supply chain. Edges and nodes of the model, their names and acronyms are taken from Hamilton et al. (2020). ZP stands for zooplankton, NPP for net primary production, DOM for dissolved organic matter, FM&O for fishmeal and oil, FO for fish oil, and PP for phytoplankton. All Flows are enumerated from r_1 till r_{41} . Major flows include direct consumption of wild fish (r_{18}), omega-3 fed for aquaculture ($r_{26} - r_{32}$), aquaculture supply ($r_{25}, r_{33} - r_{39}$), losses ($r_{17}, r_{22}, r_{23}, r_{24}$), recycling (r_{19}, r_{40}) and final supply (r_{41}). System boundaries of our model are indicated in a gray dashed line. Flows outside our model boundaries ($r_1 - r_{10}$) are constant. In aquaculture, 'others' refers to milkfish, perch, and other freshwater species. 'Carp/cat/cyp' stands for carps, catfish and cyprinids nei. Unfed aquaculture encompasses mollusks, algae and carps that require no inputs of omega-3 and are net producers of omega-3.

Table 1

Information on major flows in our model in kilo tonnes per year (kt y^{-1}). Each flow (row) includes a description, the flow's current estimated value (taken from Hamilton et al. (2020) and detailed in Fig. 3a) and its permissible bounds in the model. Flows $r_1 - r_{10}$ are held constant and serve as exogenous inputs to our model.

Flow #	Description	Value (kt y^{-1})	Permissible values in the model (kt y^{-1})
r_4	Primary production	1400,000	1400,000
r_8	Wild catch	645	645
r_9	Harvested krill	6	6
r_{10}	Freshwater catch	20	20
r_{15}	By-products to FM&O	31	0–31
r_{20}	FO for human consumption	44	0–44
r_{25}	Unfed aquaculture (mollusks, algae and carps)	80	0–80
r_{33}	Crustaceans (aquaculture)	36	0–36
r_{34}	Salmon and trout (aquaculture)	40	0–40
r_{35}	Eel (aquaculture)	0.2	0–0.2
r_{36}	Marine finfish (aquaculture)	5	0–5
r_{37}	Freshwater tilapia (aquaculture)	2.2	0–2.2
r_{38}	Others (milkfish, perch, and other freshwater species) in aquaculture	0.5	0–0.5
r_{39}	Carp/cat/cyp (carps, catfish and cyprinids nei) in freshwater aquaculture	140	0–140

includes a more detailed description of the model and the sensitivity analysis we performed to examine our results.

Mass conservation dictates that omega-3 mass must always be conserved. However, since some specific aquaculture species are net producers of omega-3, they can add to overall supply such that their total output in the model will surpass total inputs in the form of feed. Similarly, other species are net consumers of omega-3 and therefore their net output of omega-3 will be lower than their total feed inputs. Carps, for example, receive omega-3 from feed but also source it from their environment and/or efficiently elongate short fatty acids

molecules (ALA) into omega EPA and DHA long chains. Ultimately, their omega-3 content is higher by a factor of roughly 52 than the omega-3 in the feed they were given (Hamilton et al., 2020). In contrast, fish like salmon require larger amounts of omega-3 feed but produce lower amounts of omega-3 as food and are thus net consumers of omega-3.

To derive omega-3 conversion efficiencies (ωCR) we compared the EPA+DHA content of each species' feed input with its food output. Such an approach assumes an average global aggregate-level value that is a snapshot of current management practices, feeding rations, biophysical parameters, and species-specific capabilities to synthesize or retain omega-3 (Hamilton et al., 2020). Sector wide changes – for example in feeding practices or changes in environmental conditions – can reduce or increase these conversion efficiencies, but we assume these are constants in our model. As such, ωCR act as multipliers in the model: when a certain amount of feed is fed into an aquaculture compartment the resulting output (food) is that feed value multiplied by its group-specific ωCR .

Our model explores inefficiencies and loss by focusing on the supply-side structural changes in production (aquaculture), byproduct utilization (Ciriminna et al., 2019; Soldo et al., 2019), repurposing unavoidable food waste as FM&O (recycling), and reducing consumer avoidable food waste (Fig. 2 and Fig. 3c). As an intermediate step to understand the results of our fully-optimized model, we created an intermediate scenario, where we only enabled changes in aquaculture production portfolio to occur (Fig. 3b). Such an approach enabled comparing the relative contribution of changes in aquaculture production volumes with the other strategies to the overall omega-3 final supply gains.

To ensure that the optimization scheme would search for optimal yet realistic production volumes in both optimization scenarios all aquaculture species flows (carps, catfish and cyprinids nei, tilapia, eels, milkfish, salmon/trout, crustaceans, and marine finfish) had a lower bound of zero and an upper bound defined according to their current production volumes (Table 1). Additionally, in the fully-optimized scenario (Fig. 2 and Fig. 3c) the utilization of byproducts (r_{17} , and r_{22}) and unavoidable and avoidable food waste (r_{23} and r_{24} , respectively) were

increased by 50% of their current estimates. Our 50% increase in byproduct utilization is based on an estimate of a potential for a 50% increase in byproduct utilization as predicted by Jackson and Newton (2016). In terms of food loss, we estimated a 50% decrease in avoidable food waste at the retail/consumer level in line with the Sustainable Development goal target (SDG 12.3) which aims to cut per capita food waste at the consumer and retailer level by half. For unavoidable food waste (r_{23}), we also assumed a 50% increase in utilization, through an assumed central processing system, similar to those in Europe, which could hypothetically reach byproduct utilization efficiencies up towards 90%. To avoid re-utilizing these fish byproducts as food (which the model would ideally lean towards given its objective function of optimizing final supply), we added further constraints to this scenario. For example, gains in reducing unavoidable waste were redirected to FM&O (r_{40}) and the gains of fisheries byproducts (r_{17}) were directed as by-products to FM&O (r_{15}) rather than whole and processed wild fish for consumption (r_{18}). Unavoidable waste to FM&O (r_{40}) is the only flow that is not present in the original omega-3 supply chain as detailed by Hamilton et al. (2020) (Fig. 3a) and was added only to our fully-optimized model (Fig. 3c).

2.4. Limitations of the model

Limitations and caveats of the model are worth noting. First, our model provides a global average outlook, masking regional differences between supply and requirement of omega-3 that result from specific local fish availability, trade, and consumption patterns. Our model optimized omega-3 regardless of its origin, and therefore did not take into account important issues such as fish grade, palatability, market dynamics, or other behavioral or cultural considerations which will be instrumental in order to facilitate policies tailored to local contexts. For example, to utilize omega-3 efficiently, our model directed byproducts to the production of FM&O for aquaculture. FM&O from byproducts are generally of lower quality compared to whole fish and are therefore mainly used for species such as tilapia, catfish, and carp, while premium FM&O from whole fish is used for salmon and shrimp. Such differences in FM&O qualities are not captured in our model. Second, focusing on a single essential nutrient can mask potential tradeoffs in the amount and composition of other nutrients, including amino acids, lipids, and other macro- and micronutrients. This can also mask other salient features of aquaculture, including its environmental impacts, toxins, or microplastics. Finally, our model treats EPA and DHA as a single element although we acknowledge that some species might shift the EPA/DHA ratio, which might have implications to human health (AbuMweis et al., 2021).

2.5. Omega-3 requirements for human health

A minimal level of omega-3 is a critical component of a healthy human diet. To estimate the overall amount of omega-3 required to support healthy diets for the global human population (referred to hereafter as omega-3 requirement in short), we multiplied per capita age-sex health recommendations for omega-3 consumption by the global median variant of annual human population as predicted by the UN for six global regions (Africa, Asia, North America, Oceania, Europe, and South America) between 2020 and 2100 (UN Department of Economic and Social Affairs, 2019).

For adults, we used 250 mg d^{-1} per capita as a minimal requirement for omega-3 intake for cardiovascular benefits (Rimm et al., 2018). For children, we built on FAO recommendations (FAO, 2008) suggesting per capita intakes of 100–150 mg d^{-1} for children aged 2–4 yr, 150–200 mg d^{-1} for ages 4–6 yr, and 200–250 mg d^{-1} for ages 6–10. Because UN population predictions are given in categorical age groups (i.e., 0–4 and 5–9 years), we adjusted FAO recommendations to make them compatible with the UN age cohorts. Specifically, for ages 0–4 we assumed omega-3 nutrient requirement was 100 mg d^{-1} per child to account for

infants' (<2 yr) lower intake; for ages 5–9 we took the average value of the FAO's recommendations for children aged 4–6 and 6–10 years (i.e., 200 mg d^{-1}). Global nutrient requirement for omega-3 was then estimated for each year between 2020 and 2100 (Fig. 4) by multiplying daily per capita requirements by the predicted human population in each geography and age group over a year. See supplementary data for further information.

3. Results

3.1. Final supply of omega-3 under different scenarios

Our optimization model reconfigures the flows of omega-3 in order to maximize final supply for human consumption, circumventing inefficient pathways and avoiding allocating omega-3 to non-food purposes. Our results for the fully-optimized scenario suggest that final supply of omega-3 can increase by as much as 50% over the current baseline production rate of 420 to 627 kt y^{-1} (Fig. 2), without increasing overall aquaculture production quotas, or wild seafood and freshwater catches. The increase in final supply is enabled by structural changes in aquaculture (i.e., how feed is allocated between fed aquaculture species), by utilization of byproducts and reductions in food waste. Non-food uses (e.g. 'FM&O for other purposes') are avoided, which enables diverting these baseline flows (Hamilton et al., 2020) into food purposes, contributing to the increase in final supply.

Omega-3 is used as feed input in aquaculture in various carnivorous or omnivorous species, which result in either less omega-3 in the final output or more depending on its unique omega-out-omega-in conversion ratio (ωCR) (see Section 2), which determines whether the species is a net consumer or producer of omega-3. While these conversion ratios are assumed constant, the model has the option to allocate the existing omega-3 feed to each species as it sees fit without exceeding their production volume.

By diverting omega-3 FM&O only to aquaculture species with high ωCR (e.g., carps, catfish and cyprinids nei), more wild fish can be channeled towards direct consumption (instead of FM&O), increasing overall final supply of omega-3. With a final supply of 627 kt y^{-1} , our model predicts that optimal omega-3 supply will be achieved when $\approx 40\%$ of omega-3 is sourced from aquaculture (including FM&O for direct consumption) and 60% by directly consuming wild caught fish.

Because ωCR per species effectively act as multipliers, when their value is above 1, diverting more omega-3 feed to these high ωCR can improve aquaculture's average ωCR and would boost overall efficiency. For example, carps, catfish, and cyprinids nei have the highest conversion ratio (≈ 52), while salmon has a low ωCR of 0.4. When feed is diverted from salmon to catfish, carps, and other cyprinids, less FM&O is required to reach current omega-3 outputs and consequently more omega-3 can be diverted to direct consumption as wild fish. However, despite the above logic, the model allocated omega-3 also to salmon production, effectively losing omega-3.

To get a clearer understanding of how the model optimizes the flows of omega-3 across the supply chain compared to present baseline quotes and why it assigned omega-3 feed to salmon, we created an intermediate scenario where only the supply-side of production (aquaculture and wild fish mixtures) was allowed to change with no changes in byproduct utilization or food waste mitigation, and compared it to current baseline omega-3 supply chain (Hamilton et al., 2020) and our fully-optimized scenario (Fig. 3). Key values discussed below are shaded in yellow in Fig. 3 for each of the three scenarios.

Excluding unfed aquaculture, in the 'business-as-usual' baseline scenario (Hamilton et al., 2020) (Fig. 3a) 243 kt y^{-1} of omega-3 flows of fishmeal and fish oil feed (FM&O) produce 224 kt y^{-1} of total omega-3 flows from aquaculture. Consequently, aquaculture's net average ωCR is 224/243 or 0.9. Final supply for that scenario, including the contribution of wild-caught fish, is 420 kt y^{-1} (Fig. 3a).

In the intermediate scenario (Fig. 3b), the optimization model first

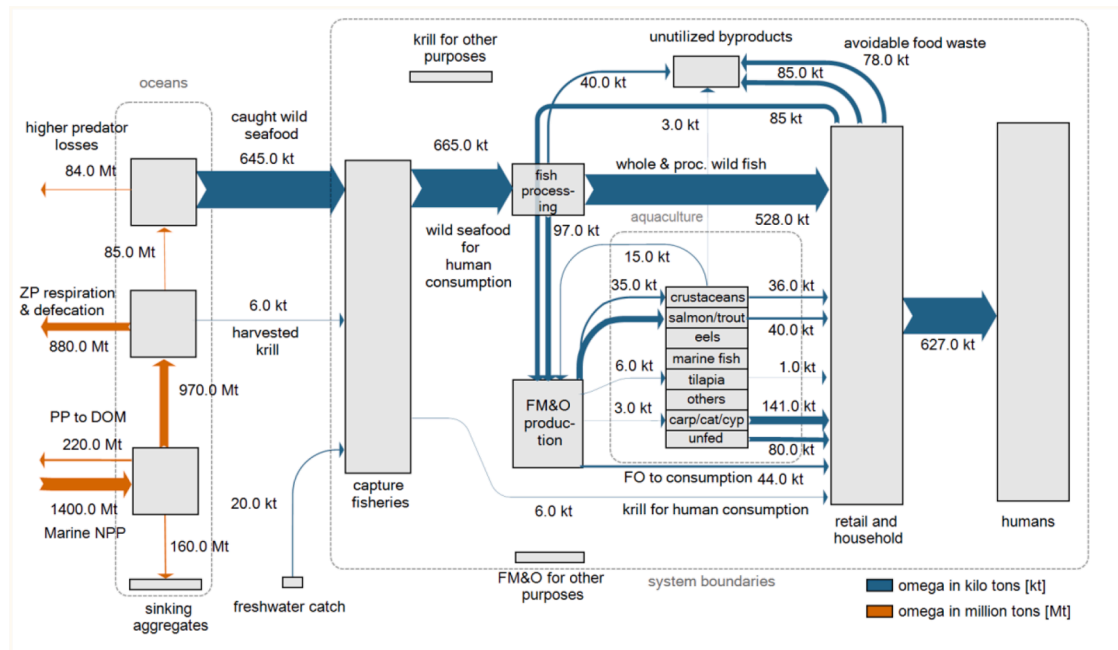


Fig. 2. Globally fully-optimized omega-3 supply chain using flux balance analysis. Compartments of the model, their names and acronyms are identical to Hamilton et al. (2020) to enable easy comparison. ZP stands for zooplankton, NPP for net primary production, DOM for dissolved organic matter, FM&O for fishmeal and oil, FO for fish oil, and PP for phytoplankton. Values are in units of kt (blue) or Mt (orange) omega-3 mass per year. Arrow width is proportional to the mass of omega-3 flows. Optimized final supply (627 kt y^{-1}) is 50% higher than current baseline supply (Hamilton et al., 2020) of 420 kt y^{-1} . This is enabled through changes in aquaculture production portfolio and consequently in the volume of wild caught fish consumed directly, improved byproduct utilization and demand-side recycling and mitigation of food waste. Non-food purposes (e.g. 'FM&O' for other purposes) are not assigned any flows by the optimization but are left as references to the original network (Hamilton et al., 2020). In aquaculture, 'others' refers to milkfish, perch, and other freshwater species. 'Carp/cat/cyp' stands for carps, catfish and cyprinids nei. Unfed aquaculture encompasses mollusks, algae, and carps that require no inputs of omega-3 and are net producers of omega-3. See Table 1 and Supplementary data for further details. The system boundaries of our model are indicated in a dashed gray rectangle.

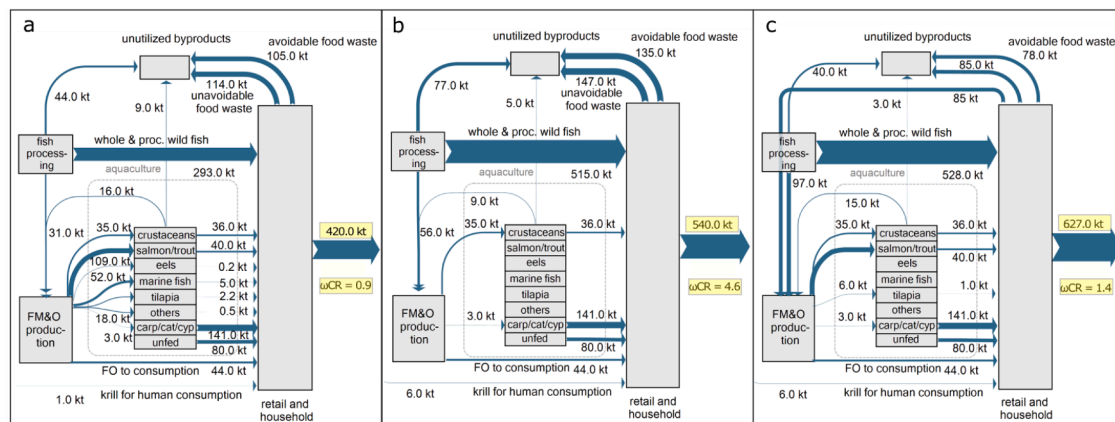


Fig. 3. Present and optimized omega-3 scenarios. Comparison between current omega-3 supply chain as detailed by Hamilton et al. (2020) (panel a), the optimized intermediate scenario (panel b), and the fully-optimized scenario (panel c and Fig. 2) are presented focusing on the system boundaries of the model, a subset of the entire global omega-3 network. Omega-3 values are presented in kt mass per year. Important values including final supply and aquaculture's average ωCR are highlighted with yellow backgrounds for each of the scenario. In aquaculture, 'others' refers to milkfish, perch, and other freshwater species. 'Carp/cat/cyp' stands for carps, catfish, and cyprinids nei. FM&O refers to fishmeal and oil and FO for fish oil. Unfed aquaculture encompasses mollusks, algae, and carps that require no inputs of omega-3 and are net producers of omega-3. See Table 1 and Supplementary data for further details.

diverted as much omega-3 feed as possible to the highest ωCR flow (carps, catfish and cyprinids nei). When this flow reached its defined upper bounds, the model then moved to allocate feed to the second highest ωCR flow (in this case crustaceans, $\omega\text{CR} = 1.02$) until its limit is reached. This allocation continues as long as the ωCR of the fed aquaculture species is higher than the average conversion ratio of wild capture fish (i.e. $\omega\text{CR} = 0.8$) at which point, it becomes more efficient to directly consume the wild caught instead of using it as aquaculture feed. Because the other major seafood groups that were modelled had ωCR

values of <0.4 , the optimization scheme did not assign any production volumes to them. Ultimately, aquaculture used 38 kt y^{-1} of omega-3 of FM&O as feed to eventually yield 177 kt y^{-1} of omega-3 from aquaculture, resulting in an overall average ωCR of $177/38$ or 4.6 (Fig. 3b). Adding wild caught omega-3, total supply resulted at 540 kt y^{-1} , 30% more than baseline final supply as indicated in Fig. 3a.

In our fully-optimized scenario (Fig. 3c which is a subset of Fig. 2), we added to the intermediate scenario above the ability to increase byproducts utilization and reduce food waste (see Section 2 for further

details). Aquaculture's average ω CR is $218/153=1.4$. Final supply of omega-3 increased to 627 kt y^{-1} , 16% more than the intermediate scenario (Fig. 3b) and 50% more than baseline final supply (Fig. 3a). Although aquaculture's average ω CR was reduced to 1.4 – more than three times less than the intermediate scenario (Fig. 3b) – the fully-optimized scenario produced more final supply of omega-3 than the intermediate scenario.

Because byproducts are not used for direct human consumption (due to model specifications) and are rather utilized and repurposed as aquaculture feed in the optimization scenario (Fig. 3c), aquaculture's volume of production increased (218 kt y^{-1} compared to 177 kt y^{-1} in the intermediate scenario, Fig. 3b). Because the constraints we imposed ensured that aquaculture production did not exceed current production volumes per species, as more feed was made available through recycling byproducts the model diverted omega-3 production to species with decreasing ω CR (e.g., salmon and tilapia), which were otherwise not chosen in the intermediate scenario. This explains why salmon was assigned with an omega-3 feed flow despite having a lower ω CR than wild fish (Fig. 2). While average aquaculture ω CR decreased in this scenario, overall production of aquaculture increased and consequently final supply increased relative to the baseline (Fig. 3a) and intermediate scenario (Fig. 3b).

Interestingly, when we changed the percentage of byproduct utilization at retail and household level and food waste repurposing across a large range from its chosen value of 50% (see Section 2), final supply (627 kt y^{-1}) hardly changed, effectively forming a homeostasis. To clarify, diverting byproducts to aquaculture acts as a negative feedback loop, because as more byproducts are repurposed as feed more are diverted to increasingly less efficient species (such as salmon), and final aquaculture output converges to a fixed value, aquaculture production volume at the baseline scenario (224 kt y^{-1}), which is an upper limit in our model.

3.2. Present versus future omega-3 nutrient gap

The increases in final supply of omega-3 suggested by our model could potentially reduce the current (i.e. 2020) omega-3 nutrient gap, nearly closing the gap entirely (Fig. 4). Juxtaposed against the predicted future requirement of a growing human population, even at optimized levels, supply of omega-3 will not be enough to meet future global omega-3 requirement, especially when considering the expected

reductions in fish abundances and omega-3 concentrations due to climate change that are likely to reduce the supply.

Disaggregating global population by regions and population groups reveals that the largest increase in omega-3 nutrient requirement will be driven by large demographic shifts in Africa across an 80-year period (dark blue patch in Fig. 4). During this time, the human population in Africa is expected to triple while the composition of age groups will change substantially (from a 150% increase for ages 0–4 to 16,425% for ages +100 compared to current population). As such, the continent's overall omega-3 requirement is expected to increase by 3.5-fold. In contrast, the highest current requirement for omega-3, Asia's population, is not expected to change much and its omega-3 requirement in year 2100 will only see a modest 4% rise compared with today.

4. Discussion

Our aim was to quantitatively examine to what extent the final supply of omega-3 can be increased from present baseline using the current wild harvest base and without aquaculture expansion. We used an optimization approach to integrate previously-proposed strategies for improving efficiency and reduction of waste (Hamilton et al., 2020) into a system-level understanding of global omega-3 supply chain. Our results suggest that the omega-3 supply chain can be optimized through structural changes in aquaculture, utilization of byproducts, and reduction in losses such that the overall final supply of omega-3 will grow by up to 50%, nearly closing the present nutrient gap.

Alternatively, if final supply of omega-3 is kept constant at current capacity, the resource-use efficiency gains achieved via the model mean that this supply can be obtained with less wild caught seafood (marine seafood, krill, and freshwater catch). Reducing the overall pressure on global fisheries is crucial for reviving fish stocks, avoiding catastrophic collapses, and restoring marine ecosystems' functionality. While our analysis is focused on a single nutrient, our recommendations are aligned with other analyses, which suggest that pressures on aquatic environments could potentially be alleviated if aquaculture farming were to focus on improving the feed efficiency of species and reducing the dependence on FM&O (Klinger and Naylor, 2012; Naylor et al., 2021; Troell et al., 2014). Overall, our results underscore the need for greater efficiency and sustainable intensification of food systems as means to meet human nutrient requirements more environmentally (Clark et al., 2019; Garnett et al., 2013; Gephart et al., 2021; Rockström

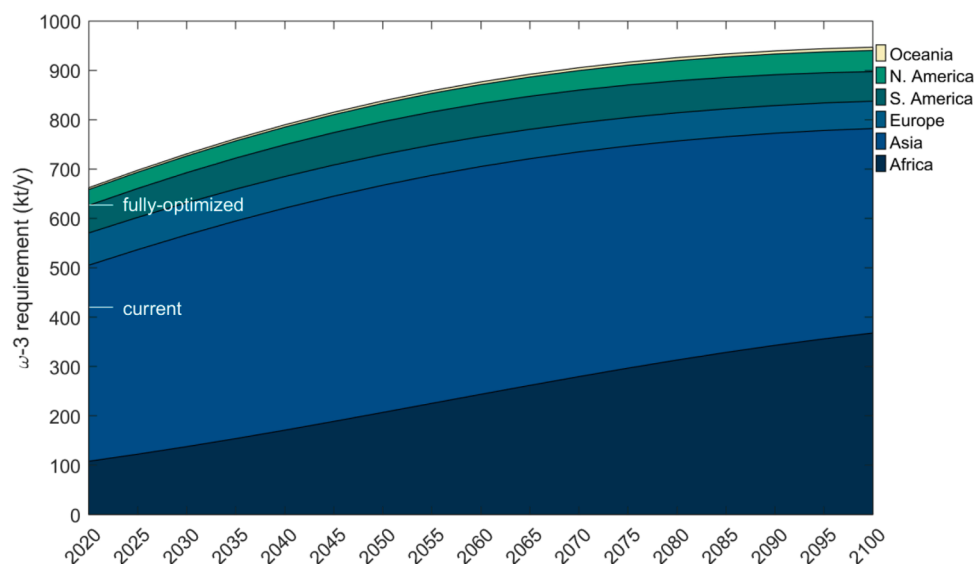


Fig. 4. Global requirement of omega-3 from year 2020 to 2100. Omega-3 requirements are disaggregated by continents based on prediction of population growth and changes in sex-age groups. As a benchmark, fully-optimized final supply of omega-3 based on our model and current final supply (Hamilton et al., 2020) are indicated.

et al., 2017; Tilman et al., 2011; Willett et al., 2019).

Many societies around the globe are currently experiencing inadequate omega-3 intakes that could be addressed through an increased supply of aquatic foods (Golden et al., 2021). Our results point to opportunities for future fisheries development to provide enough omega-3 to meet global nutrient requirement if distributed equitably. We find that feed (FM&O) should be directed to the most efficient farmed species, repurposing more wild catch towards direct consumption, and eventually increasing overall omega-3 final supply. Consequently, wild caught seafood provided the bulk of omega-3 for consumption in our model, whereas at present aquaculture and wild-caught fish contribute equally. Increasing resource use efficiency to produce more omega-3 for final supply (for the same amount of resource input) is in line with calls for sustainable management and efficient use of resources (UN's Sustainable Development Goal, SDG 12.2). Furthermore, our results illustrate that the contribution of recycling byproducts and reducing waste to final supply is on par with changes in aquaculture production portfolio (Shepon et al., 2018). Initiatives and policies that work towards achieving such goals – as indicated in SDGs 12.3 and 12.5 (reduce waste and increase its reuse and recycling and reduce losses across the supply chain) – should be prioritized.

Generally, while feed conversion ratios have been declining due to improved fish strains, feed quality, and improved husbandry, total feed requirement has been increasing rapidly due to the expansion of the aquaculture sector (Tacon, 2019). Variability of feed amounts and composition among different farmed food groups are noticeable, with groups naturally lower on the aquatic food chain (e.g., carps, catfish, tilapia, and freshwater species) more flexible in terms of type of feed use (including FM&O) and naturally carnivorous fish (salmonids, shrimp and marine species) generally more dependent on feed from animal sources. Global FM&O is allocated predominately to aquaculture, but supply has been steady over the last few decades (albeit at an increase in price) (Tacon and Metian, 2015), reflecting a decline in usage per produced fish for all species. In fact, rising FM&O prices (on account of constrained supply) has driven a transition to alternate feed sources rich in essential amino acids and fatty acids, such as soy, cassava, maize, and novel replacements, such as algae and insect meal, are being introduced (Cottrell et al., 2020). Further, an estimated 8 million tonnes of fishmeal could be made available by better utilizing seafood byproducts (Roberts et al., 2015). However, it is important to recognize that fishmeal qualities govern their use for different species. For example, salmon and shrimp require higher quality fishmeal, most of which originate from whole fish reduction, while cyprinids, tilapia, and catfish are less demanding both in terms of quality and quantity.

In our calculations we did not consider other novel sources of omega-3 that can increase supply (Tocher, 2015) or replace FM&O as feed (Cottrell et al., 2020). Even if already supplying the salmon industry with important omega-3, large scale production of micro- and macro-algae is currently still constrained by high costs, technological, and/or consumer barriers (Cottrell et al., 2020; Tocher, 2015), but future innovations will potentially increase their share in global supply. Upscaling the production of existing genetically modified terrestrial crops that produce omega-3 is possible, but in some locations public opinion and regulations related to transgenic products would hinder wide commercialization (Tocher, 2015). Ultimately, such replacements for FM&O can reduce pressures on forage fish in the long run but can introduce other environmental costs instead. Other untapped marine sources can also potentially serve as inputs to aquaculture or be consumed directly instead. Contrary to the majority of fisheries that are at or near their maximal capacity, increasing marine sources such as krill or copepods above current harvest quotas could also potentially increase overall omega-3 human supply (Rust et al., 2011; Tocher, 2015; Tou et al., 2007). However, given the large uncertainties in overall environmental impacts of krill harvest (Hewitt and Linen Low, 2000; Hill et al., 2006; Parker and Tyedmers, 2012) we did not consider increasing its provision in our model. Further, such an increase in wild harvest

would have not fallen within our attempt here to show that more omega-3 can be produced from the same environmental resource base ('sustainable intensification').

Shifting consumption patterns towards specific fish groups (e.g. carps, catfish and cyprinids) and marine wild caught seafood as a means to improve resource use efficiency as we demonstrate here is on par with a growing body of work which emphasizes dietary shifts as an environmental strategy (Poore and Nemecek, 2018; Shepon et al., 2018; Springmann et al., 2016; Tilman and Clark, 2014; Willett et al., 2019). Contrary to marine species that depend on their diet to obtain their omega-3, freshwater fish have the genetic potential and enzymatic biosynthesis capabilities to elongate omega-3 EPA+DHA from ALA and n-6 fatty acids (Rodrigues et al., 2017). Therefore, while carps have medium densities of omega-3 compared to other aquatic species (Golden et al., 2021), their innate traits make them particularly efficient from a resource usage standpoint. Because pelagic fish, freshwater fish, and non-fed species (e.g. filter feeders and bivalves) have relatively lower environmental pressures (Gephart et al., 2021) consuming these species instead of others are likely to yield improved environmental performance in addition to omega-3 related efficiency gains. Yet, such population level dietary shifts present formidable challenges (Shepherd, 2005). In the context of this study, increasing the direct consumption of omega-3-rich small pelagic wild fish will require changing perceptions of both producers and consumers (Tacon and Metian, 2009). From the consumer side, this will necessitate innovations to increase palatability and transport from distant fisheries (Kontominas et al., 2021). Notable examples of changing consumer perception are projects to introduce small nutrient-rich fish into local food systems (e.g., Castine et al., 2017). From the producer side, decision-makers may consider policies which incentivize redirecting omega-3 away from inefficient yet highly profitable fish species, prioritize the production of diverse nutrient-rich aquatic systems, and ensure access and affordability of seafood to the poor (Thilsted et al., 2016). Further, with a net flow of traded seafood to wealthier countries with low malnutrition rates (Smith et al., 2010), and ongoing inequities in wild-capture fisheries and the source and destination of their products (McCauley et al., 2018), distribution considerations are critical. The nutritional value of seafood must therefore be evaluated alongside economic considerations within trade policy.

Africa and Asia are two hotspots plagued by malnutrition and food insecurity (Development Initiatives, 2018). At the same time, many countries in these regions depend on fish supplies to meet their nutritional requirements (Golden et al., 2016). In the context of omega-3, these two continents set the highest requirement globally for this nutrient now and increasingly more in the future. These are also locations where caught fish can provide many of the nutritional shortfalls (Hicks et al., 2019) and where the potential of aquaculture to meet growing demands varies. Many countries within those regions lack aquaculture or export a large portion of production, rendering aquaculture's contribution to domestic nutritional needs as low (Golden et al., 2017). Limited growth of aquaculture in most parts of Africa is due to many factors (Troell et al., 2011) but is tied to stagnating fish availability, although fish constitutes a high proportion of animal-source foods (Beveridge et al., 2013). Future aquaculture development, particularly in Africa, should strive to maximize nutrient supply by redirecting wild caught fish to domestic supply, focusing on efficient aquaculture species, and cutting losses as we outline here.

Climate change and poor fisheries management are poised to further compromise fish-related nutrition security (Golden et al., 2016; Hilborn et al., 2020). This includes the supply of omega-3 that will likely fall due to the synergetic effects of fish stock declines (Hilborn et al., 2020), lower body size (Cheung et al., 2013), less krill (Flores et al., 2012), redistribution (Cheung et al., 2016) of catch and reduced densities (Colombo et al., 2019) as sea temperatures rise. At the same time, a growing population will have a higher overall requirement, resulting in a widening of the omega-3 gap into the future. While optimized omega-3 supply from aquatic environments as presented here is unlikely to bridge

future omega-3 requirements, this future outlook emphasizes the urgency needed in sustainably managing aquatic resources now through implementing the conclusions of our analysis in order to stave off growing omega-3 deficiencies until other sources of omega-3 (e.g. novel sources) are gradually made available on a large scale.

5. Conclusions

Omega-3 is an essential micronutrient with beneficial health impacts. Yet, globally, nutrient requirement outpaces final supply. Finding novel strategies to increase the supply of omega-3, especially towards vulnerable populations and in high demand regions, is paramount. Here we examine inefficiencies in global aquatic omega-3 production and illuminate potential pathways to produce more with the same environmental resources. Restructuring the global fisheries food system by reducing loss across the supply chains and concentrating on efficient species as well as unfed aquaculture can increase the supply of omega-3 by as much as 50%. To achieve this, overarching policies at the production, postharvest, retailer, and household levels would have to work in unison to realize the full potential of providing nutritional security with reduced environmental impacts.

Author contributions

Alon Shepon and Tamar Makov: Conceptualization, formal analysis, visualization and writing the original draft; all authors: writing – editing and reviewing.

Data sharing

The dataset as well as the code (Matlab) used for the calculations (and Fig. 4) are publicly available on [GitHub](#). Sankey diagrams (Fig. 1, 2 and 3) were produced using the eSankey software. These files are available upon contacting the lead author.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.resconrec.2022.106260](https://doi.org/10.1016/j.resconrec.2022.106260).

References

- AbuMweis, S., Abu Omran, D., Al-Shami, I., Jew, S., 2021. The ratio of eicosapentaenoic acid to docosahexaenoic acid as a modulator for the cardio-metabolic effects of omega-3 supplements: a meta-regression of randomized clinical trials. *Complement. Ther. Med.* 57, 102662 <https://doi.org/10.1016/j.CTIM.2021.102662>.
- Afshin, A., Sur, P.J., Fay, K.A., Cornaby, L., Ferrara, G., Salama, J.S., Mullany, E.C., Abate, K.H., Abbafati, C., Abebe, Z., Afarideh, M., Aggarwal, A., Agrawal, S., Akinyemiju, T., Alahdab, F., Bacha, U., Bachman, V.F., Badali, H., Badawi, A., Bensenor, I.M., Bernabe, E., Biadgilign, S.K.K., Biryukov, S.H., Cahill, L.E., Carrero, J.J., Cercy, K.M., Dandona, L., Dandona, R., Dang, A.K., Degefa, M.G., El Sayed Zaki, M., Esteghamati, A., Esteghamati, S., Fanzo, J., Farinha, C.S.E.S., Farvid, M.S., Farzadfar, F., Feigin, V.L., Fernandes, J.C., Flor, L.S., Foigt, N.A., Forouzanfar, M.H., Ganji, M., Geleijnse, J.M., Gillum, R.F., Goulart, A.C., Grosso, G., Guessous, I., Hamidi, S., Hankey, G.J., Harikrishnan, S., Hassen, H.Y., Hay, S.I., Hoang, C.L., Horino, M., Islami, F., Jackson, M.D., James, S.L., Johansson, L., Jonas, J.B., Kasaeian, A., Khader, Y.S., Khalil, I.A., Khang, Y.H., Kimokoti, R.W., Kokubo, Y., Kumar, G.A., Lallukka, T., Lopez, A.D., Lorkowski, S., Lotufo, P.A., Lozano, R., Malekzadeh, R., März, W., Meier, T., Melaku, Y.A., Mendoza, W., Mensink, G.B.M., Micha, R., Miller, T.R., Mirarefin, M., Mohan, V., Mokdad, A.H., Mozaffarian, D., Nagel, G., Naghavi, M., Nguyen, C.T., Nixon, M.R., Ong, K.L., Pereira, D.M., Poustchi, H., Qorbani, M., Rai, R.K., Razo-García, C., Rehm, C.D., Rivera, J.A., Rodríguez-Ramírez, S., Roshandel, G., Roth, G.A., Sanabria, J., Sánchez-Pimienta, T.G., Sartorius, B., Schmidhuber, J., Schutte, A.E., Sepanlou, S.G., Shin, M. J., Sorensen, R.J.D., Springmann, M., Szponar, L., Thorne-Lyman, A.L., Thrift, A.G., Touvier, M., Tran, B.X., Tyrovolas, S., Ukwaja, K.N., Ullah, I., Uthman, O.A., Vaezghasemi, M., Vasankari, T.J., Vollset, S.E., Vos, T., Vu, G.T., Vu, L.G., Weiderpass, E., Werdecker, A., Wijeratne, T., Willett, W.C., Wu, J.H., Xu, G., Yonemoto, N., Yu, C., Murray, C.J.L., 2019. Health effects of dietary risks in 195 countries, 1990–2017: a systematic analysis for the Global Burden of Disease Study 2017. *Lancet* 393, 1958–1972. [https://doi.org/10.1016/S0140-6736\(19\)30041-8](https://doi.org/10.1016/S0140-6736(19)30041-8).
- Anderson, B.M., Ma, D.W.L., 2009. Are all n-3 polyunsaturated fatty acids created equal? *Lipids Health Dis.* <https://doi.org/10.1186/1476-511X-8-33>.
- Beveridge, M.C.M., Thilsted, S.H., Phillips, M.J., Metian, M., Troell, M., 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. <https://doi.org/10.1111/jfb.12187>.
- Cao, L., Naylor, R., Henriksson, P., Leadbitter, D., Metian, M., Troell, M., Zhang, W., 2015. China's aquaculture and the world's wild fisheries. *Science* (80-). 347, 133. LP –135.
- Castine, S.A., Bogard, J.R., Barman, B.K., Karim, M., Mokarrom Hossain, M., Kunda, M., Mahfuzul Haque, A.B.M., Phillips, M.J., Thilsted, S.H., 2017. Homestead pond polyculture can improve access to nutritious small fish. *Food Secur.* 9, 785–801. <https://doi.org/10.1007/s12571-017-0699-6>.
- Cheung, W.W.L., Jones, M.C., Reygondeau, G., Stock, C.A., Lam, V.W.Y., Frölicher, T.L., 2016. Structural uncertainty in projecting global fisheries catches under climate change. *Ecol. Modell.* 325, 57–66. <https://doi.org/10.1016/j.ecolmodel.2015.12.018>.
- Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W.Y., Palomares, M. L.D., Watson, R., Pauly, D., 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nat. Clim. Chang.* 3, 254–258. <https://doi.org/10.1038/nclimate1691>.
- Ciriminna, R., Scurria, A., Avellone, G., Pagliaro, M., 2019. A Circular Economy Approach to Fish Oil Extraction. *ChemistrySelect* 4, 5106–5109. <https://doi.org/10.1002/SLCT.201900851>.
- Clark, M.A., Springmann, M., Hill, J., Tilman, D., 2019. Multiple health and environmental impacts of foods. *Proc. Natl. Acad. Sci. U. S. A.* <https://doi.org/10.1073/pnas.1906908116>.
- Colombo, S.M., Rodgers, T.F.M., Diamond, M.L., Bazinet, R.P., Arts, M.T., 2019. Projected declines in global DHA availability for human consumption as a result of global warming. *Ambio* 49, 865–880. <https://doi.org/10.1007/s13280-019-01234-6>.
- Cottrell, R.S., Blanchard, J.L., Halpern, B.S., Metian, M., Froehlich, H.E., 2020. Global adoption of novel aquaculture feeds could substantially reduce forage fish demand by 2030. *Nat. Food* 1, 301–308. <https://doi.org/10.1038/s43016-020-0078-x>.
- Development Initiatives, 2018. 2018 Global Nutrition Report: Shining a light to Spur Action On Nutrition. Bristol, UK.
- Edwards, J.S., Covert, M., Palsson, B., 2002. Metabolic modelling of microbes: the flux-balance approach. *Environ. Microbiol.* 4, 133–140. <https://doi.org/10.1046/j.1462-2920.2002.00282.x>.
- FAO, 2020. The State of World Fisheries and Aquaculture 2020. Sustainability in Action. Rome.
- FAO, 2008. Fats and Fatty Acids in Human nutrition: Report of an Expert consultation, Report no. 91. Geneva.
- Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B.A., Milinevsky, G., Nicol, S., Reiss, C., Tarling, G.A., Werner, R., Bravo Rebollo, E., Cirelli, V., Cuzin-Roudy, J., Fielding, S., Groeneveld, J.J., Haraldsson, M., Lombana, A., Marschoff, E., Meyer, B., Pakhomov, E.A., Rombolá, E., Schmidt, K., Siegel, V., Teschke, M., Tonkes, H., Toullec, J.Y., Trathan, P.N., Tremblay, N., Van De Putte, A.P., Van Franeker, J.A., Werner, T., 2012. Impact of climate change on Antarctic krill. *Mar. Ecol. Prog. Ser.* 458, 1–19. <https://doi.org/10.3354/MEPS09831>.
- Garnett, T., Appleby, M.C., Balmford, A., Bateman, I.J., Benton, T.G., Bloomer, P., Burlingame, B., Dawkins, M., Dolan, L., Fraser, D., Herrero, M., Hoffmann, I., Smith, P., Thornton, P.K., Toulmin, C., Vermeulen, S.J., Godfray, H.C.J., 2013. Sustainable intensification in agriculture: premises and policies. *Science* (80-) 341, 33–34. <https://doi.org/10.1126/science.1234485>.
- Gephart, J.A., Henriksson, P.J.G., Parker, R.W.R., Shepon, A., Gorospe, K.D., Bergman, K., Eshel, G., Golden, C.D., Halpern, B.S., Hornborg, S., Jonell, M., Metian, M., Miffill, K., Newton, R., Tyedmers, P., Zhang, W., Ziegler, F., Troell, M., 2021. Environmental performance of blue foods. *Nature* 597, 360–365.
- Gerster, H., 1998. Can adults adequately convert α -linolenic acid (18:3n-3) to eicosapentaenoic acid (20:5n-3) and docosahexaenoic acid (22:6n-3)? *Int. J. Vitam. Nutr. Res.* 68, 159–173.
- Gladyshev, M.I., Arts, M.T., Sushchik, N.N., 2009. Preliminary estimates of the export of omega-3 highly unsaturated fatty acids (EPA+DHA) from aquatic to terrestrial

- ecosystems. *Lipids in Aquatic Ecosystems*. Springer, New York, pp. 179–210. <https://doi.org/10.1007/978-0-387-89366-2.8>.
- Golden, C.D., Allison, E.H., Cheung, W.W.L., Dey, M.M., Halpern, B.S., McCauley, D.J., Smith, M., Vaitla, B., Zeller, D., Myers, S.S., 2016. Nutrition: fall in fish catch threatens human health. *Nature* 534, 317–320. <https://doi.org/10.1038/534317a>.
- Golden, C.D., Koehn, J.Z., Shepon, A., Passarelli, S., Free, C.M., Viana, D., Matthey, H., Eurich, J.G., Gephardt, J.A., Fluet-Chouinard, E., Nyboer, E.A., Lynch, A.J., Kjelleve, M., Bromage, S., Charlebois, P., Barange, M., Vannuccini, S., Cao, L., Kleinsner, K.M., Rimm, E.B., Danaei, G., DeSisto, C., Kelahan, H., Fiorella, K.J., Little, D.C., Allison, E.H., Fanzo, J., Thilsted, S.H., 2021. Aquatic foods to nourish nations. *Nature*.
- Golden, C.D., Seto, K.L., Dey, M.M., Chen, O.L., Gephardt, J.A., Myers, S.S., Smith, M., Vaitla, B., Allison, E.H., 2017. Does aquaculture support the needs of nutritionally vulnerable nations? *Front. Mar. Sci.* 4, 1–7. <https://doi.org/10.3389/fmars.2017.00159>.
- Gregg, W.W., Rousseaux, C.S., 2019. Global ocean primary production trends in the modern ocean color satellite record (1998–2015). *Environ. Res. Lett.* 14, 1–9. <https://doi.org/10.1088/1748-9326/ab4667>.
- Hamilton, H.A., Newton, R., Auchterlonie, N.A., Muller, D.B., 2020. Systems approach to quantify the global omega-3 fatty acid cycle. *Nat. Food* 1, 59–62.
- Hewitt, R.P., Linen Low, E.H., 2000. The Fishery on Antarctic Krill: defining an Ecosystem Approach to Management. *Rev. Fish. Sci.* 8, 235–298. <https://doi.org/10.1080/10641260091129224>.
- 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., MacNeil, M.A., 2019. Harnessing global fisheries to tackle micronutrient deficiencies. *Nature* 574, 95–98. <https://doi.org/10.1038/s41586-019-1592-6>.
- Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., Kurota, H., Little, L.R., Mace, P., McClanahan, T., Melnychuk, M.C., Minto, C., Osio, G.C., Parma, A.M., Pons, M., Segurado, S., Szuwalski, C.S., Wilson, J.R., Ye, Y., 2020. Effective fisheries management instrumental in improving fish stock status. *Proc. Natl. Acad. Sci.* 117, 2218–2224. <https://doi.org/10.1073/PNAS.1909726116>.
- Hill, S.L., Murphy, E.J., Reid, K., Trathan, P.N., Constable, A.J., 2006. Modelling Southern Ocean ecosystems: krill, the food-web, and the impacts of harvesting. *Biol. Rev.* 81, 581–608. <https://doi.org/10.1017/S1464793106007123>.
- Jackson, A., Newton, R., 2016. Project to model the use of fisheries by-products in the production of marine ingredients with special reference to omega-3 fatty acids EPA and DHA. doi:10.13140/RG.2.2.21237.19687.
- Jayedi, A., Shab-Bidar, S., 2020. Fish consumption and the risk of chronic disease: an umbrella review of meta-analyses of prospective cohort studies. *Adv. Nutr.* 11, 1123–1133. <https://doi.org/10.1093/advances/nmaa029>.
- Jiao, J., Li, Q., Chu, J., Zeng, W., Yang, M., Zhu, S., 2014. Effect of n-3 PUFA supplementation on cognitive function throughout the life span from infancy to old age: a systematic review and meta-analysis of randomized controlled trials. *Am. J. Clin. Nutr.* 100, 1422–1436. <https://doi.org/10.3945/ajcn.114.095315>.
- Kirby, Derbyshire, E., 2018. Omega-3/6 fatty acids and learning in children and young people: a review of randomised controlled trials published in the last 5 years. *J. Nutr. Food Sci.* 8, 1–10. <https://doi.org/10.4172/2155-9600.1000670>.
- Klinger, D., Naylor, R., 2012. Searching for Solutions in Aquaculture: charting a Sustainable Course. *Annu. Rev. Environ. Resour.* 37, 247–276. <https://doi.org/10.1146/annurev-environ-021111-161531>.
- Kontominas, M.G., Badeka, A.V., Kosma, I.S., Nathanailides, C.I., 2021. Innovative seafood preservation technologies: recent developments. *Anim. an open access. J. from MDPI* 11, 1–40. <https://doi.org/10.3390/ANI11010092>.
- Kwasek, K., Thorne-Lyman, A.L., Phillips, M., 2020. Can human nutrition be improved through better fish feeding practices? a review paper. *Crit. Rev. Food Sci. Nutr.* <https://doi.org/10.1080/10408398.2019.1708698>.
- Lotze, H.K., Tittensor, D.P., Bryndum-Buchholz, A., Eddy, T.D., Cheung, W.W.L., Galbraith, E.D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J.L., Bopp, L., Büchner, M., Bulman, C.M., Carozza, D.A., Christensen, V., Coll, M., Dunne, J.P., Fulton, E.A., Jennings, S., Jones, M.C., Mackinson, S., Maury, O., Niiranen, S., Oliveros-Ramos, R., Roy, T., Fernandes, J.A., Schewe, J., Shin, Y.J., Silva, T.A.M., Steenbeek, J., Stock, C.A., Verley, P., Volkholz, J., Walker, N.D., Worm, B., 2019. Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proc. Natl. Acad. Sci. U. S. A.* 116, 12907–12912. <https://doi.org/10.1073/pnas.1900194116>.
- McCauley, D.J., Jablonicky, C., Allison, E.H., Golden, C.D., Joyce, F.H., Mayorga, J., Kroodsm, D., 2018. Wealthy countries dominate industrial fishing. *Sci. Adv.* 4. https://doi.org/10.1126/SCIADV.AAU2161/SUPPL_FILE/AAU2161_SM.PDF.
- McCloskey, D., Pálsson, B.Ø., Feist, A.M., 2013. Basic and applied uses of genome-scale metabolic network reconstructions of *Escherichia coli*. *Mol. Syst. Biol.* 9, 661. <https://doi.org/10.1038/msb.2013.18>.
- Micha, R., Khatibzadeh, S., Shi, P., Fahimi, S., Lim, S., Andrews, K.G., Engell, R.E., Powles, J., Ezzati, M., Mozaffarian, D., 2014. Global, regional, and national consumption levels of dietary fats and oils in 1990 and 2010: a systematic analysis including 266 country-specific nutrition surveys. *BMJ* 348. <https://doi.org/10.1136/bmj.g2272>.
- 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., Troell, M., 2021. A 20-year retrospective review of global aquaculture. *Nature* 551–563. <https://doi.org/10.1038/s41586-021-03508-0>.
- Orth, J.D., Thiele, I., Pálsson, B.Ø., 2010. What is flux balance analysis? *Nat. Biotechnol.* 28, 245–248. <https://doi.org/10.1038/nbt.1614>.
- Parker, R.W.R., Tyedmers, P.H., 2012. Life Cycle Environmental Impacts of Three Products Derived from Wild-Caught Antarctic Krill (*Euphausia superba*). *Environ. Sci. Technol.* 46, 4958–4965. <https://doi.org/10.1021/ES2040703>.
- Poore, J., Nemecek, T., 2018. Reducing food’s environmental impacts through producers and consumers. *Science* (80-) 360, 987–992. <https://doi.org/10.1126/science.aaa0216>.
- Rimm, E.B., Appel, L.J., Chiuve, S.E., Djoussé, L., Engler, M.B., Kris-Etherton, P.M., Mozaffarian, D., Siscovick, D.S., Lichtenstein, A.H., 2018. Seafood long-chain n-3 polyunsaturated fatty acids and cardiovascular disease: a science advisory from the American heart association. *Circulation* 138, e35–e47. <https://doi.org/10.1161/CIR.0000000000000574>.
- Roberts, C.A., Newton, R.W., Bostock, J., Prescott, S., Honey, D.J., Telfer, T.C., Walmsley, S.F., Little, D.C., Hull, S.C., 2015. SARF106: a Risk Benefit Analysis of Mariculture as a means to reduce the Impacts of Terrestrial Production of Food and Energy.
- Rockström, J., Williams, J., Daily, G., Noble, A., Matthews, N., Gordon, L., Wetterstrand, H., DeClerck, F., Shah, M., Steduto, P., de Fraiture, C., Hatibu, N., Unver, O., Bird, J., Sibanda, L., Smith, J., 2017. Sustainable intensification of agriculture for human prosperity and global sustainability. *Ambio* 46, 4–17. <https://doi.org/10.1007/s13280-016-0793-6>.
- Rodrigues, B.L., Canto, A.C.V.D.C.S., Da Costa, M.P., Da Silva, F.A., Mársico, E.T., Conte, C.A., 2017. Fatty acid profiles of five farmed Brazilian freshwater fish species from different families. *PLoS ONE* 12, e0178898. <https://doi.org/10.1371/journal.pone.0178898>.
- Rust, M.B., Barrows, F.T., Hardy, R.W., Lazur, A., Naughten, K., Silverstein, J., 2011. The future of aquafeeds: NOAA Technical Memorandum NMFS F/SPO-124.
- Salem, N., Eggersdorfer, M., 2015. Is the world supply of omega-3 fatty acids adequate for optimal human nutrition? *Curr. Opin. Clin. Nutr. Metab. Care* 18, 147–154. <https://doi.org/10.1097/MCO.0000000000000145>.
- Shepherd, R., 2005. Influences on food choice and dietary behavior. *Forum Nutr.* 57, 36–43. <https://doi.org/10.1159/000083752>.
- Shepon, A., Eshel, G., Noor, E., Milo, R., 2018. The opportunity cost of animal based diets exceeds all food losses. *Proc. Natl. Acad. Sci. U. S. A.* 115, 3804–3809.
- Smith, M.D., Roheim, C.A., Crowder, L.B., Halpern, B.S., Turnipseed, M., Anderson, J.L., Asche, F., Bourillón, L., Guttormsen, A.G., Khan, A., Liguori, L.A., McNevin, A., O’Connor, M.I., Squires, D., Tyedmers, P., Brownstein, C., Carden, K., Klinger, D.H., Sagarin, R., Selkoe, K.A., 2010. Sustainability and global seafood. *Science* (80-) 327. <https://doi.org/10.1126/science.1185345>.
- Soldo, B., Šimat, V., Vlahović, J., Skroza, D., Ljubenkov, I., Generalić Mekinić, I., 2019. High quality oil extracted from sardine by-products as an alternative to whole sardines: production and refining. *Eur. J. Lipid Sci. Technol.* 121, 1800513. <https://doi.org/10.1002/EJLT.201800513>.
- Springmann, M., Godfray, H.C.J., Rayner, M., Scarborough, P., 2016. Analysis and valuation of the health and climate change cobenefits of dietary change. *Proc. Natl. Acad. Sci.* 113, 4146–4151. <https://doi.org/10.1073/pnas.1523119113>.
- Tacon, A.G.J., 2019. Trends in Global Aquaculture and Aquafeed Production: 2000–2017. *Rev. Fish. Sci. Aquac.* 28, 43–56. <https://doi.org/10.1080/23308249.2019.1649634>.
- Tacon, A.G.J., Metian, M., 2015. Feed matters: satisfying the feed demand of aquaculture. *Rev. Fish. Sci. Aquac.* 23, 1–10. <https://doi.org/10.1080/23308249.2014.987209>.
- Tacon, A.G.J., Metian, M., 2009. Fishing for Feed or Fishing for Food: increasing Global Competition for Small Pelagic Forage Fish. *AMBIO A J. Hum. Environ.* 38, 294–302. <https://doi.org/10.1579/08-A-574.1>.
- Thilsted, S.H., Thorne-Lyman, A., Webb, P., Bogard, J.R., Subasinghe, R., Phillips, M.J., Allison, E.H., 2016. Sustaining healthy diets: the role of capture fisheries and aquaculture for improving nutrition in the post-2015 era. *Food Policy* 61, 126–131. <https://doi.org/10.1016/j.foodpol.2016.02.005>.
- Tilman, D., Balzer, C., Hill, J., Belfort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. *Proc. Natl. Acad. Sci. U. S. A.* 108, 20260–20264. <https://doi.org/10.1073/pnas.1116437108>.
- Tilman, D., Clark, M., 2014. Global diets link environmental sustainability and human health. *Nature* 515, 518–522. <https://doi.org/10.1038/nature13959>.
- Tocher, D.R., 2015. Omega-3 long-chain polyunsaturated fatty acids and aquaculture in perspective. *Aquaculture* 449, 94–107. <https://doi.org/10.1016/j.aquaculture.2015.01.010>.
- Tocher, D.R., Betancor, M.B., Sprague, M., Olsen, R.E., Napier, J.A., 2019. Omega-3 Long-Chain Polyunsaturated Fatty Acids, EPA and DHA: bridging the Gap between Supply and Demand. *Nutrients* 11, 89. <https://doi.org/10.3390/nu11010089>.
- Tou, J.C., Jaczynski, J., Chen, Y.C., 2007. Krill for human consumption: nutritional value and potential health benefits. *Nutr. Rev.* 65, 63–77. <https://doi.org/10.1111/j.1753-4887.2007.tb00283.x>.
- Troell, M., Hecht, T., Beveridge, M., Stead, S., Bryceson, I., Kautsky, N., Mmochi, A., Ollevier, F., 2011. Mariculture in the WIO region “Challenges and Prospects”. W, WIOMSA Book Series No. 11. v.
- 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., Gren, Å., Kautsky, N., Levin, S.A., Nyborg, K., Österblom, H., Polasky, S., Scheffer, M., Walker, B.H., Xepapadeas, T., de Zeeuw, A., 2014. Does aquaculture add resilience to the global food system? *Proc. Natl. Acad. Sci.* 111, 13257–13263. <https://doi.org/10.1073/pnas.1404067111>.
- Wang, D.D., Li, Y., Chiuve, S.E., Stampfer, M.J., Manson, J.A.E., Rimm, E.B., Willett, W. C., Hu, F.B., 2016. Association of specific dietary fats with total and cause-specific

- mortality. *JAMA Intern. Med.* 176, 1134–1145. <https://doi.org/10.1001/jamainternmed.2016.2417>.
- Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., Garnett, T., Tilman, D., DeClerck, F., Wood, A., Jonell, M., Clark, M., Gordon, L.J., Fanzo, J., Hawkes, C., Zurayk, R., Rivera, J.A., De Vries, W., Majele Sibanda, L., Afshin, A., Chaudhary, A., Herrero, M., Agustina, R., Branca, F., Lartey, A., Fan, S., Crona, B., Fox, E., Bignet, V., Troell, M., Lindahl, T., Singh, S., Cornell, S.E., Srinath Reddy, K., Narain, S., Nishtar, S., Murray, C.J.L., 2019. Food in the Anthropocene: the EAT–Lancet Commission on healthy diets from sustainable food systems. *Lancet* 393, 447–492. [https://doi.org/10.1016/S0140-6736\(18\)31788-4](https://doi.org/10.1016/S0140-6736(18)31788-4).
- UN Department of Economic and Social Affairs, Population Division, 2019. World Population Prospects 2019.