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REVIEW



Feed-food competition in global aquaculture: Current trends and prospects

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Abstract

Feed-food competition is the allocation of resources that can be used to feed humans to animal feed instead, a current but unsustainable practise not well documented for aquaculture. Here, we analysed feed-food competition in aquaculture using two measures; natural trophic levels (TLs) and species-specific human-edible protein conversion ratios (HePCRs). The HePCR equals the ratio of human edible protein in feed (input) to the human edible protein in animal produce (output). To provide prospects on aquaculture's potential to convert human inedible by-products into edible biomass, data on aquaculture production were collected and categorized based on natural TLs. HePCRs were computed for four aquaculture species produced in intensive aquaculture systems: Atlantic salmon, common carp, Nile tilapia and whiteleg shrimp. Under current feed use, we estimated that the carp, tilapia and shrimp considered were net contributors of protein by requiring ~0.6 kg of human edible protein to produce 1 kg of protein in the fillet/meat. Considering soya bean meal and fishmeal as food-competing ingredients increased the HePCR to \sim 2 and turned all of the casestudy species into net consumers of protein. To prevent this increase, the use of highquality food-competing ingredients such as fishmeal, or soya bean products should be minimized in aquaculture feed. In the future, the role of aquaculture in circular food systems will most likely consist of a balanced mix of species at different TLs and from different aquaculture systems, depending on the by-products available.

KEYWORDS

aquatic food, circular food system, feed efficiency, human edible feed, sustainable aquaculture, trophic level

1 | INTRODUCTION

Humanity is facing the challenge of feeding the world's growing population while staying within planetary environmental boundaries. As the current food system exceeds many planetary boundaries, a promising way forward is to build circular food systems. In which

feed-food competition. $^{1-3}$ In this paradigm, farm animals, including aquaculture species, should not consume human edible biomass but instead convert by-products from crops, livestock and fisheries that are inedible for humans, into edible biomass. In addition to these by-products, animals in circular food systems can also convert plant-

based food waste and grass resources into food.

biomass from arable land and water bodies is prioritized for human food and other basic needs rather than for animal feed, thus reducing

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To date, discussions of feed-food competition in aquaculture have largely addressed the use of fishmeal, and for a good reason: 9% of fisheries landings are transformed into fishmeal and fish oil,4 of which 90% can be considered food-grade.⁵ These studies often focused on the fish-in: fish-out ratio (FIFO) as an indicator for feed efficiency of aquaculture species. The FIFO differs greatly among species. For example, in 2009, salmon had a FIFO of around 5 and shrimp around 1.5.6 Over the years, the FIFO has decreased to around 0.3 for global aquaculture. An important reason for this decrease is that there is a growing trend to replace fishmeal with plant-based protein sources, such as soy protein concentrate.^{8,9} These replacement ingredients, however, also often cause feed-food competition because they can be used directly as food.^{8,9} In addition, plant-based ingredients, such as soya-bean-based ingredients, could influence feed-food competition indirectly by increasing land use for the production of animal feed instead of human food.

Nevertheless, fish and shellfish are rich in macronutrients (e.g., protein, fat) and micronutrients (e.g., calcium, iron, zinc, selenium; vitamins A, B and D; iron)^{10–12} and can be a valuable addition to a healthy diet even when consumed in small amounts.¹⁰ In fact, fish is the main source of essential omega-3 long-chain polyunsaturated fatty acids in human diets.¹³ Furthermore, farmed fish convert feed into food relatively efficiently.¹⁴ For example, Atlantic salmon has a feed conversion efficiency similar to that of chicken, and both are better than those of most other farmed animals.¹⁵ To determine the unique role of aquaculture in the transition towards healthy and circular food systems, more insight is needed into feed-food competition in global aquaculture.

One way to do so is to explore an animal's natural ability to upgrade specific by-products into food. This ability is determined by animal species, breed, and production-system intensity, and varies greatly among the more than 400 fish and shellfish species farmed in aquaculture. Here, we used the natural trophic level (TL) as an indicator of an animals' natural ability to upgrade specific by-products from human food. 9,15 Aguatic species at low TLs, such as primary producers (algae) and filter feeders (e.g., mussels, oysters) do not consume human edible biomass and therefore do not contribute to feed-food competition. Similarly, herbivorous species at low TLs have enzymes that can digest dietary fibres and other carbohydrates that humans cannot. Aquaculture species at higher TLs-omnivores and carnivores species-have diets that are more similar to those of humans and are well adapted to convert fish or other animal-based by-products into food. We therefore hypothesize that feed-food competition increases as the natural TL in aquaculture increases. To date, however, insight into the ability of individual aquaculture species from different natural TLs to convert by-products into food is lacking.

Another way to gain insight into feed-food competition is to use the HePCR to quantify the net contribution of farmed fish to the supply of human edible protein. The HePCR equals the ratio of human edible protein in feed (input) to the human edible protein in the animal product (output). Much quantification of HePCR has focused on livestock. In general, monogastric animals consume more protein than they produce (i.e., HePCR > 1) while grass-fed ruminants can produce

more protein than they consume (i.e., HePCR < 1). HePCRs are reported for a variety of animals in several countries, ¹⁶ including England (beef, lamb, pig, poultry ¹⁷), Austria (beef, veal, swine, chicken, turkey, sheep, goat ¹⁸) and Ireland (beef, pig ¹⁹), but have not been estimated for aquaculture species. In aquaculture, only the human ediblity of the feed has been estimated. Insights into the conversion efficiency of human edible feed protein into aquatic protein (i.e., quantifications of HePCR), however, are lacking.

Here, we analysed feed-food competition in aquaculture using both criteria: natural TLs and species-specific HePCR. We addressed the current status and trends in aquaculture production based on TLs and calculated HePCRs of current intensive aquaculture systems. The HePCRs were calculated for case studies of four key aquaculture species: Atlantic salmon, common carp (*Cyprinus carpio*), whiteleg shrimp (*Litopenaeus vannamei*) and Nile tilapia (*Oreochromis niloticus*).

2 | METHODS

2.1 | Global aquaculture production

To contextualize our findings about feed-food competition, we first reviewed generic data on aquaculture production by retrieving production (wet weight) and economic data (USD) at global and continental levels from FishstatJ.²⁰ To develop an overview of current aquaculture production (reference year 2019), we selected the 50 species produced most (in wet weight).²⁰

2.2 | Natural trophic levels

We first quantified the relative contribution of each TL to current global aquaculture production (in kg wet weight and edible protein), aggregated by species groups. To this end, we categorized production data of the 50 aquaculture species produced most by TL range. Each species' natural TL (1–5) was based on information from FishBase²¹ (Figure 1), shown to be a good data source for the trophic ecology of finfish.²² Because FishBase does not include data on molluscs or crustaceans, their natural TLs were extracted from the literature (refer to Tables A1 and A2 for details). If the TL of a species was unknown, that of a closely related species was assumed to apply. As primary producers, all seaweeds were assigned to TL 1.

Species were subsequently grouped by TL range based on the nine divisions of the International Standard Statistical Classification of Aquatic Animals and Plants²³: aquatic plants; freshwater fish; molluscs; crustaceans; diadromous fish; marine fish; miscellaneous aquatic animals; miscellaneous aquatic animal products; and whales; seals and other aquatic mammals.

We expressed the relative contribution of each TL range to current global aquaculture in terms of edible protein by multiplying each species' production volume (wet weight) by its edible yield and protein content. Edible yield was defined as fillet yield for finfish species and as meat yield for molluscs and crustaceans, as shells and exoskeletons were considered inedible. Because seaweeds have other uses besides food, we multiplied total seaweed production per species by the proportion used as human food, which was derived from Naylor et al. 24 Seaweed produced for food was assumed to be completely human edible. If the edible yield of a species was unknown, that of a closely related species was assumed (refer to Tables A1 and A2 for details).

The protein content of individual fish species was collected from the U.S. Department of Agriculture (USDA) database.²⁵ When data were not available from the USDA database,²⁵ they were obtained from FishBase,²¹ standard tables of food composition in Japan²⁶ or the literature (see Tables A1 and A2 for details). Protein contribution was based on raw fish, and cooking losses were not included.

We then quantified the trend in the mean TL of aquaculture production globally and by continent from 1980–2019. We collected

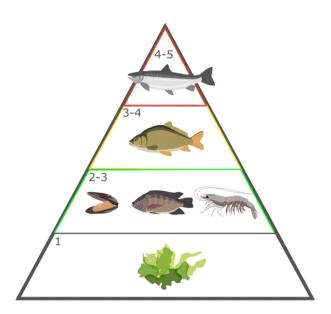


FIGURE 1 Overview of natural trophic levels of key aquaculture species. 4–5: Atlantic salmon, 3–4: common carp, 2–3: mussels, Nile tilapia, whiteleg shrimp, 1: Seaweeds.

data on annual production and the natural TL of the 25 species produced most (wet weight) globally and categorized them by continent. The method for collecting data on production, natural TL, and the grouping of species was the same as that used for analysing the global natural TL.

2.3 | Human edible protein conversion ratios

To embed HePCR results in the existing aquaculture literature, we also calculated the protein conversion ratio (PCR), as an indicator of feed efficiency.

2.3.1 | Case studies

To obtain an initial impression of feed-food competition in aquaculture at the species level, calculations were performed for four case-study species—three finfish (one from each natural TL) and one crustacean—chosen based on two criteria: having the highest economic value and being produced in intensive systems. Consequently, we selected: Atlantic salmon (TL 4–5), common carp (TL 3–4), Nile tilapia (TL 2–3) and whiteleg shrimp (TL 2–3).

2.3.2 | Data sources

PCR, HePCR $_{\rm e}$ and HePCR $_{\rm d}$ were calculated for each species (Box 1). For the ingredients in the diets, we focused on the grow-out phase. Diets for common carp, Nile tilapia and whiteleg shrimp were based on confidential surveys with five people active in the aquaculture feed industry. They were asked to estimate the feed composition for each species for intensive cultivation in 2020. The mean of the suggested diets was used as diet composition in this study (Table 1). The diet composition of Atlantic salmon was based on the feed used for Atlantic

BOX 1 Protein conversion ratio (PCR), human edible protein conversion ratio (HePCR_e) and human digestible protein conversion ratio (HePCR_d) adapted from Laisse et al.²⁷ and Mottet et al.¹⁶

$$\begin{aligned} &\textbf{1.} \quad \textbf{PCR} = \frac{Protein in feed}{Human \ edible \ protein \ in \ fillet/meat} = FCR \times \frac{\sum\limits_{j=1}^{n} Feed_{j} \times PC_{j}}{CP_{j} \times HE_{j}} \\ &\textbf{2.} \quad \textbf{HePCR}_{\textbf{e}} = \frac{Human \ edible \ protein \ in \ feed}{Human \ edible \ protein \ in \ fillet/meat} = FCR \times \frac{\sum\limits_{j=1}^{n} Feed_{j} \times CP_{j} \times HE_{j}}{CP_{i} \times HE_{j}} \\ &\textbf{3.} \quad \textbf{HePCR}_{\textbf{d}} = \frac{Human \ digestible \ protein \ in \ fillet/meat}{Human \ digestible \ protein \ in \ fillet/meat} = FCR \times \frac{\sum\limits_{j=1}^{n} Feed_{j} \times CP_{j} \times HE_{j}}{CP_{i} \times HE_{j} \times DIAAS_{j}} \\ &\textbf{3.} \quad \textbf{HePCR}_{\textbf{d}} = \frac{Human \ digestible \ protein \ in \ fillet/meat}{Human \ digestible \ protein \ in \ fillet/meat} = FCR \times \frac{\sum\limits_{j=1}^{n} Feed_{j} \times CP_{j} \times HE_{j} \times DIAAS_{j}}{CP_{i} \times HE_{i} \times DIAAS_{j}} \end{aligned}$$

where *i* the aquaculture species considered, *j* the ingredients of the diets consumed by the animal. FCR is the feed conversion ratio of the animal, Feed the proportion of the feed that is ingredient (*j*), CP is the crude protein content (%), HE the human edibility and DIAAS the digestible indispensable amino acid score (%).

TABLE 1 Mean ingredient composition of the diets of the four selected aquaculture species.

	Diet composition (%)							
Ingredient	Atlantic salmon ^a	Common carp ^b	Whiteleg shrimp ^b	Nile tilapia ^b				
Animal-based ingredients								
Blood meal	-	-	-	1.4				
Feather meal	-	-	1.1	3.0				
Fish meal	12.1	1.7	12.0	1.0				
Krill meal	-	-	2.0	-				
Meat and bone meal	-	9.0	-	6.4				
Poultry meal	-	8.3	9.3	8.0				
Plant-based ingredients								
Cassava meal	-	3.3	-	8.0				
Corn bran	-	-	-	0.2				
Corn gluten meal	0.7	-	1.5	1.2				
Corn meal	-	5.0	-	4.4				
Distillers grains	-	6.0	-	0.9				
Faba beans	3.6	-	-	-				
Guar protein	4.3	-	-	-				
Pea flower	2.5	-	-	-				
Pea protein concentrate	1.4	-	-	-				
Rapeseed meal	-	3.3	-	-				
Rice bran	-	15.7	3.8	8.2				
Soy lecithin	-	-	1.1	-				
Soy protein concentrate	20.9	-	2.3	-				
Soya bean meal	-	28.3	31.3	27.8				
Sunflower meal	3.4	-	-	-				
Wheat gluten meal	9.8	-	2.0	-				
Wheat meal	-	3.3	5.0	17.8				
Wheat bran	-	7.3	2.8	5.0				
Wheat flour	6.5	-	18.8	1.4				
Other (e.g., oils, vitamins, minerals, other additives)	34.6	8.7	7.3	5.3				

Note: Only ingredients included as protein sources were considered. The diets selected were assumed to reflect commercial diets.

salmon aquaculture in Norway in 2020.²⁸ The assumed range in feed conversion ratio (FCR) of each species was based on FCRs found for these species for intensive production systems in the literature (Table 3). The crude protein content of diet ingredients was calculated based on the International Aquaculture Feed Formulation database³⁶ (Table 2). The human edibility of each feed ingredient was defined as either food-competing (1 in Equation 2,3) or non-food-competing (0 in Equation 2,3) based on Sandström et al.⁹ and Mottet et al.¹⁶ (Table 2). Both studies reported the same human edibility for most ingredients, except for soya bean meal and fishmeal. Sandström et al.⁹ considered fishmeal made from whole fish food-competing but fishmeal made from fish by-products non-food-competing, while Mottet et al.¹⁶ considered all fishmeal non-food-competing. Furthermore, while soy protein concentrate is food-competing, soya bean meal is considered non-food-competing.

competing because it is a by-product of soya bean oil production, and the meal is used almost entirely as a feed ingredient. However, soya bean differs from all other ingredients in that its by-product (soya bean meal) is the primary driver of soya bean production. As a result, soya bean meal can be considered an indirect competitor to human food, ¹⁶ which Mottet et al. ¹⁶ did, but Sandstrom et al. ⁹ did not. To capture these differences, we created two scenarios, in which soya bean meal and fishmeal were considered (1) non-food-competing or (2) food-competing. For fishmeal, we used a human edibility of 0.66 instead of 1 to represent that 27% of fishmeal is made up of by-products (non-food) and that 90% of the whole fish used to create fishmeal can be considered food grade. ⁵ For the human edibility of the output of the species, we focused on the current habits of eating primarily fillets. To represent protein quality, we included the digestible indispensable amino acid score (DIAAS) for the selected fish

^aAas et al.²⁸

bMean ingredient inclusion based on confidential surveys. Number of diets included for common carp: 3, whiteleg shrimp: 4 and Nile tilapia: 5.

species and the feed ingredients (Table 2). The Food and Agriculture Organization of the United Nations (FAO) recommends the DIAAS⁴¹ as a measure of protein quality. The DIAAS reflects the content of the first limiting indispensable amino acid in a feed/food ingredient relative to the requirement for the same amino acid by humans.⁴¹ We used the amino acid requirement pattern for a 6-month to 3-year-old child as the reference protein's amino acid profile, similar to studies by Laisse et al.⁴² and Ertl et al.,³⁹ and as recommended by the FAO.⁴¹ The DIAASs of feed ingredients were extracted from Ertl et al.³⁹ or, if not included by them, estimated using their method.³⁷ Due to a lack of data on the human ileal amino acid digestibility of fish fillets, the DIAASs of the case-study species were calculated based on amino acid scores from the USDA,²⁵ assuming an amino acid digestibility of 94% for fillets/meat.⁴¹

3 | RESULTS

3.1 | Global aquaculture production

Volumes of global aquaculture productions are increasing, driven by the growth of the sector in Asia. In 2019, global aquaculture (including seaweed and algae) reached a total production of 97 M ton (wet weight), an ~50% increase compared to that of 10 years previously (62 M in 2009). The contribution to global production, however, differed considerably among continents: Asia dominated (90%, with 60% of the total from China alone) followed by the Americas (4%), Europe (3%), Africa (2%) and Oceania (0.2%). Africa showed the highest growth over the previous 10 years (130%); its growth >2.5 times the growth of China. Interestingly, the continent (Asia) and country (China) that produced the largest volume, had the lowest economic values, while the continents with the lowest volumes (Oceania, Europe and the Americas) have the highest economic values.

3.2 | Trophic levels

The contribution of each aquaculture species groups to global aquaculture production in 2019 varied (Figure 2).

In 2019, TL 2–3 produced the most wet weight (59%) and edible protein (60%). Although dominated by freshwater fish and molluscs, it was the TL range with the greatest diversity of species groups produced. In general, aquaculture species at lower TL (TL 1–3) contributed less to global protein production than to global aquaculture wet-weight volumes. For aquatic plants, this is due to their high water and low protein content whereas fish from low TLs have lower edible yields than at higher TLs.

Globally, over the past 40 years, the mean natural TL of aquaculture species increased slightly (Figure 3a), but it differed greatly among regions, especially China and Europe. In Europe, it increased due to the large increase in production of diadromous fish (especially Atlantic salmon) over the past 35 years. Since 2002, Europe was also the continent with the highest mean TL (Figure 3a,b). In contrast, the mean TL of aquaculture species in Asia/China

remained relatively low and stable over the past 30 years (1985–2015) due to higher growth of production of freshwater fish, molluscs and aquatic plants than that of other species groups (Figure 3c).

3.3 | Human edibility of fish diets

In scenario 1 (soya bean meal and fishmeal non-competing), Atlantic salmon had the highest percentage of food-competing ingredients in the diet (45%) (Figure 4a) because soy protein concentrate was the primary protein source. Common carp, whiteleg shrimp and Nile

TABLE 2 Plant and animal ingredients crude protein content and digestible indispensable amino acid scores (DIAAS).

Product	Protein content (%) ^a	DIAAS
Food-competing ingredients + s	soya bean meal + fishmeal	
Animal-based ingredients		
Fish meal	65	67 ^b
Plant-based ingredients		
Cassava meal	3	17 ^c
Corn meal	8	42 ^d
Faba beans	26	61 ^b
Pea flower	16	63 ^e
Pea protein concentrate	54	67 ^f
Soy protein concentrate	65	115 ^b
Soya bean meal	47	97 ^d
Sunflower meal	30	47 ^d
Wheat meal	17	40 ^d
Wheat flour	13	40 ^d
Non-food-competing feedstuff		
Animal-based ingredients		
Blood meal	86	-
Feather meal	81	-
Krill meal	58	-
Meat and bone meal	37	-
Poultry by-product meal	60	-
Plant-based ingredients		
Corn bran	9	-
Corn gluten meal	68	-
Distillers grains	45	-
Guar protein	65	-
Rapeseed meal	35	-
Rice bran	13	-
Wheat gluten meal	78	-
Wheat bran	15	-

aUSDA.25

bINRA.37

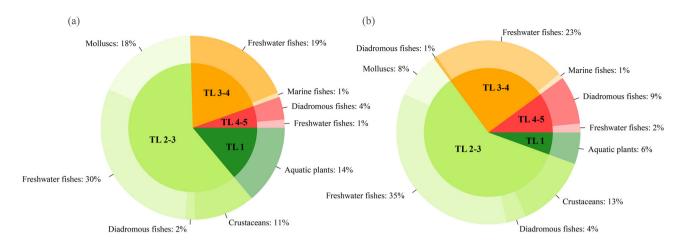
^cDe Vries-Ten Have et al.³⁸

dErtl et al.39

 $^{^{}m e}$ Amino acid profile from IAFFD $^{
m 36}$ and protein digestibility from INRA. $^{
m 37}$ $^{
m f}$ Adapted from Mathai et al. $^{
m 40}$

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Global aquaculture production in 2019 per trophic level (TL) expressed as (a) wet weight or (b) edible protein. FIGURE 2

tilapia had a lower percentage of food-competing ingredients in their diets (3%, 12% and 12%, respectively), with wheat products providing most edible protein (Figure 4a).

In scenario 2 (soya bean meal and fishmeal food-competing), the percentage of human edible protein increased for all diets, ranging from 49% to 65% (Figure 4b), because soya bean meal was the main protein source in the diets of common carp, whiteleg shrimp and Nile tilapia and fishmeal was included in the diets of Atlantic salmon and whiteleg shrimp. Atlantic salmon and whiteleg shrimp had the highest percentages of food-competing ingredients in their diets (59% and 65%, respectively). Ingredients included in the aquaculture diets in relatively large percentages that were not food-competing included livestock by-products, gluten meals and cereal bran.

3.4 **Conversion ratios**

The PCR ranged from 3.4 to 8.7 for the case-study species (Table 3). Atlantic salmon converted protein the most efficiently, followed by whiteleg shrimp and then common carp and Nile tilapia, both of which had similar PCRs. Differences in PCR among species were caused by differences in the FCR, edible yield and protein content of the feed. Compared to the other species, Atlantic Salmon had the lowest FCR and highest fillet/meat yield.

In scenario 1, Atlantic salmon was the only species with an HePCR_e greater than 1 (range: 1.5-2.0; Figure 5a) and thus consumed more human edible protein than it produced. The HePCR_e of the other species lay below 1 (range: 0.2-1.0), implying that they produced more human-edible protein than they consumed. Values of HePCR_d, which considers protein digestibility, were lower than those of HePCR_e due to the relatively higher quality of fillet protein than feed protein (Figure 5).

In scenario 2, all four species were net consumers of protein: HePCR_e increased to 2.0-4.6 (Figure 5a), while the HePCR_d increased to 1.7-3.5 (Figure 5b). The range of HePCR_{e/d} of Atlantic salmon including or excluding soya bean meal and fishmeal overlapped,

indicating smaller changes in the human edibility of protein in salmon diets compared to those of other species.

DISCUSSION

Given the diversity of aquaculture species, the present study was intended as a starting point for exploring and analysing feed-food competition for additional species, systems and locations.

4.1 **Synthesis**

We worked from the assumption that aquaculture offers great potential to produce food while avoiding feed-food competition. We used natural TLs as a starting point to analyse feed-food competition, as the natural ability of an animal to upgrade specific by-products into food can determine its role in a circular food system. In both Europe and the Americas, Atlantic salmon was the species at a high TL (TL 4-5), whose production was largest and grew the most rapidly, which drove the increase in average produced natural TL. Feeding compound feeds has generally resulted in aquaculture diets with an effective TL lower than that of natural diets (natural TL).43 This decrease may appear positive if assuming that diets at lower TLs generally cause less feed-food competition because they include more plant-based ingredients and less fishmeal. However, when fishmeal is replaced by soy protein concentrate, as for salmon, the positive impact on feed-food competition is not apparent because soy protein concentrate is human edible and has higher protein quality (i.e., a higher DIAAS) than fishmeal. As a result, species at a naturally high TL, such as salmon, continue to receive relatively higher quality (plantbased) ingredients, resulting in highly human edible diets.

When investigating feed-food competition in the present study, classifying soya bean meal and fishmeal as either foodcompeting or non-food-competing ingredients had large influence on the net contribution to protein supply of the four aquaculture

FIGURE 3 Mean trophic level (TL) of aquaculture production by continent, with China separate from Asia and development of species groups in Europe and China (a) Mean trophic level of aquaculture production by continent and globally. (b) Development of species groups in Europe. (c) Development of species groups in China.

species. When we considered them as human-edible, not only did species at a high trophic (i.e., salmon) appear as net consumers of protein, but so did species at a lower TL, (i.e., common carp, whiteleg shrimp and Nile tilapia). Soya bean meal is the ingredient used most in aquaculture compound feeds.⁸ Although soya bean meal itself is considered inedible, ^{9,16} its production is the main

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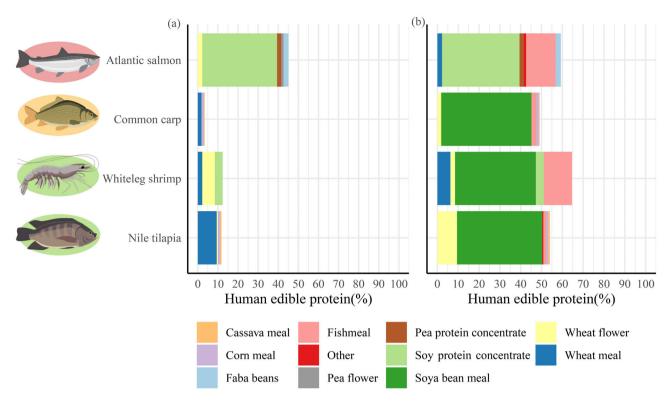


FIGURE 4 Human-edible protein ingredients as percentage of the total protein of the diets for the selected species. (a) Scenario 1 (fish meal and soya bean meal are non-food-competing ingredients) and (b) Scenario 2 (fish meal and soya bean meal are food-competing ingredients).

TABLE 3 Feed conversion ratios (FCR), fillet/meat yield, protein contents and crude protein conversion ratio (PCR) for the four case-study species from literature and the present study.

	Literature		Present study Protein content (%)		
Species	FCR	Fillet/meat yield	Fillet/meat	Feed	PCR
Atlantic salmon	1.1-1.4 ^a	56 ^e	21.4 ^h	36.7	3.4-4.4
Common carp	1.5-1.8 ^b	45 ^e	17.8 ^h	30.9	6.0-7.1
Whiteleg shrimp	1.2-2 ^c	52 ^f	20.4 ^h	38.1	4.0-6.7
Nile tilapia	1.3-2.0 ^d	37 ^g	20.1 ^h	32.1	5.6-8.7

^aBalseiro et al.²⁹ and Aas et al.²⁸

driver of land use. 16 Soya bean meal causes indirect feed-food competition, as the land used to produce soya bean meal could have been used to grow food crops for direct human consumption.44 Although fishmeal does not require land its production can lead to overfishing and of greenhouse gas emissions. 45 Replacing soya bean meal in aquaculture feeds would reduce feed-food competition in aquaculture drastically.

When soya bean meal and fishmeal were considered foodcompeting, Nile tilapia, which has a low TL, had the highest HePCR, while Atlantic salmon, which has a high TL, had the lowest HePCR. This may seem surprising, because Atlantic salmon and whiteleg shrimp had the highest percentage of human-edible protein in their feed. However, the low HePCR of Atlantic salmon can be explained by its relatively high growth rate and feed efficiency,

^bSuprayudi et al.³⁰

^cCao et al.³¹

^dWatanabe et al.³²

^eMalcorps et al.³³

fKim et al.34

^gRutten et al.³⁵

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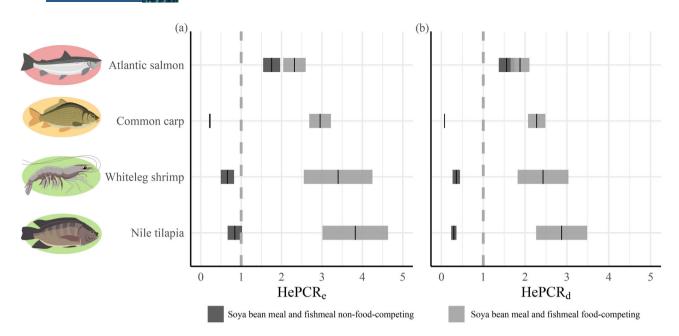


FIGURE 5 Human-edible protein conversion ratio (HePCRe) and human digestible protein conversion ratio (HePCRd) for selected aquaculture species in intensive production systems. (a) Human-edible protein feed and fillet/meat protein and (b) human digestible protein feed and fillet/meat digestible protein. Vertical lines indicate means, and bars indicate a range related to variability in the feed conversion ratio. Values less than 1 indicate net production of protein, while values greater than 1 indicate net consumption of protein.

due, among other things, to years of selective breeding. ⁴⁶ In addition, when kept in intensive systems, species at a naturally low TL such as Nile tilapia are often fed high-quality protein (e.g., soya bean meal) to increase growth rates and decrease FCR. Thus, intensive aquaculture systems do not optimally align with the natural ability of species at a low TLs to upgrade lower quality by-products or natural biomass. For these species, extensive systems as well as ecological intensification, for example, nutritious ponds, are better suited.

4.2 | Feed-food competition in aquaculture compared to livestock

Compared to livestock, absolute feed-food competition in aquaculture is relatively small, because aquaculture represents for only a small percentage (\sim 1.2%) of global feed consumption, compared to that of cattle (73%), pigs (20%) and poultry (7%). Looking only at global human-edible feed consumption, however, aquaculture represents a larger percentage (3.8%), likely related to the relatively high protein requirements of fed aquaculture species. Overall, most gain to reduce feed-food competition is to be made with livestock.

Directly comparing the HePCR of livestock and aquaculture is hampered by differences in metabolism and housing. The most logical comparison with monogastric species, such as poultry and pigs. When their HePCR ratios are compared, broilers (HePCR $_{\rm e}\sim5.2$) and industrially produced pigs (HePCR $_{\rm e}\sim4.5$) have higher HePCRs than the aquaculture species examined (HePCR $_{\rm e}$: 0.2–2). 16

4.3 | Limitations of this study

We attempted to approach feed-food competition scenarios in aquaculture using all available information and objective criteria, but improvements are always possible. First, information on complete feed formulation in this study was obtained for three of the four selected species by confidential surveys of people in the aquaculture feed industry. Feed formulation, however, changes constantly and differs by region. We mitigated the influence of this uncertainty by developing a mean diet formulation per species based on multiple diets representative of the same period. However, still some bias for a specific region could be present and the diets used may not completely reflect global practise. Assessing diets by region and over time lay beyond the scope of this study, but doing so would provide valuable knowledge in the transition towards circular food systems. Second, the feed quantity and growth rate were not always available for each life stage of the aquaculture species selected, thus FCR could not be estimated for each life stage. Consequently, we estimated HePCR for the grow-out phase only. As this phase has most influence on HePCR (i.e., most compound feed is consumed during it), including other phases seems unlikely to influence our conclusions. Third, we considered only protein efficiency in this study; however, because fish have a high-fat content, investigating the efficiency with which aquaculture species upgrade lipids could be a valuable next step. Overall, as an initial estimate of feed-food competition, we included multiple feeds and FCR per species, which provide a range for the HePCR. Future studies could focus on the entire life cycle of one specific system and species, as HePCR depends on the animal, its feed and efficiency and, to the definition of human edible products. 17,27,42 These types of studies could provide more detailed estimates of

feed-food competition in aquaculture; nevertheless, more data should be available for these studies.

Another limitation of this study was related to its scope, as we focused only on intensive systems to the enable comparison of HePCRs between species at low versus high TLs and between aquaculture and livestock. Most aquaculture species, however, are produced in extensive or semi-intensive systems, especially finfish species at a low TL, in which they can obtain (some of) their nutritional requirements from the natural environment. As the efficiency of converting by-products is affected by species as well as production systems, ⁴⁷ we need to analyse comparative case studies of specific species and production systems. In other words, we need to compare HePCRs of the same species produced in different systems and at different intensities.

4.4 | Implications of this study for future-food systems

Animals can play an important role in circular food systems by upgrading by-products; therefore, the transition towards circular systems should emphasize minimizing feed-food competition, 48,49 for both livestock and aquaculture. To ensure a net contribution of aquaculture to food security, focus should be placed not only on feed efficiency metrics, such as FCR, but also HePCR. For example, the present study, showed that Atlantic salmon, despite having a relatively low FCR, consume more protein than they produce (HePCR > 1), indicating the importance of HePCR.

In recent years, an increasing number of animal and plant-based by-products have been used as aquaculture feeds. ^{50,51} For example, according to recent estimates livestock by-products and fishmeal from fish by-products could replace 99% of the fishmeal made from whole fish. ⁹ Besides using by-products, the literature also suggests using novel protein sources to replace fishmeal, such as insects, algae and yeasts; however, the global potential to replace fishmeal with these sources, remains unclear. ⁵² Moreover, novel protein sources that cause feed-food competition should not be incorporated into aquaculture feeds. For example, if insects are used as fish feed they should not be fed with by-products that can be fed to the fish directly, such as slaughter waste, but rather alternative biomass streams, such as manure. A combination of novel protein sources and by-products could replace current food-competing ingredients.

To further encourage the feed industry to develop and apply innovations to increase by-product use, ¹¹ the government could develop targets for the inclusion of by-products in aquatic feeds for feeding companies or tax the use of food-grade feed materials. ⁹ Alternatively, certification schemes such as the Aquaculture Stewardship Council, Best Aquaculture Practices and SafeFeed/Safe Food (SF/SF) Certification Program, ⁴³ could include targets for the inclusion of by-products in aquatic feed. To monitor the efficacy of these policies or certification schemes, we are in need of indicators of feed-food competition, ⁵³ such as HePCR.

A final strategy to optimize the role of aquaculture in the food system is to increase the edible yield of harvested species. If humans would consume not only fillets but also all edible parts (Table S2), the HePCR $_{\rm e/d}$ would decrease by 27% for Atlantic salmon, 37% for common carp, 21% for whiteleg shrimp, and 35% for Nile tilapia. Consuming a larger fraction of the fish therefore has an environmental benefit, as it allows for a better use of all raw materials and primary resources (lands, freshwater, energy) used through the life cycle of the fish.

The role of aquaculture in circular food systems will most likely consist of a balanced mix of species at different TLs and from different aquaculture systems, depending on the by-products available. Species at high TLs are specifically adapted to use highquality by-products from animal-based food, such as fisheries and livestock by-products, while those at lower TLs could be fed plantbased by-products or be produced in non-fed aquaculture systems. If aquaculture species are fed mainly by-products, however, the availability and quality of these by-products would determine new boundaries for production and consumption. Hence, the consumption of aquatic species will no longer be determined by the demand, but by the amount of aquatic food that can be produced from by-products. Therefore, shifting towards circular food systems, requires changing not only production systems but also consumption patterns, especially in high-income countries. Diets should gradually contain more plant-based products and fewer animal-based products.² Combinations of socio-economic and institutional measures,² education and promotion of circular thinking, but also reduction of taxes for circular products⁵⁴ could all help achieve the change towards more circular food production.

5 | CONCLUSIONS

The mean natural TL in global aquaculture production has increased over time. If this trend continues, feed-food competition may also increase assuming that aquaculture feed at a higher TL contains more human edible ingredients. When considering only ingredients directly edible by the diet of the species at the highest TL, Atlantic salmon, had by far the highest human edibility. Nevertheless, in this scenario, less than 50% of each of the diets was human edible, and common carp, whiteleg shrimp and Nile tilapia were net producers of protein. When soya bean meal and fishmeal were also considered food competing ingredients, the percentage of human edibility increased substantially for all diets except that of Atlantic salmon, and all species were net consumers of protein. Because soya bean meal is the feed ingredient most used in aquaculture, replacing it with non-food-competing protein sources is an important step towards reducing feed-food competition in aquaculture and towards circularity. The role of aquaculture in circular food systems will most likely consist of a balanced mix of species at different TLs and from different aquaculture systems, depending on the by-products available. As the natural TL is not the only factor that influences feed-food competition, future research should focus on including more species (e.g., diets, FCRs) and systems (e.g., intensities).

AUTHOR CONTRIBUTIONS

Anne-Jo Riel, van: Conceptualization; data curation; formal analysis; methodology; visualization; writing – original draft. Marit Aleida Jantien Nederlof: Conceptualization; supervision; writing – review and editing. Killian Chary: Conceptualization; supervision; writing – review and editing. Geert Frits Wiegertjes: Conceptualization; supervision; writing – review and editing. I. J. M. de Boer: Conceptualization; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX

TABLE A1 Protein content (%), edible yield(%) and trophic level of the 50 aquaculture species most produced globally in 2019.

Species	Description	Value	References
Japanese kelp	Protein	1.5-2.9	55,56
	Edible yield	100	a
	Trophic level	1	b
Grass carp(=White amur)	Protein	15.2-20	57,58
	Edible yield	36-54	59
	Trophic level	2	21
Whiteleg shrimp	Protein	18.8-21.4	25
	Edible yield	52	34
	Trophic level	2.5	60
Cupped oysters nei	Protein	5-10	25
	Edible yield	6-18	61
	Trophic level	2	С
Silver carp	Protein	16.1-17.2	57
·	Edible yield	34-39	62
	Trophic level	2	21
Nile tilapia	Protein	18.1-26.1	25,58,63
	Edible yield	31-45	64,65
	Trophic level	2	21
Common carp	Protein	17.5-18	25,63
Common carp	Edible yield	36-54	61
		3.1	21
lanamasa samast akali	Trophic level		
Japanese carpet shell	Protein	6.1-14.9	26
	Edible yield	35-40	26 c
0.11	Trophic level	2	
Catla	Protein	14.9	58
	Edible yield	32.2-33.7	66
	Trophic level	2.8	21
Bighead carp	Protein	24.3	67
	Edible yield	30.2-32.9	68
	Trophic level	2.8	21
[Carassius spp]	Protein	19.9	69
	Edible yield	42.8	70
	Trophic level	3.1	21
Striped catfish	Protein	12.6-18	25,63,71,7
	Edible yield	50.4	73
	Trophic level	3.1	21
Atlantic salmon	Protein	19.9-25.4	25,63
	Edible yield	62.5-65	63,74
		4.5	21
Wakame	Protein	1.9-2.7	26,56,75
	Edible yield	100	a
	Trophic level	1	b
Freshwater fish nei	Protein	17.5	d
	Edible yield	39.5	d
	Trophic level	3.1	21

TABLE A1 (Continued)

ABEL A1 (Continued)			
Species	Description	Value	Reference
Red swamp crawfish	Protein	7.4-8	76
	Edible yield	20.4-20.9	76
	Trophic level	2.5	77
Nori nei	Protein	1.2-4.5	26
	Edible yield	100	а
	Trophic level	1	b
Roho labeo	Protein	19.7	78
	Edible yield	35.6-36.2	66
	Trophic level	2.2	21
Scallops nei	Protein	13.5	26
	Edible yield	50	26
	Trophic level	2	c
Milkfish	Protein	20.5-21.1	25,61
ministr	Edible yield	61	61
	Trophic level	2.4	21
Torpedo-shaped catfish nei	Protein	18.2	79
Torpedo-snaped Catristi nei	Edible yield		
	,	38.9-46.7 3.5	79
Marine molluscs nei/Sea mussels nei	Trophic level		21
Marine moliuscs nei/Sea musseis nei	Protein	11.2	61
	Edible yield	24	61 c
	Trophic level	2	
Tilapias nei	Protein	17.6	61
	Edible yield	37	61
	Trophic level	2	21
Rainbow trout	Protein	19.9	25
	Edible yield	56-65	80
	Trophic level	4.1	21
Constricted tagelus	Protein	8.1	26
	Edible yield	65	26
	Trophic level	2.5	21
Laver (Nori)	Protein	4.8-5.1	81
	Edible yield	100	a
	Trophic level	1	b
Chinese mitten crab	Protein	18.9	82
	Edible yield	24.2	82
	Trophic level	2.5	83
Giant tiger prawn	Protein	15.9-25.8	25
	Edible yield	52	e
	Trophic level	2.5	e
Wuchang bream	Protein	17.9-18.3	84
-	Edible yield	36	61
	Trophic level	3.4	21
Marine fish nei	Protein	17.5	f
	Edible yield	39.5	f
	Trophic level	3.5	21
	Tropfile level	0.5	21

TABLE A1 (Continued)

Species	Description	Value	References
Black carp	Protein	16.5	85
	Edible yield	30.6	68
	Trophic level	3.2	21
Cyprinids nei	Protein	17.5	61
	Edible yield	54	61
	Trophic level	2.8	21
Pacific cupped oyster	Protein	8.5	61
	Edible yield	10	61
	Trophic level	2	С
Yellow catfish	Protein	12	86
	Edible yield	42-57	g
	Trophic level	3.5	21
Pangas catfish nei	Protein	14.7	25,63,71,72
· ·	Edible yield	50.4	73
	Trophic level	3.1	21
Mrigal carp	Protein	19.9	78
	Edible yield	37.6-39.3	66
	Trophic level	2.4	21
Largemouth black bass	Protein	15.7	87
Zangerneuth, stadit saud	Edible yield	34-35	88
	Trophic level	3.8	21
Blood cockle	Protein	12.5-13.9	26
BIOGG COCKIC	Edible yield	40	26
	Trophic level	2	с
Snakehead	Protein	17.7	89
Shakeread	Edible yield	30-37	89
	Trophic level	4.4	21
Channel catfish	Protein	15.2	25
Channel Cathon	Edible yield	42-57	90
	Trophic level	4.2	21
Silver barb	Protein		
Sliver Darb		18.4	58
	Edible yield	50.1 2.4	91 21
Disco NPIs (Plants Is Is all d	Trophic level		21 h
Blue-Nile tilapia hybrid	Protein	18.1-26.1	h
	Edible yield	31-45	
	Trophic level	2	21
Chilean mussel	Protein	8.3-14.1	25
	Edible yield	40	26
	Trophic level	2	
Amur catfish	Protein	15.8	92
	Edible yield	36-50	90
	Trophic level	4.4	21
Pond loach	Protein	16.1-17	93
	Edible yield	100	26
	Trophic level	3.2	21

(Continues)

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TABLE A1 (Continued)

Species	Description	Value	References
Asian swamp eel	Protein	17.8	21
	Edible yield	60	i
	Trophic level	2.9	21
Fusiform sargassum	Protein	1.4-2	94
	Edible yield	100	а
	Trophic level	1	b
Giant river prawn	Protein	17.4-18.5	95
	Edible yield	26.1-42.1	95,96
	Trophic level	2.55	97
Japanese eel	Protein (g/100 g)	19.6	21
	Edible yield (%)	60	i
	Trophic level	3.6	21

Note: References include letters that indicate the assumptions made.

TABLE A2 Protein content and edible yields of fillet and by-product fractions for the four selected species.

		Fillet	Heads	Frames	Trimmings	Skin	Viscera	Shell	Tail	Total edible yield (%)
Atlantic Salmon ^a	(%) of whole body	56	10	10	8	5	11	-	-	
	Edible yield (%)	100	37	57	81	100	0	-	-	77
	Protein (%)	21	17	19	18	23	12	-	-	
Common carp ^a	(%) of whole body	43	17	9	8	9	14	-	-	
	Edible yield (%)	100	44	90	46	100	0	-	-	72
	Protein (%)	18	13	17	15	19	11	-	-	
Whiteleg shrimp ^{b,c}	(%) of whole body	56	34	-	-	-	-	8	3	
	Edible yield (%)	100	100	-	-	-	-	100	100	100
	Protein (%)	20	7	-	-	-	-	8	8	
Nile tilapia ^{d,e}	(%) of whole body	37	25	13	12	6	6	-	-	
	Edible yield (%)	100	44	90	46	100	0	-	-	71
	Protein (%)	20	13	17	15	19	6	-	-	

^aMalcorps.³³

^aEdible yield of seaweeds was assumed to be 100%.

^bTrophic level of seaweeds is 1 as primary producers.

 $^{^{\}rm c}\text{Trophic}$ levels of mussels was assumed to be 2 as herbivorous filter feeders.

^dAverage freshwater fish.

^eAssumed same as whiteleg shrimp.

^fAssumed average marine fish.

^gAssumed same as channel catfish.

^hAssumed same as Nile tilapia.

ⁱAssumed same as European eel.

bKim.34

cLui.98

^dSuliemani.⁹⁹

eEdible yield (%) and the protein (%) of heads, frames, trimmings, and skin was assumed the same as Common carp.