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The Fish Behind Fish Feed: Rethinking Transparency Using DNA Tools

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ABSTRACT

Aquaculture is now the fastest growing food sector and may be a promising solution to increasing seafood demands. Yet, carnivorous aquaculture species such as salmon and seabass continue to rely on fishmeal and fish oil (FMFO), which are derived largely from pelagic fish that are sometimes key to the food security of some coastal nations. This reliance on wild-caught resources fuels debates around the ethics, sustainability and socio-economic impacts of transforming edible fish into feed. Despite growing concerns, traceability and transparency around the origin and composition of FMFO is limited, leaving feed ingredients largely invisible to customers, consumers and policymakers. We argue that this opacity erodes trust and hinders informed debate and conversation around the growth of aquaculture, its sustainability, and ethical concerns regarding just and equitable food systems. Here, we highlight how DNA metabarcoding of commercial feed samples offers a promising transparency tool by revealing a wide diversity of species, far beyond what labels disclose. If aquaculture is to demonstrate that it supports global food security, this blind spot around fish feed will need to be addressed urgently. Increased transparency on FMFO sourcing and composition could rebuild public trust, empower producers, consumers and regulators, and safeguard the livelihoods of coastal communities by ensuring a just pathway to aquaculture production.

1 | Fed Aquaculture, a Double-Edged Sword

Aquaculture production has become the fastest growing food sector and has now surpassed wild caught seafood production in terms of quantity produced (FAO 2024). For fed species, the purchase of animal feed is often the largest expenditure of total production cost (> 15% of production cost) (Einarsson et al. 2019). The aquaculture sector encompasses a diverse range of organisms with varying degrees of impact on ecosystems, including algae and shellfish, omnivorous fish like tilapia (*Oreochromis* sp.) and cyprinids and carnivorous species like Atlantic salmon (*Salmo salar*) and European seabass (*Dicentrarchus labrax*) (Belton et al. 2020; Chiu et al. 2013). Although fed aquaculture is often brought forth as a path to improving nutrient intake and livelihoods, it is also at the centre of a contentious debate (Froehlich et al. 2025) and has even been characterised by some authors as 'a false solution' to increasing seafood demands and world hunger (Belton et al. 2020; Sumaila et al. 2022). Indeed, the last few years have seen a proliferation of articles and dossiers highlighting the potential links between FMFO production

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Etymology of Ghot: George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

and the impoverishment of some coastal communities, namely in West Africa (Greenpeace Africa and Changing Markets 2021; Healy et al. 2025; Rothstein 2024). Despite this, the share of fed aquaculture continues to increase and now represents 73% of the sector (FAO 2024), raising questions around the production of fish feed and its impact on both marine and terrestrial ecosystems (Clawson et al. 2025; Cottrell et al. 2025; Leadbitter et al. 2025).

At present, the European Union only meets 37% of its demand in aquaculture (EUMOFA 2024) and imports most of the aquaculture products it consumes from Norway. Meanwhile, and despite the low relative proportion of FMFO in their feed, the sheer magnitude of tilapia and carp aquaculture in China is a key drivers behind its position as the world's largest fish meal importer (Chiu et al. 2013). Along with Europe and the United-States as leading consumers of Atlantic salmon, China's increasing demand for high-value fin fish may encourage the growing production of carnivorous species (Budhathoki et al. 2025), possibly increasing pressure on wild fish stocks unless viable alternatives are developed (Boissat et al. 2025; Cao et al. 2015).

2 | Feeding High-Value Fish: Equity Concerns in Global FMFO Use

Several species of important commercial values in high income countries such as salmon and seabass are fed with pellets which often contain a mixture of terrestrial and marine products. Fatty carnivorous fin fish species are usually destined to consumers in high income countries (Majluf et al. 2024), but are highly dependent on global FMFO providers, some of whom obtain resources, often small pelagic fish species high in omega-3, from low-income countries, creating an imbalance in the distribution of protein and nutrient resources (Cashion and Le Manach 2017; Deme et al. 2022; Majluf et al. 2017, 2024; Westgaard et al. 2017). This imbalance in the supply chain and in who benefits from it has raised criticism, and concerns continue to emerge around the transformation of food-grade fish into fish feed (Cashion and Le Manach 2017). Indeed, studies show that nutrient retention is higher if small pelagic species such as sardines, herrings, mackerel and anchovies, are used for direct human consumption rather than fish feed (Willer et al. 2024). Bearing in mind these considerations, the sector of fed carnivorous species aquaculture is expected to continue growing, with the production of salmon, one of the most lucrative aquaculture species, projected by the Norwegian seafood and aquaculture market intelligence company Kontali to increase by 40% from 2023 to 2033 (4 million tons) (Boissat et al. 2025).

The reliance on small pelagic species, such as the Peruvian anchoveta (*Engraulis ringens*), the world's largest fishery and their fluctuating stocks and quotas compounded by climate change, has driven the FMFO sector to expand and diversify its raw material sources. Markets such as those from West African coastal states represent relatively recent additions (Braham et al. 2024; Deme et al. 2022; Shea et al. 2025). In countries such as Mauritania, Senegal and the Republic of The Gambia, rapid proliferation of fish processing factories and deteriorating environmental conditions have been linked to overexploitation and decline of local stocks (Braham et al. 2024; SFP 2025). With the global FMFO trade projected to increase (Boissat et al. 2025) and its supply chain likely to become more complex (Shea et al. 2025), best practices should be put in place to prevent the over-exploitation of resources and ensure that local communities can benefit from this trade and not see their livelihoods impacted.

In Europe, the overfishing and lack of comprehensive quota agreements on some key pelagic species used for FMFO production such as Atlantic mackerel (*Scomber scombrus*) or blue whiting (*Micromesistius poutassou*) are threatening the certification of salmon aquaculture. As a result, some producers have considered veering away from species like blue whiting (NAPA 2024), but given how much feed production depends on this species in Europe (EUMOFA 2025), this would require a major revaluation of providers and source species, some of which may come from countries with less capacity to manage their stocks sustainably and responsibly. In doing so, European feed companies risk shifting the environmental and ethical burden of harvest onto third countries.

3 | The Limits of Reduced Dependence on FMFO

As an attempt to decrease its dependence on marine ingredients and provide some buffer against the unpredictable fluctuations of the pelagic fisheries sector, the fish feed sector has largely decreased its relative use of FMFO in salmon feed, from 89% in 1990 to 22% in 2020 (Aas et al. 2022). Simultaneously, feed producers have increased their use of byproducts and trimmings from fish destined for human consumption (Boissat et al. 2025). Despite this relative decrease in marine ingredients from forage fish, the steady growth of fed aquaculture means that the demand for fish meal and fish oil has remained relatively constant over the last decade (Newton et al. 2023). Despite these marked improvements however, the salmon aquaculture sector is now facing a challenging conundrum: the reduction of marine ingredients in the diet has led to a dramatic fall of beneficial marine fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) content in the flesh, affecting the nutritional content of salmon (Sprague et al. 2016). Furthermore, life cycle assessments (LCA) of FMFO and modelling studies have argued that terrestrial sources of ingredients might be less sustainable than marine sources (Clawson et al. 2025; Cottrell et al. 2025; Kok et al. 2026).

These stumbling blocks and the limited availability of widely accepted solutions can erode trust in the sector, leading to unanswered questions and making the consumption of carnivorous aquaculture species controversial. A recurrent criticism stems from the lack of transparency over the ingredients used by the feed industry and the opacity of parts of the global FMFO supply chain (Shea et al. 2025). Given the unstable nature of small pelagic fish, the sector has developed a large array of possible marine ingredients, some of which are deemed less environmentally and socially sustainable than others. Based on personal relations and informal conversations with industry representatives, we observe that some FMFO producers have invested in robust internal traceability systems, allowing them to track data on origin, toxicology and quality of specific batches at any point in time. Yet given the prevalent lack of traceability at the global scale and given the mixed nature of animal feed, it remains difficult for consumers, including aquaculture farms themselves (Chiu et al. 2013), to evaluate the sustainability of the feed they are provided with.

4 | A Blind Spot on Feed Labels

The EU and the UK have some of the world's strongest seafood labelling and traceability requirements including the recently revised Fisheries Control Regulation (EC 2023/2842), and the Common Market Organisation (CMO) for fisheries and aquaculture products (EU 1379/2013) and the UK Fish Labelling Regulations 2013, which retains text from the CMO. As such, the CMO lays down the principles of mandatory consumer information for seafood, stating that species name (commercial and scientific), production method, catch or farmed area, amongst other details, must be provided to the final consumer. Despite this, critical gaps remain, such as the lack of adequate labels for prepared and preserved seafood products destined for human consumption, which are exempt from Article 35 of the CMO. Given that the majority of FMFO produced is reserved for animal feed, it largely falls outside the seafood provenance traceability and transparency rules in place both in the UK and the EU and is mostly regulated through sanitary control rules. As a result, imported FMFO destined for animal feed is excluded from the import catch certificates in the UK and in the EU (EC 1005/2008), and any information on species, provenance, production method and flag state is lost, unless provided voluntarily. Furthermore, consumer labelling rules in Europe and the UK (EU 1379/2013; UK Fish Labelling Regulations 2013) don't apply to aquafeed products, leading to labels with minimal information (Figure S1). As a result, once the fish are aggregated into FMFO, provenance information is no longer required and the type of information available will differ greatly between producers (Hornborg and Langeland 2024).

In an attempt to respond to some of the concerns around the lack of transparency in the supply chain and the absence of stringent traceability regulations, the feed industry has engaged in a number of initiatives and certification schemes, each varying in the rigidity of their demands and verification processes; though the nature of highly processed fish feed can make it difficult to verify claims. In this context, reliable transparency tools that can be used at any point of the supply chain could become powerful allies in making the whole sector more transparent and sustainable.

4.1 | A Case Study Using DNA to Investigate Fish Feed Composition

Genetic tools have been used extensively to tackle the lack of transparency in some branches of the seafood supply chain, uncovering repeated instances of mislabelling and highlighting the species and food sectors most affected (Cawthorn et al. 2018; Cusa et al. 2025; Lorusso et al. 2024; Luque and Donlan 2019; Miller and Mariani 2010). In a sector where products are highly processed prior to export and where many ingredients go into the making of a single final product, such as fish feed, DNA metabarcoding, with its ability to simultaneously sequence complex mixtures and parse their diverse content based on taxonomy, holds the power to inform stakeholders, authorities and certification bodies on the raw materials used.

Despite this, the use of genetic tools to uncover the composition of FMFO and fish feed remains relatively unused at the moment but see (Galal-Khallaf et al. 2016; Ido and Miura 2022; Mokhtar et al. 2022). Baetscher et al. 2023 explored some of the primers best suited for the analysis of mixed fish products and identified that Cytochrome C Oxidase subunit I (COI) markers were ideal for the identification of most of the taxa tested. Here, we carried out the first attempt to evaluate the content of fish feed opportunistically sampled in the UK and destined for a variety of species, using the mlCOIintF and jgHCO2198 primers, designed to target a 313 bp fragment of the COI gene across all eukaryotes (Geller et al. 2013; Leray et al. 2013), and using an Illumina MiSeq platform for sequencing (Supporting Information).

4.2 | Results and Discussion: More Fear Than Harm?

The results of 30 fish feed samples acquired from five feed companies in Europe and used in the farming of cyprinids, trout, salmon (adults and hatchery) in the UK show a wide diversity of aquatic species, none of which were indicated in the vague package labels which typically listed 'fish meal' and 'fish oil' (Figure S1). Excluding taxa contributing to $<0.1\%$ of the total sequence reads recovered, which may have represented accidental traces and 'noise' associated with the production process (Deagle et al. 2019; Ido and Miura 2022; McInnes et al. 2017), our dataset revealed 33 fish species, 17 of which could have originated from whole fish and 16 of which most likely originated from fish by-products and trimmings (Table S1) (see Supporting Information for methodological details on laboratory procedures and bioinformatics analyses, and for the raw MOTU table which includes taxonomic assignments). The majority of species that might have been derived from whole fish originated from the Northeast Atlantic, highlighting the importance of local FMFO providers to the production of fish feed in Europe (Figure 1a).

Though read numbers are not entirely representative of species abundance in a sample, particularly in aqueous environmental DNA samples, it has the potential of informing on some of the most prevalent species, especially in samples of concentrated fish material (Deagle et al. 2019; Di Muri et al. 2020; Luo et al. 2023; McInnes et al. 2017). In this case, blue whiting (*Micromesistius poutassou*), Atlantic herring (*Clupea harengus*), capelin (*Mallotus villosus*) and Atlantic mackerel (*Scomber scombrus*) were by far the most prominent fish species overall, indicating a strong dependence on regional supply chains for most of the feed samples (Table S1, Figure 1b).

Feed was separated in seven categories, based on its target species and life stage, including (a) salmon grower feed ($n=9$), (b) salmon hatchery and nursery feed ($n=6$), (c) trout grower feed ($n=4$), (d) trout hatchery and nursery feed ($n=3$), (e) carp grower feed ($n=3$), (f) mixed hatchery and nursery feed ($n=4$) and (g) reproduction feed ($n=1$). Hatchery and nursery feed are destined for fish larvae, fry and early juvenile stages, whereas grower feed is destined for the post-smolt or

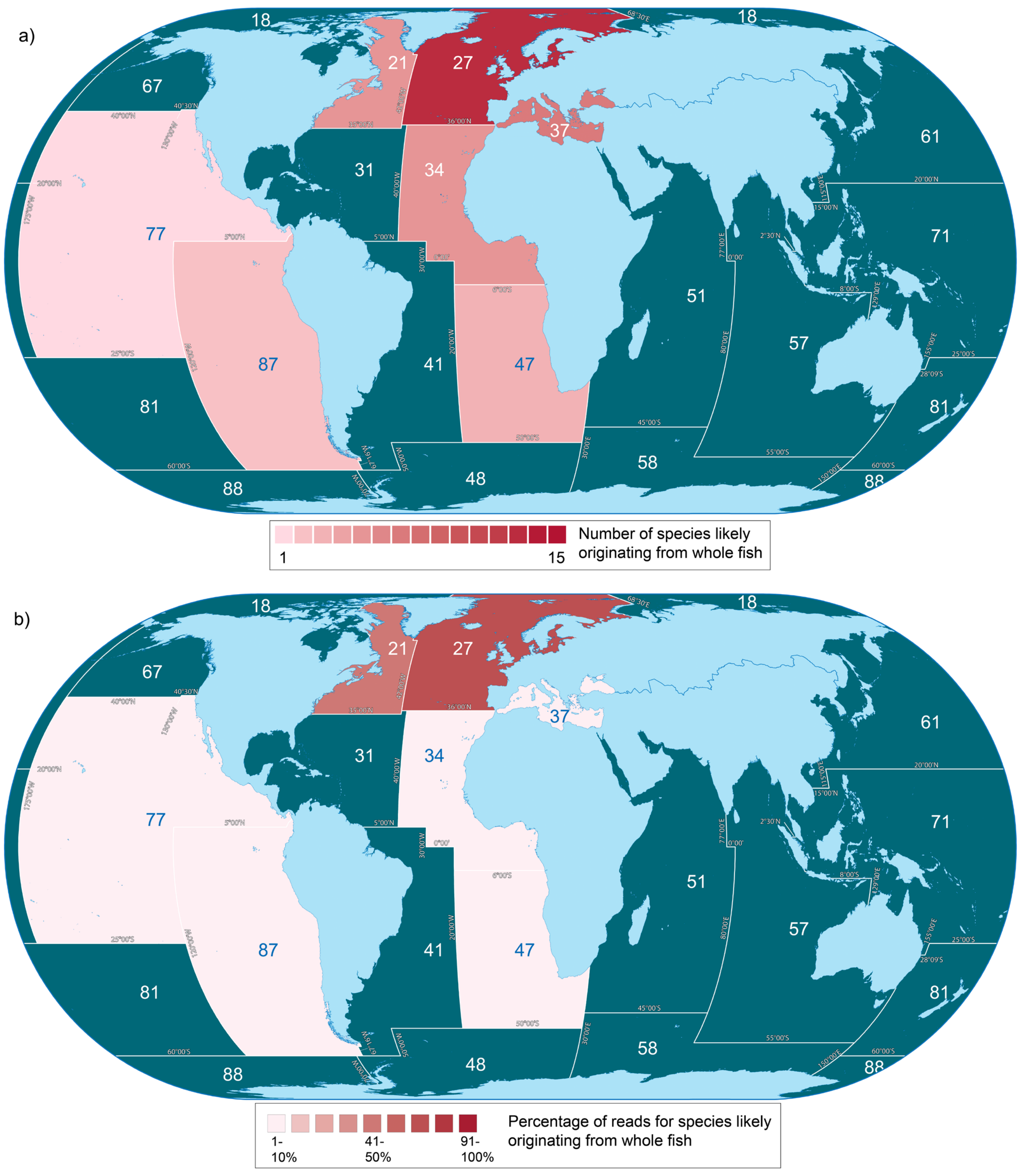

FIGURE 1 | Map of the Major Fishing Areas as divided and numbered by the Food and Agriculture Organisation (FAO) for management purposes (Map layer retrieved from: https://fish-commercial-names.ec.europa.eu/fish-names/fishing-areas_en). Overlaid are layers showing the global distribution of species identified in fish feed through DNA metabarcoding and likely derived from whole fish using (a) species count and (b) species relative contribution in terms of percentage of reads. Species distribution ranges were obtained from FishBase (see Table S1) and mapped according to FAO Major Fishing Areas; a species for whom the geographical range expands to several FAO Fishing Areas was counted in each area to reflect the true possible distributional range of all species identified in the feed.

post-fingerling stages and is reserved for fish that are rapidly increasing weight until they reach market size. Reproduction feed, on the other hand, is destined for mature broodstock and is not developed to enhance growth but rather to promote gonad development, spawning success and to ensure egg quality. Some feed types exhibited a higher diversity of marine ingredients, illustrating their dependence on a diverse supply chain. Namely, salmon grower, hatchery and nursery feed displayed a wider range of species, mostly oily pelagic species like Atlantic herring, Atlantic mackerel, capelin and sprat (*Sprattus sprattus*), silver smelt (*Argentina silus*) and boarfish (*Capros aper*) and included some alternative lower trophic level species such as lanternfish (Mictophiformes) or krill (Euphasiacea). In general, however, the salmon feed analysed largely contained Northeast Atlantic species with the exception of Peruvian anchoveta, which was present in much lower read proportion compared to key Northeast Atlantic pelagics. Feed destined for trout grower, hatchery and nursery, as well as mixed hatchery and nursery, also displayed a wide range of species with a dominance of Northeast Atlantic species. Although occurring in low read count, Madeiran sardinella (*Sardinella maderensis*) and Pacific thread herring (*Opisthonema libertate*) were detected in trout grower feed (Figure 2), indicating possible imports from West African and Southwest American coastal States. The straddling stock of Madeiran sardinella, also known as flat sardinella, is showing a worrying decline (Braham et al. 2024). Its detection in feed, albeit exhibiting extremely low read numbers, warrants further investigation. The largest proportion of reads in reproduction feed was assigned to European pilchard (*Sardina pilchardus*) (Figure 2). Though this species is found across a large geographical area, the majority of its fisheries in Europe are reserved for human consumption (Silva et al. 2015), with some of the by-products from canneries being used by the FMFO industry. Recently, fleets in Morocco and Mauritania are fishing European pilchard extensively for the purpose of FMFO production and export a large portion of it to Europe, notably to Spain, France and Denmark (EUMOFA 2025). European pilchard exported from Morocco for aquafeed purposes is currently under scrutiny as the stock has declined sharply and large uncertainties remain around stock status and management (SFP 2025). Carp grower feed contained the lowest diversity of fish species, with blue whiting, Atlantic herring and capelin dominating the composition.

The observed difference in proportion of these key species is most likely a factor of the different supply chains providing FMFO for feed production and could reflect divergences in raw material quality needs. As visualised in a PCA plot (see Supporting Information for methodological details on ordination analyses), the types of ingredients used appear to vary with company, as well as targetted aquaculture species and life stages (feed type). Similar trends can be observed in the nMDS provided in the Supporting Information (Figure S3). The feed type however appears to be the main driver of feed composition and salmon grower, hatchery and nursery feed shows a strong relationship with the presence of pelagic fish species whereas carp, trout grower and reproduction feed display a wider range of ingredient sources including terrestrial and by-products (i.e., yellowfin and skipjack tuna trimmings) (Figure 3).

Terrestrial ingredients were composed of grains and animal byproducts, namely poultry for which a large number of reads were detected, but also swine and beef with lower read counts (Figure 4a–c). In general, and based on read proportion, mammal byproduct appeared higher in salmon feed, though it

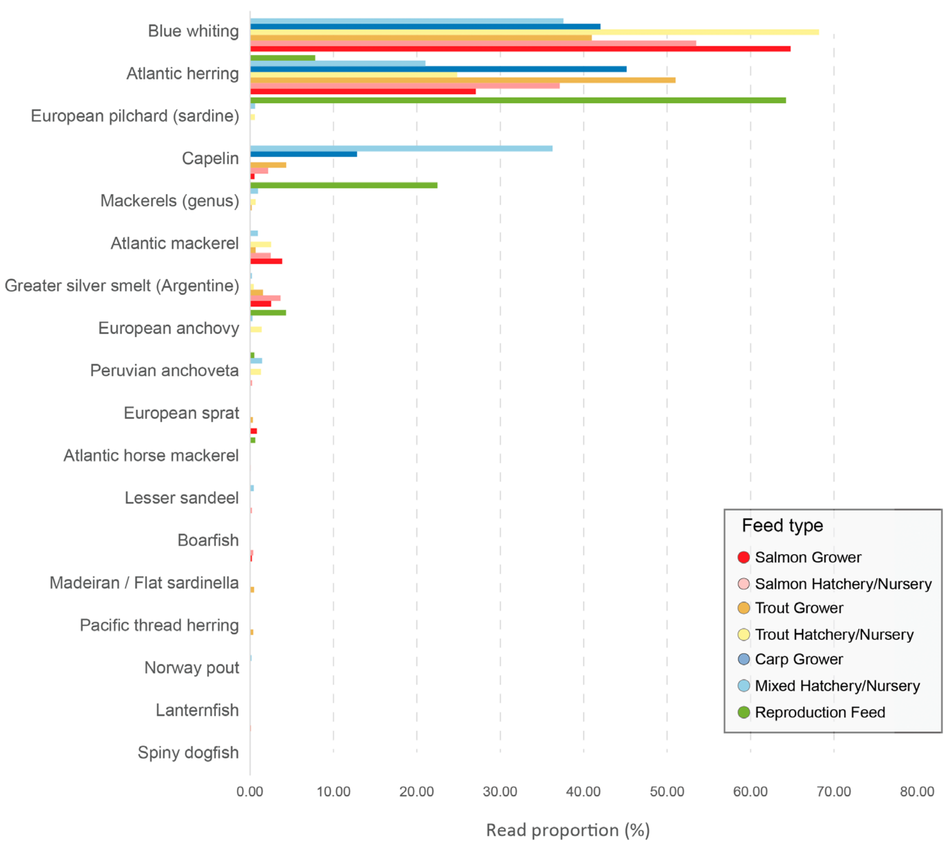

FIGURE 2 | Bar graph indicating the read proportion in percentage for the species most likely to be derived from whole fish.

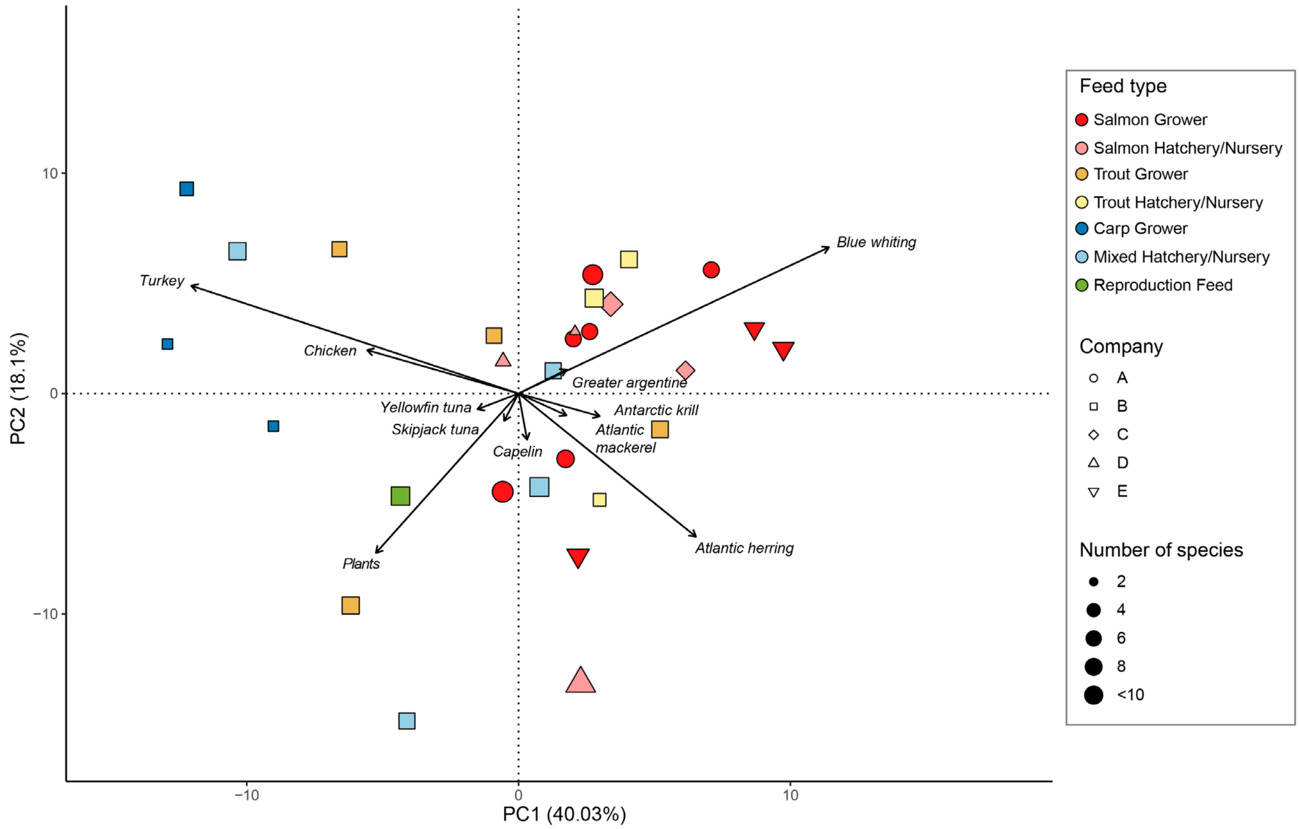

FIGURE 3 | Principal Component Analysis (PCA) showing the distribution of feed per feed type (including target species and life stage) and companies (A–E) based on the composition of feed ingredients as identified using metabarcoding. Points represent individual feed samples grouped and principal components explain 58% of the variation observed. Arrows show how variables contribute to the principal components with length indicating variable importance and direction indicating contribution to axes.

remained low compared to marine ingredients. In four of the samples, black soldier fly (*Hermetia illucens*) was detected as a component of the feed, supporting the growing importance of alternative sources for raw ingredients. These four samples belonged to a single company which openly advertises the use of black soldier fly meal on their website; the read numbers for the insect were low (< 5K), possibly indicating their limited contribution to overall feed composition. The presence of terrestrial ingredients in salmon feed reflects recent trends to decrease dependence on marine ingredients and brings into question the sustainability trade-offs between marine and terrestrial provenance of feed ingredients (Clawson et al. 2025; Kok et al. 2026).

4.3 | Possible Limitations and Improvements of Genetic Tools for FMFO Transparency

Like any method, DNA metabarcoding for FMFO has limitations and can be improved through robust proof-of-concept studies. At the moment, caution should be exercised when attempting to interpret eDNA read abundance data in a quantitative way, due to the known issue of primer bias with universal primers (Sickel et al. 2023). FMFO processing and refining may also degrade DNA, while crude or refined fish oil may contain PCR inhibitors (Zhao et al. 2025), or simply contain DNA in very low amount as observed with other processed oils (Vahdani et al. 2024). Furthermore, the lower the cut-off (in this case 0.1%) of total reads, the higher the chance of catching species that were not fished, for example the stomach content of whole fish, or trace DNA present in the processing plant and environment. This issue is particularly important as detecting species present in low quantities in FMFO can be highly relevant in terms of conservation and analysis of the supply chain. The presence of mould mites (*Tyrophagus putrescentiae*) in our samples appears to negatively affect read recovery (Figure S2) suggesting that sample quality and degradation level can significantly affect the results and return false negatives (i.e., species that are present but are not detected due to degraded DNA). Differences in raw material quality and FMFO output are common in this sector, as preservation methods, processing times, and transport conditions vary. Any study using DNA metabarcoding for species identification of FMFO or animal feed product will need to take these limitations in consideration and possibly run proof-of-concept studies before drawing hard conclusions from the results.

5 | Towards Transparency in the Aquafeed Industry

The aquaculture feed industry has recently come under increased scrutiny and skepticism over its ability to sustain itself without harming fishing resources and coastal communities. The limited public transparency on the composition of the feed is fueling this criticism. Calls for stronger transparency are rapidly emerging, pressing the sector into developing the necessary

FIGURE 4 | Sunburst plots illustrating the proportion of meal types (e.g., plant meal, fish meal, bird/feather meal, mammal by-product meal, insect meal, crustacean meal, etc.) for each feed type (based on target species and life stage) for (a) salmon feed (b) trout feed and (c) carp and mixed feed.

tools to document the origin of raw material (Hornborg and Langeland 2024).

In the majority of our samples randomly obtained across the UK, the bulk of the species detected were sourced from the Northeast Atlantic, and although the sustainability and efficacy of FMFO production in this region have recently been put into question despite a relatively high share of trimmings (Cottrell et al. 2025), the reliance on relatively local fish supplies may alleviate ethical concerns around the source of the product. In general, however, the high diversity of fish noted in our case study highlights the reliance of the industry on available raw products, but also its ability to adjust and diversify feed content. As demonstrated by this genetic analysis, the lack of adequate labels means that users of the feed and consumers of the fish raised on that feed, have very limited information about its composition. Based on our results, we argue that improved transparency could benefit rather than harm the sector. Integrity and ethical concerns are one of the most important drivers of consumer trust (Khamitov et al. 2024), and when confronted with concerning allegations on sourcing, a lack of transparency on product content undermines the sector's ability to respond adequately.

To address current societal concerns, improve trust and foster data driven discussions on the viability of a growing aquaculture sector, the industry should regularly disclose information on the species and origin of the raw material they use. Such information could be made publicly available in sustainability reports but should ideally be displayed on feed packages, allowing for full transparency behind any given feed. More standardised, structured and efficient traceability methods must be developed and adopted throughout the supply chain. Given the growing concerns around the sourcing of feed and the expected growth of the aquaculture industry, adequate traceability and improved transparency behind feed production are key elements that must be systematically adopted by the sector; and without progress on these fronts, consumer confidence may deteriorate.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Final feed pellet bag for salmon illustrating a typical list of ingredients where any information on the species or origin of the fish used to produce meal and oil included in the feed is lost. **Figure S2:** Read numbers of food grade material in aquafeed compared to read number of mould mites (*Tyrophagus putrescentiae*). **Figure S3:** Patterns of samples dissimilarities visualised through a non-metric multidimensional scaling (nMDS). **Table S1:** List of the species identified with a minimum cut-off of 0.1% of total reads and arranged by class with, for fish species, information on their most likely provenance originating from FishBase. **Data S1:** faf70080-sup-0002-Supinfo2.csv. **Data S2:** faf70080-sup-0003-Supinfo3.csv.