



Global adoption of novel aquaculture feeds could substantially reduce forage fish demand by 2030

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With the global supply of forage fish at a plateau, fed aquaculture must continue to reduce dependence on fishmeal and oil in feeds to ensure sustainable sector growth. The use of novel aquaculture feed ingredients is growing, but their contributions to scalable and sustainable aquafeed solutions are unclear. Here, we show that global adoption of novel aquafeeds could substantially reduce aquaculture's forage fish demand by 2030, maintaining feed efficiencies and omega-3 fatty acid profiles. We combine production data, scenario modelling and a decade of experimental data on forage fish replacement using microalgae, macroalgae, bacteria, yeast and insects to illustrate how reducing future fish oil demand, particularly in high-value species such as salmonids, will be key for the sustainability of fed aquaculture. However, considerable uncertainties remain surrounding novel feed efficacy across different life-cycle stages and taxa, and various social, environmental, economic and regulatory challenges will dictate their widespread use. Yet, we demonstrate how even limited adoption of novel feeds could aid sustainable aquaculture growth, which will become increasingly important for food security.

Aquaculture is one of the fastest growing sources of animal protein globally, with approximately half of total production requiring external feed inputs¹. Aquafeeds typically include fishmeal and oil extracted from small pelagic forage fish, such as herrings, sardines and anchovies, and to a lesser extent from fish trimmings and discards¹. Fishmeal and oil were originally used as palatable and inexpensive feed ingredients efficient at supplying the protein and fatty acid requirements of farmed aquatic species². However, with global forage fish catches stagnant since the 1980s, the price of fishmeal and oil has increased alongside the demand for aquaculture, pig and poultry feeds^{3,4}. Furthermore, the use of forage fish for feed has been criticized for its impact on marine ecosystems^{5,6} and for diverting these nutritious, small fish away from human consumption⁷. To secure sustainable growth in the fed aquaculture industry, producers have found (and must continue to find) feeds that reduce or exclude forage fish ingredients without compromising the economic value, or fish consumption benefits for human health, that aquaculture confers.

Numerous raw materials have been tested and adopted to reduce fishmeal and oil inclusion in aquafeeds. Soy, corn, cassava, wheat and canola have been used as protein and oil sources in aquafeed as the price gap with forage fish widens^{8–10}. However, high proportions of fibre and anti-nutritional factors¹¹ in these crops can impair species growth performance and health, and increase feed and nutrient waste^{11–13}. Livestock by-products, mesopelagic fish species (for example, myctophids) and discards and trimmings from fishery and aquaculture sectors can provide suitable protein and/or lipids for aquafeeds, but may present sustainability issues or policy restrictions^{5,14}. Products from mixed mesopelagic fish hauls can contain excessive heavy metal concentrations^{15,16}. Fisheries trimmings and by-products are expected to supply a growing proportion of fishmeal and oil over the next decade¹, but will probably be insufficient

to meet projected demands by 2050³ and may also affect the nutritional quality of farmed fish¹. In response to these challenges, novel aquafeed materials, such as macroalgae, single-cell proteins (microalgae, bacteria or yeasts), insects or genetically modified crops have been developed^{17,18}.

It is unclear how new ingredients can scale on a global level or support sustainable feeding practices. Studies on fishmeal or oil replacement using novel aquafeed ingredients have yielded mixed effects on species growth and nutritional content. To address this uncertainty, we synthesize published information on farmed species feed efficiencies, dietary composition and feeding practices with national aquaculture production data. Using these data and published aquaculture growth scenarios, we calculate the sector's global forage fish demand by 2030. We then identify, synthesize and model 10 years of experimental fishmeal and oil replacement data focused on the integration of micro- and macroalgae, bacteria and yeasts, or insect ingredients. Changes to feed conversion ratios (feed intake/weight gain) and nutritional content (via the omega-3 index; see Methods) are assessed to identify thresholds of forage fish replacement with equivalent performance to forage fish-based diets. Finally, we evaluate how novel feeds could reduce forage fish demand compared with soy (a major feed crop) and explore barriers to their wider adoption.

Results

Projected future forage fish demands. Future demands for forage fish will depend on numerous socioeconomic and environmental factors influencing fed aquaculture growth. We build on recent work examining limits to forage fish supply to 2050³ by focusing on three key shorter-term scenarios to 2030 to explore these uncertainties. We use United Nations aquaculture growth projections¹ as our business-as-usual scenario (2030 BAU), and two alternative futures

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Table 1 | Aquaculture growth scenarios used for future forage fish demand calculations

2030 production scenario	Description	Global change in production relative to 2015 (%)
BAU	Based on projected production increases by 2030 from the FAO ¹ . Production is expected to increase by 28% in more economically developed countries, 46% in least developed countries and 36% everywhere else.	+37
Rap.Gr	Reflects the faster aquaculture growth scenario from the World Bank ¹⁹ . Production is predicted to grow 50% faster than BAU in all countries.	+56
Cons.Shft	Growth rates mirror the accelerated shifts in consumer preference in the China scenario from the World Bank ¹⁹ . Production of salmonids, shrimps, crustaceans and tunas triple the BAU tonnage, while all other groups are held at BAU levels.	+98

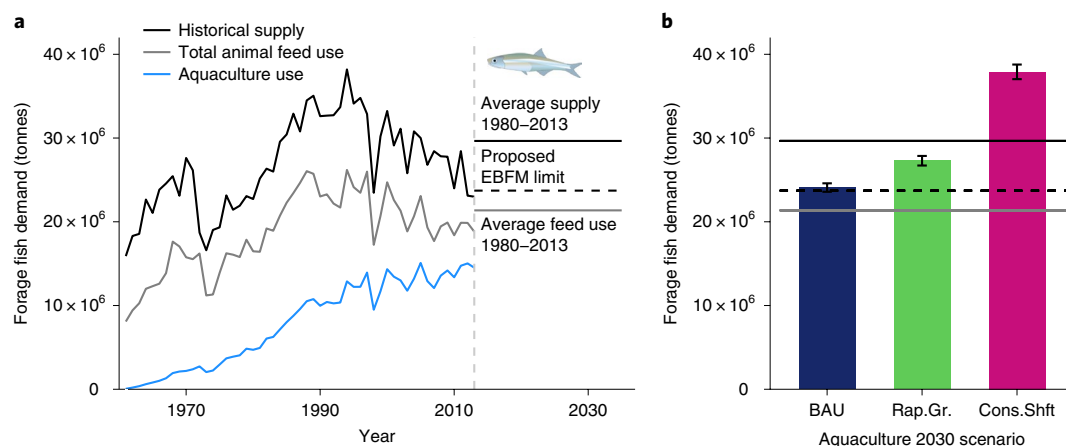


Fig. 1 | Historical supply, feed use and projected aquaculture demand for forage fish across 2030 growth scenarios. a, Historical supply of forage fish (taken as landings of the top 20 forage fish species by biomass from ref. ⁵⁵, making up >90% of reported global forage fish landings³) and aquaculture use through time (estimated by interpolation and extrapolation of the proportion of forage fish feeds used by aquaculture in 1960, 1980 and 2010 (ref. ⁴) and applied to FAOSTAT feed use data⁵⁶). **b,** Mean simulated forage fish demand from aquaculture in 2030 across different aquaculture growth scenarios using diets with current forage fish inclusion rates. Error bars represent s.d. ($n=500$ simulations). Anchoveta icon in **a** courtesy of T. Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

based on the World Bank's IMPACT model projections¹⁹. The first is a scenario of more rapid growth in aquaculture that may be seen with greater shifts towards pescatarian diets^{19,20} (2030 Rap.Gr). The second is a scenario reflective of accelerating consumer preference for high-value seafood in China, already being observed with increasing affluence and demographic change¹⁹ (2030 Cons.Shft) (Table 1). For each scenario, both the change in total production quantity and the species composition of production across different countries and aquatic taxa (with differing diets and efficiencies) contribute to varying levels of demand in forage fish equivalents (Supplementary Fig. 1).

Global forage fish supplies have remained stagnant since 1980, averaging ~29 million tonnes, with ~70% of these landings used for animal feeds (Fig. 1a). Of the fraction used for feed, an increasing proportion has been used by aquaculture (Fig. 1a), which we estimate to be 16.9 million tonnes in forage fish equivalents in 2015 (s.d.: $\pm 364,215$ tonnes based on 500 simulations), in close agreement with recent estimates³. Under current diets (that is, typical fishmeal and oil inclusion rates across taxa; see Supplementary Table 1), we calculate that demand would increase to over 24 million tonnes by 2030 under a BAU scenario, to over 27 million tonnes under more rapid industry growth and to approximately 38 million tonnes with accelerated demand for high-value species from Chinese consumers, far exceeding historical supply of forage fish (Fig. 1b). Supply-demand mismatches may be exacerbated further if calls for greater adoption of ecosystem-based fisheries management (EBFM) are realized, which suggest there should be 20% reductions in catch to improve ecosystem effects of forage fish extraction²¹ (Fig. 1b).

New ingredients for forage fish sparing. Novel aquafeed ingredients can offer rich sources of both protein and lipids²² that may help reduce aquaculture's demand for forage fish. Some microalgae species naturally synthesize key omega-3 polyunsaturated fatty acids (for example, eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA)), which are crucial for the energetic and growth needs of naturally carnivorous farmed species²². Macroalgae can provide an important protein source with favourable concentrations of key amino acids, such as methionine¹⁷. Bacterial-based feeds offer high protein contents and the capacity to be grown on low-cost substrates with minimal land or water footprints^{23,24}. Yeasts possess favourable amino acid compositions relative to fishmeal and can be produced from lignocellulosic biomass, such as agricultural or forestry waste²⁵. Insects could provide an important source of protein¹⁷ and can convert organic side-stream products (manure, cellulosic or human food waste) into protein-rich feed-stuffs^{26,27}. However, the quality of substrates influences the value of insects as feed, with low-quality substrates yielding low-quality lipids, poor feed conversion ratios or failure to reach harvestable size^{26–29}. While numerous trade-offs associated with novel feed ingredients will be central to their scalability and uptake, here we focus on their global potential within the context of feed efficiency and nutritional content.

We identified 264 scientific articles relevant to our search criteria (Supplementary Table 2) covering 12 farmed animal groups across microalgae, bacteria and yeast, insects and soy ingredients, replacing either fishmeal, fish oil or both (see Methods). For fishmeal replacement studies, we aggregated bacteria and yeasts given

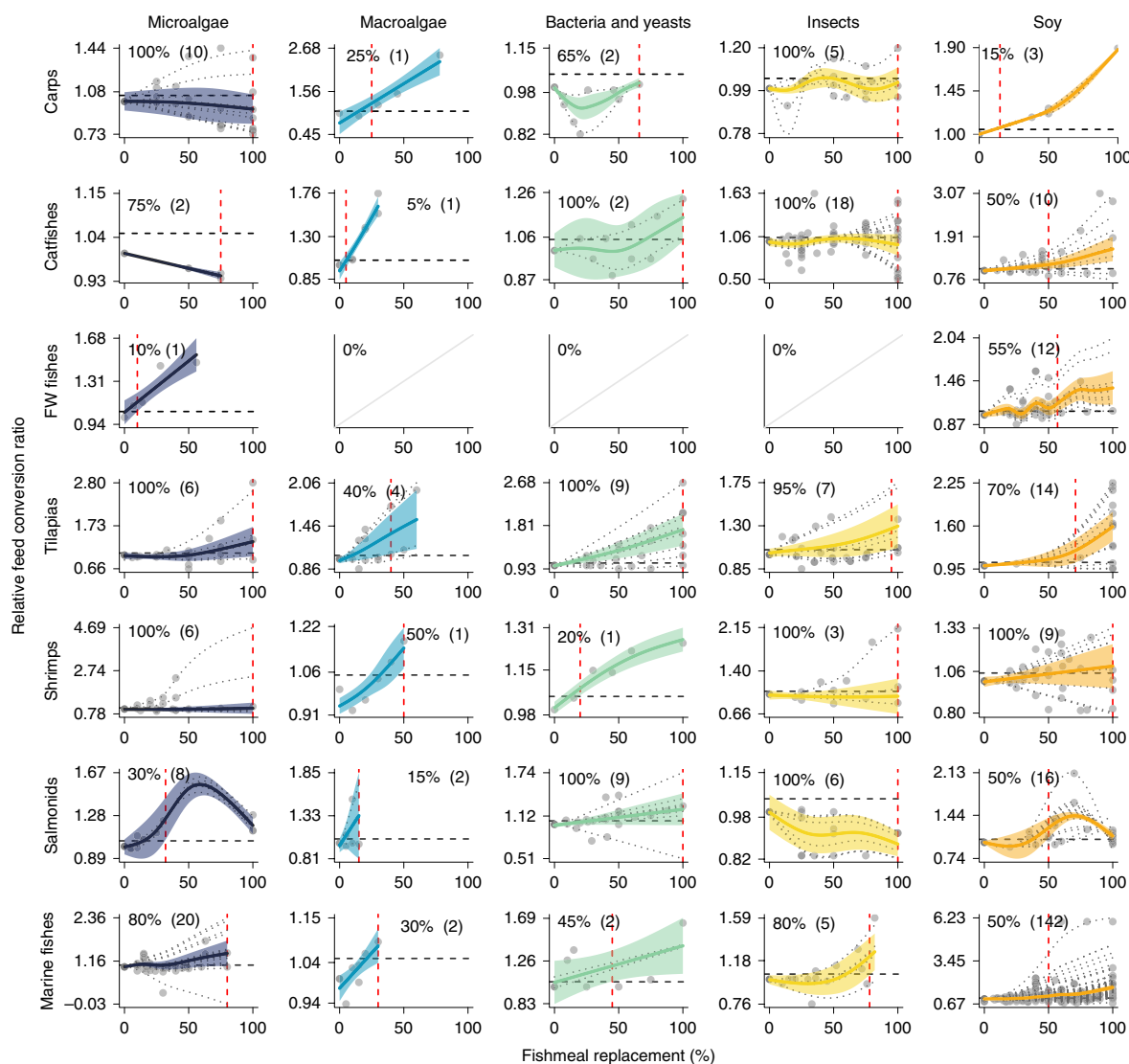


Fig. 2 | Relative change to feed conversion ratios with fishmeal replacement for different animal groups across novel feed types. Solid coloured lines and shading represent fitted mixed-effects model mean responses and 95% confidence intervals, respectively. Vertical dashed lines in red indicate plausible fishmeal replacement levels before feed conversion rates increase beyond 5% (horizontal dashed lines) of reference diets. Percentages on each plot represent thresholds to the nearest 5%. Plots with diagonal lines indicate no/insufficient data identified by a systematic search. Numbers in brackets represent the study sample size for each taxa-feed combination. FW, freshwater.

their functional similarity¹⁷, and to allow for larger sample sizes in the feed–taxa combinations. We limited our analysis to aggregates of carps, catfishes, tilapia, other freshwater fishes (for example, snakeheads, striped bass and Nile perch), shrimps, salmonids and marine fishes (for example, groupers, Atlantic cod and red drum) as an insufficient number of studies for other groups prevented model fitting. Nonetheless, these taxa provide good coverage of the fed sector, contributing >90% of aquaculture’s global forage fish demand (Supplementary Fig. 1). In total, 46% of all studies addressed marine species, largely due to the richness of species farmed. Of the novel feeds, microalgae (18.7%) and insects (16.9%) represented the greatest proportion of the studies, in contrast with 53% that focused on soy, highlighting the uneven effort in experimental work across feed ingredients.

Fishmeal replacement and feed efficiency. We found that fishmeal replacement in feed generally increases species’ feed conversion ratios. In other words, more feed is required for a given mass gain, making the feed less efficient (Fig. 2). Insect-based diets had

the least detrimental effect (median effective replacement=100%) and macroalgae the most (median = 50%) detrimental effect on feed conversion ratios when replacing fishmeal on average across all animal groups (Fig. 2 and Supplementary Table 3). However, there is considerable variability around replacement trends within feed and animal groups and among studies (Fig. 2). For example, no clear change to catfish feed conversion ratios occurred with 100% fishmeal replacement using bacteria-/yeast- or insect-based feeds, yet soy-based diets led to clear increases in feed conversion ratios after 50% fishmeal replacement (Fig. 2).

Fish oil replacement and omega-3 profiles. Fish oils provide key nutritional benefits for the growth, health and maintenance in farmed aquatic species⁸, and nutritional benefits for fish and seafood consumers. Freshwater species such as carps, catfishes and tilapias do not usually need fish oil within their diets. However, when freshwater fishes, salmonids and marine fishes were fed soy-based diets to replace fishmeal, there was an increase of 1–1.5% inclusion of fish oil at the fishmeal replacement threshold (Fig. 2 and Supplementary

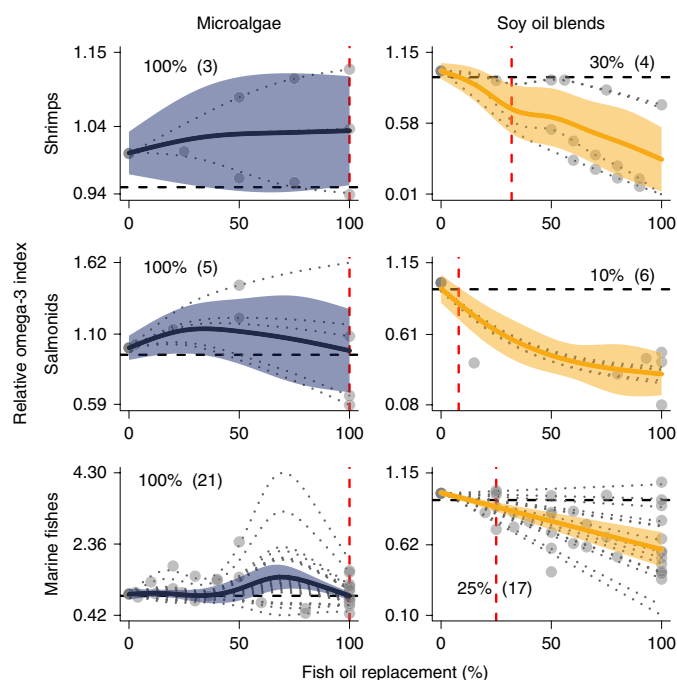


Fig. 3 | Relative change to the omega-3 index in species tissues following fish oil replacement. Solid coloured lines and shading represent fitted mixed-effects model mean responses and 95% confidence intervals, respectively. Vertical dashed lines indicate the threshold where the omega-3 index decreases beyond 5% of reference diets (horizontal dashed lines). Percentages on each plot represent thresholds to the nearest 5%. Numbers in brackets represent the sample size for each experimental group. Only whole-body and fillet samples were used for the fatty acid data. All values in the plots are summarized in Supplementary Table 2.

Fig. 2), which we account for in our forage fish demand calculations. In contrast, algae, bacteria/yeast and insect-based feeds used for fishmeal replacement led to decreases in fish oil inclusion in marine fishes (Supplementary Fig. 2). However, fish oil replacement did not affect feed conversion ratios on average in the studies identified (Supplementary Fig. 3). We instead focus on how fish oil replacement influences the composition of fatty acid profiles in fish tissues—specifically, the relative changes in the proportion of fatty acids represented by EPA and DHA (herein, the omega-3 index), which are highly unsaturated fatty acids known to confer important human health benefits when consumed^{30,31}.

Fish oil replacement experiments largely focused on shrimps, salmonids and marine fishes as the main consumers of fish oil globally³². Microalgae are the only new ingredients considered here that are frequently used to replace fish oil (one study for fish oil replacement by yeast was omitted due to insufficient data for modelling). When compared with soy-oil blends as the baseline, which often contain canola or linseed oil, microalgal diets showed greater promise in fish oil minimization on average, with 100% of fish oil able to be replaced for salmonids, shrimps and marine fishes without clear changes to the omega-3 index in animal tissues (Fig. 3). Using soy oil or soy-oil blends allowed only 30, 10 or 25% fish oil replacement in marine fishes, salmonids and shrimps, respectively, before there were clear decreases in the omega-3 index in animal tissues (Fig. 3). Thus, microalgal meals appear to considerably outperform soy counterparts in preserving the omega-3 profiles in high-value species such as salmon, shrimp and marine species.

Global potential of novel aquafeeds. Quantifying the maximum theoretical global reductions in forage fish demand from novel feeds

requires applying the highest thresholds of plausible fishmeal and oil replacement identified in the previous section across all feeds for each taxon. Under these conditions, our simulations predict that aquaculture's global forage fish demand reduces dramatically to between 8 and 10 million tonnes for all 2030 growth scenarios—below historical or EBFM supply limits, or even historical feed use (BAU = 8.48 ± 0.24 million tonnes; Rap.Gr = 9.65 ± 0.28 million tonnes; Cons.Shft = 10.27 ± 0.32 million tonnes; Fig. 4a (optimal global use)). While global adoption of novel feeds across all taxa is probably unrealistic, feeds containing new ingredients are increasingly available for high-value species such as salmon^{33,34}. Applying maximum plausible replacement to salmonid and shrimp diets only, fed aquaculture's simulated forage fish demand still reduces below historical supply and stricter EBFM supply limits (BAU = 8.48 ± 0.24 million tonnes; Rap.Gr = 9.65 ± 0.28 million tonnes; Cons.Shft = 10.27 ± 0.32 million tonnes; Fig. 4b (salmonids and shrimps only)).

However, reducing fish oil inclusion in feeds is far more efficient at reducing forage fish demand than lowering fishmeal inclusion. Even when replacing fishmeal across all taxa to the maximum threshold identified in Fig. 2, forage fish demand remains far higher in 2030 than when only salmon and shrimp have both fishmeal and oil replaced, or when just fish oil is replaced across salmonids, shrimps and marine fishes (Fig. 4c (fishmeal only) and Fig. 4d (fish oil only)). This is particularly true under the 2030 Cons. Shft scenario ($33.74 + 8.67$ million tonnes forage fish demand) where the production of fish oil-dependent marine fish, salmonids, tunas, shrimps and other crustaceans increases by a factor of three between 2015 and 2030.

Discussion

Maintaining aquaculture's demand for forage fish below historical supply limits is already possible using novel feed ingredients that are currently available, although with varying potential across species and economies. Naturally non-piscivorous fish, such as carps and tilapias, respond well to complete fishmeal elimination from feeds, whereas high-value species such as salmonids appear more sensitive, becoming less efficient in converting feed to biomass. However, total fish oil elimination from salmonids, shrimps and marine fish diets appears possible, with no clear change to the omega-3 index in the tissues of the farmed species. Removing fish oil yields the greatest reductions in global forage fish demand (Fig. 4) because considerably more forage fish is needed to yield a tonne of fish oil than a tonne of fishmeal³². Thus, current innovations targeting reductions in fish oil show great promise for sustainably fed aquaculture growth.

Notably, of all the novel protein sources, insects provided the greatest capacity for fishmeal replacement across all taxa, and microalgae holds far greater potential for fish oil replacement than soy-oil-based feeds. However, we acknowledge that this analysis is limited by the systematic search process that identified the experimental data, and that other ingredients for fishmeal and oil replacement exist. For instance, we did not investigate the effects of fish oil replacement using lipids from insects, yeasts or genetically modified crops such as omega-3-enriched canola, due to a paucity of experimental data.

The variation in the efficiency of different new ingredients across taxa illustrates the continued challenge imposed by physiological differences between non-obligate carnivores and species such as salmon. Nonetheless, the variability in novel feed efficiency among studies within taxa–feed groups highlights how influential feeding or supplementation regimens, complementary ingredients, species or production systems are for the utility of novel feeds. Further innovation in feed manufacturing technologies and feed nutrition will therefore be fundamental for producing more efficient feeds with the desired physical characteristics that continue to reduce fishmeal and oil inclusion across multiple taxa into the future².

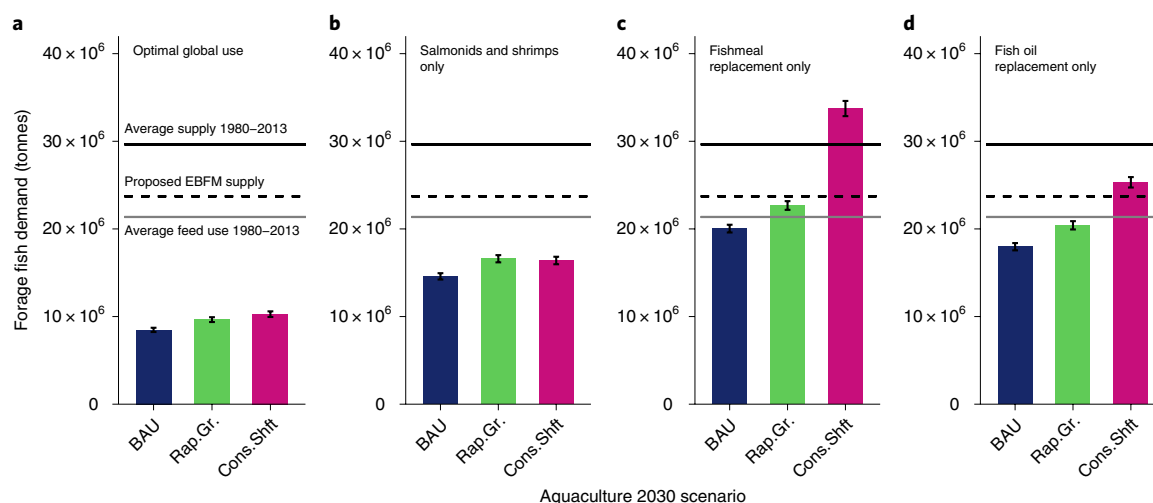


Fig. 4 | Simulated global forage fish savings across animal groups with the incorporation of novel feed ingredients under different aquaculture growth scenarios to 2030. a–d. Global forage fish demand is simulated with: uptake of novel feeds across all taxa (a); novel feed use constrained to global salmonid and shrimp production (b); uptake of novel feed across all taxa limited to fishmeal sparing only (c); and uptake of novel feed across all taxa limited to fish oil sparing only (d). Bars represent mean demand ($n = 500$ simulations) for each scenario and error bars represent s.d.

Numerous technical and socioeconomic factors challenge the widespread use of novel feeds. For example, relatively small production volumes mean algal meals and other microbial biomass still provide a limited market contribution compared with traditional feed commodities^{17,35}. Extracting algae oil from biomass is also a costly process relative to fish oil, and one that is complicated by the need to protect long-chain polyunsaturated fatty acids against oxidation³⁶. However, while current prices and production scales of algal meals limit their global implementation, our results show that targeted interventions on fish-oil-dependent species could still drive a substantial reduction in global forage fish demand. Indeed, since 2017, both insect³⁷ and algal meal and oils³⁸ have been approved for commercial salmon feed use in the European Union. For producers around the world, local-scale market access to novel feeds, the value of the farmed species, production scales, culture systems, financial resources at the farm level and novel feed costs will contribute towards the rate of uptake^{1,36,39}. Social acceptance of novel feed ingredients may also influence market success, particularly if genetic modification is used to improve desirable fatty acid profiles³⁶. However, consumer awareness of feed sustainability is growing, along with acceptance to pay premiums for responsibly produced food^{33,40}, which may support the growth of novel feeds.

Novel feed ingredients will be particularly important if, as we assume here, future demand for fish oil is likely to determine absolute demand for marine resources⁵. Future fishmeal and oil supply from forage fish resources is highly uncertain as populations are highly variable, are closely coupled to environmental conditions and can be sensitive to fishing pressure⁴¹. Consequently, the use of whole trash fish and fishery discards will probably continue supplying animal protein to farmed species in some countries instead of proper and adequate compounds feeds⁴². While we do not explicitly model the use of these resources here, our range of dietary fishmeal inclusions and feed conversion ratios are extremely conservative across taxa⁴³, and deliberately underestimate demand coming from these systems to account for diverse sources of fishmeal and oil. Furthermore, while the development of novel feeds may lower forage fish demand from the aquaculture sector, it is important to reiterate that only changes in fisheries management are likely to lead to reduced biomass extracted from marine ecosystems³.

Numerous uncertainties regarding aquafeed composition and sustainability have implications for our results. Published data

have been highly skewed towards juvenile life stages (92% of studies within our analysis were conducted on juveniles), and uneven research effort (and thus sample size) across taxa–feed combinations influences the reliability of our results. Thus, it is not clear whether these replacement thresholds are reasonable across the entire life cycle of farmed species. Despite this, fish-free feeds for sub-adult and adult fish are commercially available, so the replacement thresholds we identify here can be used to inform replacement targets that would achieve the decreases in demand we simulate. We recognize that measuring changes to the proportional contribution of DHA and EPA to total fatty acid content in animal tissues as a metric of nutritional content has limitations. Changes to absolute quantities of EPA, DHA and total fatty acid contents in animal tissues are details hidden in this ratio. However, absolute quantities are not consistently reported in experimental data, and the omega-3 index we use provides us with a comparable measure of the change in quality of fatty acids in animal tissues as fish oil is replaced. Finally, the best standardized, multi-taxon data on fishmeal and oil inclusion rates, feed conversion ratios or cross-sectoral comparisons are still only available in older publications^{4,32,39}, creating a challenge for the growing body of sustainability research trying to keep pace with the rapidly evolving aquaculture sector.

Broader environmental consequences of using novel feeds over traditional feeds are poorly understood⁴⁴. Microalgal feeds can perform well in terms of cumulative environmental energy extraction compared with reference fish feeds, but performance relies on feed composition and fossil fuel use may still be higher³⁷. Similarly, insect feed conversion ratios and overall energy use can be as high as for conventional livestock^{29,45,46}. Greater understanding of a standardized and comparable suite of environmental impacts (beyond the capacity to replace forage fish) across different feed types needs to be addressed if meaningful decisions about the sustainability of future aquafeeds are to be made.

Future work should aim to prioritize low-cost and complementary ingredients that may be more widely accessible to low-value production systems that otherwise depend on aquatic resources with poor economic, social and environmental efficiency. Further investigations on novel aquafeeds across all dimensions of sustainability are needed as shifting human dietary preferences and demographic change may drive rapid increases in demand for seafood in the next decade.

Methods

We synthesized a broad body of published datasets and scientific literature on aquaculture growth, the potential of novel feeds to replace forage fish ingredients, and current and future forage fish demand. By first combining national aquaculture production data with published information on farmed species growth efficiencies, dietary composition and industry growth scenarios, we calculated and compared historical forage fish supply with projected demand by 2030 under different growth scenarios. To understand how alternative novel feeds can help ameliorate disparities between historical forage fish supply and projected demand, we then assembled a broad body of published experimental data on fishmeal and oil replacement by novel feed ingredients to model their influence on species growth and nutritional content. While assuming reasonable tolerance thresholds for producers, we applied these results to previous forage fish demand calculations to assess whether novel feeds alone will be sufficient to keep the demands from fed aquaculture below historical supply of forage fish. We performed all data analyses in this study using R statistical software⁴⁷.

Aquaculture growth scenarios. For production biomass values for fed aquaculture species until 2015, we used data from the Food and Agriculture Organization (FAO) FishStatJ database (1950–2015 global production dataset; www.fao.org/fishery/topic/166235/en). We then used published growth scenarios to calculate the plausible production potential by 2030, which enabled us to simulate future forage fish demand. The first scenario from the FAO (2030 BAU) simulates a 37% increase in aquaculture growth in developing countries, a 28% increase in developed nations and a 46% increase in the least developed countries¹. We drew the other two scenarios from the World Bank's IMPACT model projections⁴⁸. Our second scenario (2030 Rap.Gr) addresses the possibility of faster aquaculture growth with technological progress, which enables the supply of a given unit of biomass at a lower cost¹⁹. This may be particularly relevant if demand for fish increases under shifts towards more pescatarian human diets in the future^{3,20}. Under this scenario, we increased growth rates from BAU by 50%¹⁹. The third scenario for production in 2030 (2030 Cons.Shft) reflects a case where increasingly affluent Chinese consumers increase demand threefold (mirrored by production change) for high-value products such as salmon, shrimp and other crustaceans (Supplementary Fig. 1).

Calculating forage fish demand. To calculate current and future forage fish demand, we employed the generalized modelling approach of Froehlich et al.³. Across the three different production scenarios outlined above (2030 FAO, 2030 Rap.Gr, 2030 Cons.Shft), we calculated forage fish demand for fish group i in country j as:

$$FF_{ij} = \text{Prod}_{ij} \times \text{Prop}_i \times \text{FCR}_i \times \text{FMFO}_i \times \text{Cv} \quad (1)$$

where demand (FF) is the product of production biomass (Prod; 2015 or 2030), the proportion of biomass that is fed (Prop), the feed conversion ratio (FCR; feed input divided by biomass output) and the proportional dietary contribution of fishmeal and oil (FMFO) converted into biomass equivalents of forage fish (Cv)³².

We took ranges of values for proportions of biomass that are fed, and predicted 2015 and 2020 dietary contributions from fishmeal and oil from Tacon and Metian^{32,39}, as well as feed conversion ratios from Froehlich et al.³. These dietary forage fish inclusion rates, and feed efficiencies, were used for current diets as well as the starting point for the 2030 simulations. From the range of values for the proportion biomass that is fed, the highest value was assumed for all 2030 scenarios. For each animal group in each country, we sampled randomly from the uniform range of values presented in Supplementary Table 1. For each animal group–country combination, we sampled from feed conversion ratios, fishmeal and oil inclusion, and fed proportions independently account for regional differences in production efficiencies, technology and feed practices that influence forage fish demand from a given production unit. We then repeated the above simulations 500 times to obtain mean demand while quantifying uncertainty from between- and within-country differences.

Forage fish replacement data. To identify relevant data on the growth and nutritional effects of fishmeal and oil replacement by novel feeds, we conducted a systematic search of the experimental aquaculture literature. We focused on soy as the major crop-based substitute for forage fish, along with new ingredients that are not yet a substantial global source of human food (microalgae, macroalgae, bacteria/yeasts and insects). In Google Scholar and Scopus databases, we applied the predefined search terms outlined in Supplementary Table 4 for each feed ingredient separately. Different search terms within each ingredient were defined through a preliminary search of Google Scholar using (for example) “algae” or “bacteria” with the rest of the search string to find common model organisms to include. We defined animal group terms by the broad groups and key species outlined in Tacon and Metian³⁹ and Pahlow et al.⁴⁸ and subsequently adjusted them through the same process as is outlined above for feed ingredients. In Scopus, all searches looked for the search terms in document titles, abstracts and keyword fields, and we reviewed all of the results returned for inclusion in our study. In Google Scholar, we reviewed all items returned until five consecutive pages yielded no further relevant studies, as is consistent with systematic search methods⁴⁹.

For an experimental study to be included in our analysis, it needed to:

1. Be published between 2008 and 2018, to isolate recent trends in the growth and nutritional effects of forage fish replacement;
2. Replace fishmeal and/or oil ingredients using soy, algae, bacteria, yeast or insects (solely or in combination with other ingredients);
3. Explicitly illustrate forage fish sparing rather than supplementation with novel feed ingredients;
4. Numerically (not just graphically) describe the influence of fishmeal or oil replacement on animal growth through the feed conversion ratio (or the feed efficiency ratio where we took the inverse);
5. Numerically (not just graphically) describe the influence of fish oil replacement on the nutritional value of animal tissue through the changes in DHA and EPA concentrations as a percentage of total fatty acids (or where at least DHA, EPA and total fatty acids were calculable);
6. Detail the complete dietary composition of reference (0% forage fish replacement) and experimental diets so we could quantify trade-offs between fishmeal replacement and dietary fish oil (and vice versa) and account for them when calculating forage fish demand.

Metrics for growth efficiencies and nutritional content. There are a number of indices that experimental studies and producers use to assess growth rates and the nutritional value of farmed aquatic animals at the start of, during and after feeding trials. Growth parameters can include a combination of the total weight gain (percentage change between final and initial weight), specific growth rate (difference in the natural logarithm of the final and initial weight normalized by the duration of the feed trial), feed efficiency ratio (weight gain divided by feed input), feed conversion ratio (feed input divided by weight gain) or protein efficiency ratio (weight gain divided by protein input). Here, we adopted the feed conversion ratio as our growth metric of interest because: (1) the results directly reflect the forage fish demand calculations; and (2) feeds are one of the greatest overheads for aquaculture producers (for example, 50% of total production costs for salmon)⁵⁰ and substantial increases to feed conversion ratios may equate to lower profits per unit of biomass produced.

As a metric of nutritional value in farmed species tissues, we adopt a metric similar to the omega-3 index used in the human health studies—the sum of DHA and EPA as a proportion of total fatty acids within animal tissues following fish oil replacement trials. We note that decisions on nutritional substitutability of a given feed ingredient normally use several metrics of change to fatty acid content, including total omega-3 polyunsaturated fatty acid content, the ratio of EPA to DHA content, or a ratio of total omega-3 to total omega-6 fatty acid ratios among others⁵¹. Nonetheless, the relative change to both DHA and EPA as a proportion of total fatty acid content provides a useful, unitless metric of the degree of fatty acid composition change in animal tissues. While the omega-3 index we use here is analogous to those used in human nutritional studies, it should be noted that they are not the same. In humans, the omega-3 index is used to describe the sum of EPA and DHA as a fraction of total fatty acids in the blood as an indication of human health^{31,52,53}. We do not claim that our use of this fraction describes anything about fish health; it is merely a useful tracker of the change to fatty acid composition within the same species as fish oil is replaced.

From each individual study, we extracted the mean effect of forage fish replacement on either the feed conversion or fatty acid ratios to represent a single point within our data. To judge plausible replacement levels of fishmeal and oil, we assumed producers will only be willing to replace forage fish ingredients in feeds if a reasonably similar feed conversion ratio or fatty acid profile is achieved. We arbitrarily hold this similarity to within 5% of reference diets, given that there will be a price or even belief system component to why a manufacturer or producer may want to use a novel feed over fishmeal and oil. We standardize the detection of any change beyond this threshold as the point at which 95% confidence intervals of fitted statistical models (detailed below) increase or decrease >5% past reference diet values for feed conversion ratios or omega-3 indices, respectively.

Modelling growth and nutritional effects of forage fish replacement. Given the range of fed animal species, ingredient species or forms, amino acid or enzyme supplementations, attractants, pellet sizes or production environments used, it is not surprising that even studies replacing forage fish with the same ingredients within animal groups yield different results for growth or fatty acid contents. To calculate average responses to fishmeal and oil replacement while accounting for these variables, we combined experimental data for each feed type, animal group and model at what level of forage fish replacement feed conversion or omega-3 indices, respectively, increase or decrease beyond 5% of reference diets. To reflect the nonlinear trends in growth or nutritional content with replacement across different studies, we fitted smoother-spline mixed-effects (SME) models to the data on feed conversion and the omega-3 index from 0–100% fishmeal or oil replacement (or the maximum used in the feeding trial) using the *sme* R package⁵⁴. As we are interested only in relative rather than absolute changes to both of these parameters, we modelled replacement effects on relative feed conversion or fatty acid ratios for study i as a smooth function of forage fish replacement, $y_i(r)$:

$$y_i(r) = \mu(r) + v_i(r) + e_i(r) \quad (2)$$

where $\mu(r)$ is the mean function across all studies, $v_i(r)$ is study i 's deviation from the mean function, assumed to also be a smooth function of replacement, and $\epsilon_i(r)$ is the error process⁵⁴. Using the study ID as the random effect, we capture combined information on the experimental species, specific forage fish substitute and amino acid and enzyme supplementation regimens used, which would otherwise be highly collinear.

SME models are ideally suited to our dataset due to the small sample sizes, noisy observations, irregular measurements and missing data inherent from pulling independently designed experimental research together. To avoid the constraints small sample sizes impose on the number and locations of knots between polynomials within smoother splines, SME models use every measured replacement percentage point as a knot and introduce penalty parameters for lack of smoothness to avoid overfitting. We estimate these penalty parameters during model fit using the corrected Akaike information criterion, maximizing penalized likelihood. However, knot number and location were occasionally manually fitted if there were fewer observations than degrees of freedom when using the default approach outlined above. Manual fitting was honed through diagnostic checks of quantile–quantile plots and the spread of standardized residuals across forage fish replacement values and fitted values for relative feed conversion or n-3:n-6 fatty acid ratios. By plotting model outputs, we discern where (in terms of forage fish replacement levels) clear increases in the feed conversion ratio occur when 95% confidence intervals increase >5% above feed conversion ratios of reference diets. We repeat this for where confidence intervals decrease >5% below the omega-3 index for reference diets under fish oil replacement.

Finally, we combine these thresholds as limits of plausible fishmeal or oil replacement with apparent trade-offs in dietary change of the opposite ingredient (that is, for species i under a fishmeal replacement regimen from feed k):

$$\text{FMFO}_{i,k} = \sum (\text{FMFO}_i \times \Delta \text{FM}_{(\text{opt})i,k}) + (\text{FMFO}_i \times \Delta \text{FO}_{(\text{opt})i,k}) \quad (3)$$

where $\text{FMFO}_{i,k}$ is the proportional dietary contribution of fishmeal and oil, $\Delta \text{FM}_{(\text{opt})}$ is the optimal proportional replacement level of dietary fishmeal, and $\Delta \text{FO}_{(\text{opt})}$ is the proportional change in fish oil associated with $\Delta \text{FM}_{(\text{opt})}$ or vice versa. This can then be reinserted into the forage fish calculation (equation (1)):

$$\text{FF}_{i,j} = \text{Prod}_{i,j} \times \text{Prop}_i \times \text{FCR}_i \times \text{FMFO}_{i,k} \times \text{CV}$$

Applying these combined results to dietary information within forage fish demand calculations for 2030, we assess the potential for each novel feed type to keep forage fish demands of fed aquaculture below historical supply.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Aquaculture production data are publicly available and were accessed through FishStatJ³⁵. All data products used for analyses in this study are publicly available through a GitHub repository (<https://github.com/cottrellr/alternativefeeds>). All data that support this study are available from the corresponding author on request.

Code availability

All custom code produced during the analyses were generated using R statistical software version 3.4.3 and are publicly available through a GitHub repository (<https://github.com/cottrellr/alternativefeeds>).

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References

1. The State of World Fisheries and Aquaculture 2018—Meeting the Sustainable Development Goals (FAO, 2018).
2. Turchini, G. M., Trushenski, J. T. & Glencross, B. D. Thoughts for the future of aquaculture nutrition: realigning perspectives to reflect contemporary issues related to judicious use of marine resources in aquafeeds. *N. Am. J. Aquac.* **81**, 13–39 (2019).
3. Froehlich, H., Jacobsen, N. S., Essington, T. E., Clavelle, T. & Halpern, B. S. Avoiding the ecological limits of forage fish for fed aquaculture. *Nat. Sustain.* **1**, 298–303 (2018).
4. Shepherd, C. J. & Jackson, A. J. Global fishmeal and fish-oil supply: inputs, outputs and markets. *J. Fish Biol.* **83**, 1046–1066 (2013).
5. Naylor, R. et al. Feeding aquaculture in an era of finite resources. *Proc. Natl Acad. Sci. USA* **106**, 15103–15110 (2009).
6. Naylor, R. et al. Effect of aquaculture on world fish supplies. *Nature* **405**, 1017–1024 (2000).
7. Wijkstrom, U. in *Fish as Feed Inputs for Aquaculture: Practices, Sustainability and Implications* Fisheries and Aquaculture Technical Paper Vol. 518 (eds Hasan, M. & Halwart, M.) 371–407 (2009).
8. Turchini, G. M., Torstensen, B. E. & Ng, W. K. Fish oil replacement in finfish nutrition. *Rev. Aquac.* **1**, 10–57 (2009).
9. Hasan, M. R. & Halwart, M. *Fish as Feed Inputs for Aquaculture: Practices, Sustainability and Implications* (FAO, 2009).
10. Troell, M. et al. Does aquaculture add resilience to the global food system? *Proc. Natl Acad. Sci. USA* **111**, 13257–13263 (2014).
11. Francis, G., Makkar, H. P. S. & Becker, K. Antinutritional factors present in plant-derived alternate fish feed ingredients and their effects in fish. *Aquaculture* **199**, 197–227 (2001).
12. Hamilton, H. A. et al. Investigating cross-sectoral synergies through integrated aquaculture, fisheries, and agriculture phosphorus assessments: a case study of Norway. *J. Ind. Ecol.* **20**, 867–882 (2015).
13. Kokou, F. & Fountoulaki, E. Aquaculture waste production associated with antinutrient presence in common fish feed plant ingredients. *Aquaculture* **495**, 295–310 (2018).
14. Parker, R. Implications of high animal by-product feed inputs in life cycle assessments of farmed Atlantic salmon. *Int. J. Life Cycle Assess.* **23**, 982–994 (2018).
15. Olsen, R. E. et al. Can mesopelagic mixed layers be used as feed sources for salmon aquaculture? *Deep Res. Pt II* <https://doi.org/10.1016/j.dsr2.2019.104722> (2020).
16. Saunders, R. A., Hill, S. L., Tarling, G. A. & Murphy, E. J. Myctophid fish (family Myctophidae) are central consumers in the food web of the scotia sea (Southern Ocean). *Front. Mar. Sci.* **6**, 530 (2019).
17. Hua, K. et al. The future of aquatic protein: implications for protein sources in aquaculture diets. *One Earth* **1**, 316–329 (2019).
18. Pelletier, N., Klinger, D. H., Sims, N. A., Yoshioka, J. R. & Kittinger, J. N. Nutritional attributes, substitutability, scalability, and environmental intensity of an illustrative subset of current and future protein sources for aquaculture feeds: joint consideration of potential synergies and trade-offs. *Environ. Sci. Technol.* **52**, 5532–5544 (2018).
19. *Fish to 2030: Prospects for Fisheries and Aquaculture* (World Bank, 2013).
20. Tilman, D. & Clark, M. Global diets link environmental sustainability and human health. *Nature* **515**, 518–522 (2014).
21. Smith, A. D. M. et al. Impacts of fishing low-trophic level species on marine ecosystems. *Science* **333**, 1147–1150 (2011).
22. Shah, M. R. et al. Microalgae in aquafeeds for a sustainable aquaculture industry. *J. Appl. Phycol.* **30**, 197–213 (2018).
23. Mahan, K. M. et al. Production of single cell protein from agro-waste using *Rhodococcus opacus*. *J. Ind. Microbiol. Biotechnol.* **45**, 795–801 (2018).
24. Rosas, V. T., Poersch, H., Romano, L. A. & Tesser, M. B. Feasibility of the use of *Spirulina* in aquaculture diets. *Rev. Aquac.* **11**, 1367–1378 (2018).
25. Øverland, M. & Skrede, A. Yeast derived from lignocellulosic biomass as a sustainable feed resource for use in aquaculture. *J. Sci. Food Agric.* **97**, 733–742 (2017).
26. Van Huis, A. Potential of insects as food and feed in assuring food security. *Annu. Rev. Entomol.* **58**, 563–583 (2013).
27. Henry, M., Gasco, L., Piccolo, G. & Fountoulaki, E. Review on the use of insects in the diet of farmed fish: past and future. *Anim. Feed Sci. Technol.* **203**, 1–22 (2015).
28. Sealey, W. M. et al. Sensory analysis of rainbow trout, *Oncorhynchus mykiss*, fed enriched black soldier fly prepupae, *Hermetia illucens*. *J. World Aquac. Soc.* **42**, 34–45 (2011).
29. Lundy, M. E. & Parrella, M. P. Crickets are not a free lunch: protein capture from scaled organic side-streams via high-density populations of *Acheta domesticus*. *PLoS ONE* **10**, e0118785 (2015).
30. Harris, W. S. Omega-3 fatty acids and cardiovascular disease: a case for omega-3 index as a new risk factor. *Pharmacol. Res.* **55**, 217–223 (2007).
31. Von Schacky, C. Omega-3 index and cardiovascular health. *Nutrients* **6**, 799–814 (2014).
32. Tacon, A. G. J. & Metian, M. Global overview on the use of fish meal and fish oil in industrially compounded aquafeeds: trends and future prospects. *Aquaculture* **285**, 146–158 (2008).
33. Salmon novelty in France: Supermarché Match launches salmon fed with Veramaris' innovative natural marine algal oil. *Veramaris* (6 June 2019).
34. Protix presents the Friendly Salmon™, the first insect-fed salmon in the world. *Protix* (6 February 2018).
35. Vigani, M. et al. Food and feed products from micro-algae: market opportunities and challenges for the EU. *Trends Food Sci. Technol.* **42**, 81–92 (2015).
36. Sprague, M., Betancor, M. B. & Tocher, D. R. Microbial and genetically engineered oils as replacements for fish oil in aquaculture feeds. *Biotechnol. Lett.* **39**, 1599–1609 (2017).
37. Taelman, S. E. et al. Bioresource technology the environmental sustainability of microalgae as feed for aquaculture: a life cycle perspective. *Bioresour. Technol.* **150**, 513–522 (2013).
38. *Sustainability Report: Global 2017* (Skretting, 2017).
39. Tacon, A. & Metian, M. Feed matters: satisfying the feed demand of aquaculture. *Rev. Fish. Sci. Aquac.* **23**, 1–10 (2015).
40. Llagostera, P. F., Kallas, Z., Reig, L. & Amores de Gea, D. The use of insect meal as a sustainable feeding alternative in aquaculture: current situation,

- Spanish consumers' perceptions and willingness to pay. *J. Clean. Prod.* **229**, 10–21 (2019).
41. Essington, T. E. et al. Fishing amplifies forage fish population collapses. *Proc. Natl Acad. Sci. USA* **112**, 6648–6652 (2015).
 42. Cao, L. et al. China's aquaculture and the world's wild fisheries. *Science* **347**, 133–135 (2015).
 43. Chiu, A. et al. Feed and fishmeal use in the production of carp and tilapia in China. *Aquaculture* **414–415**, 127–134 (2013).
 44. Couture, J. L. et al. Environmental benefits of novel nonhuman food inputs to salmon feeds. *Environ. Sci. Technol.* **53**, 1967–1975 (2019).
 45. Oonincx, D. G. A. B. et al. An exploration on greenhouse gas and ammonia production by insect species suitable for animal or human consumption. *PLoS ONE* **5**, e14445 (2010).
 46. Oonincx, D. G. A. B. & de Boer, I. J. M. Environmental impact of the production of mealworms as a protein source for humans—a life cycle assessment. *PLoS ONE* **7**, e51145 (2012).
 47. R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2017).
 48. Pahlow, M., van Oel, P. R., Mekonnen, M. M. & Hoekstra, A. Y. Increasing pressure on freshwater resources due to terrestrial feed ingredients for aquaculture production. *Sci. Total Environ.* **536**, 847–857 (2015).
 49. Pickering, C. & Byrne, J. The benefits of publishing systematic quantitative literature reviews for PhD candidates and other early-career researchers. *High. Educ. Res. Dev.* **33**, 534–548 (2014).
 50. Fore, M. et al. Review precision fish farming: a new framework to improve production in aquaculture. *Biosyst. Eng.* **173**, 176–193 (2018).
 51. Alhazzaa, R., Nichols, P. D. & Carter, C. G. Sustainable alternatives to dietary fish oil in tropical fish aquaculture. *Rev. Aquac.* **11**, 1195–1218 (2018).
 52. Harris, W. S. The omega-3 index as a risk factor for coronary heart disease. *Am. J. Clin. Nutr.* **87**, 1997S–2002S (2008).
 53. Harris, W. S. & von Schacky, C. The omega-3 index: a new risk factor for death from coronary heart disease? *Prev. Med.* **39**, 212–220 (2004).
 54. Berk, M. sme: Smoothing-splines mixed-effects models. R package v.1.0.2 (rdr, 2018).
 55. FishStatJ (FAO, 2019).

56. FAOSTAT (FAO, 2019); <http://www.fao.org/faostat/en/#data>

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Author contributions

R.S.C. and H.E.F. designed the study. R.S.C. conducted the analysis and wrote the initial draft. J.L.B., H.E.F., B.S.H. and M.M. contributed to methodological refinements and conceptual considerations. All authors contributed to completion of the manuscript through comments and edits of the text and figures.

Competing interests

H.E.F. is a scientific advisor on the Aquaculture Stewardship Council Technical Advisory Group.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s43016-020-0078-x>.

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All analyses were conducted using custom code on R version 3.4.3.

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Aquaculture production data are publicly available and were accessed through FishStatJ25. All code and data products used for analyses in this study are publicly available through a Github repository (<https://github.com/cottrellr/alternativefeeds>). All data that support this study are available from the corresponding author on request.

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Study description	This study synthesizes global production data with published experimental data on forage fish replacement in forage fish diets. To analyze experimental data we systematically selected 264 research articles containing 446 independent studies.
Research sample	The experimental sample were identified through a systematic literature review where the key words listed in the methods section defined the search over a ten year period, 2008 - 2018. Aquaculture production data was sourced from FishStatJ.
Sampling strategy	Search terms and filters detailed in methods were applied to both Scopus and Google Scholar databases. All items identified in Scopus were reviewed for inclusion. For Google Scholar which often returns tens of thousands of articles in a search, we used an empirical standard. Once we reviewed five pages without relevant articles, the search was ended.
Data collection	Richard Cottrell collected the experimental data from published literature, extracting mean values of feed conversion ratios and change in fatty acid profiles with forage fish replacement. For each study information on study species, feed types, life stage, author and year.
Timing and spatial scale	The literature search occurred constantly from mid-August to mid-September 2018
Data exclusions	Experimental data on forage fish replacement in freshwater crustaceans and diadromous fishes were excluded from final analyses due to insufficient data points or number of studies across different feed types for model fitting. This brought the number of independent studies used down to 409.
Reproducibility	All code and data products will be available in a public Github repository (including downloaded aquaculture production data) on manuscript acceptance. All experimental data is also referenced.
Randomization	All experimental groups were defined through the taxonomic groupings of both the farmed species and species of novel feed used.
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