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Original Research Article

Impact of krill (*Euphausia superba*) meal on growth performance of aquatic animals: A meta-analysis and prospective directions

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A B S T R A C T

Antarctic krill meal (KM) (*Euphausia superba*) as a substitute for fishmeal in aquatic animal diets is gaining popularity worldwide. A quantitative approach investigating the efficacy of using this protein on the production performance of aquatic animals remains widely limited. Here, we employed a meta-analysis to quantify the overall effects (Hedges'g [*g*] value effect size) of KM on the specific growth rate (SGR), feed conversion ratio (FCR), protein efficiency ratio (PER), and survival rate (SR) of several aquaculture species. A total of 22 records published during 2006 to 2022 from different countries, targeting 14 aquatic species, were employed in the present study. Overall, KM has a high nutritional value relative to fishmeal, particularly from the high protein and amino acid composition. Dietary KM significantly increased the overall effect size of SGR ($g = 1.92$) ($P = 0.001$); the positive effect was illustrated in marine species ($g = 1.32$ to 9.10) ($P < 0.05$) and sturgeon (*Acipenser gueldenstaedtii*) ($g = 6.59$) ($P < 0.001$). The overall g value for FCR (−2.42) was significantly improved compared to the control group ($P < 0.001$). The inclusion of KM in aquatic animal diets did not affect g value of PER (1.52, 95% confidence interval: −1.04 to 4.07) and survival rate (0.08, 95% confidence interval: −0.63 to 0.79) ($P = 0.252$ and 0.208, respectively). The meta-regression models indicated that SGR of rainbow trout (*Oncorhynchus mykiss*) was significantly correlated with dietary KM by a positive linear model ($P = 0.022$). The cod and sturgeon (*A. gueldenstaedtii*) appeared to efficiently utilize krill-containing diets as illustrated by a negative linear model ($P = 0.011$ and $P = 0.024$, respectively) between dietary KM and FCR. Dietary KM positively correlated with PER for Atlantic cod ($P = 0.021$). Our meta-analysis highlighted the significant outcome of KM in diets for aquaculture species by reducing pressure on forage fish from marine resources and sparing edible foods. Specifically, including KM significantly reduced economic fish-in fish-out (eFIFO) in four taxa — the top forage fish consumers ($P < 0.05$): marine fish, salmon, shrimp, and trout. The meta-analysis revealed the decreased food-competition feedstuff in diets for important aquaculture species ($P < 0.05$) fed dietary KM. The outlook for efficient use of KM from marine resources in aquafeeds was elucidated in the present work.

1. Introduction

Antarctic krill (*Euphausia superba*) hold significant ecological and commercial value within the Southern Ocean (Nicol et al., 2012; Siegel, 2016), playing a pivotal role in the marine food chain as important prey for various predators such as whales, penguins, flying seabirds, and seals (McCormack et al., 2021). Additionally, it serves as a substantial global carbon sink (Khatiwala

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et al., 2009). The annual total krill biomass is estimated to be 379 million tonnes, constituting a significant 95% of the total capture fisheries in the Southern Ocean (Atkinson et al., 2009). The capture production of krill has significantly escalated from 59 tonnes in 1973 to 357 thousand tonnes in 2021. Notably, Norway leads in the total catch, contributing 64%, followed by China (13%), the Republic of Korea (11%), Chile (6%), and Ukraine (6%) (CCAMLR, 2023; FishStatJ, 2023).

The harvested krill undergoes processing into key commodities like oil and meal, primarily processed on vessels into ground krill, from which oil is then extracted. The remaining krill with lower oil content is directed towards the feed industry (Cappell et al., 2022). Krill oil, a significant product for human consumption in the form of tablets, generated a value of 161.5 million United States dollars from 1242 tonnes of product in 2020 (Cappell et al., 2022). Furthermore, feed-graded krill meal (KM) is a by-product of oil extraction, providing approximately 51 thousand tonnes for animal feed, valued at 98 million United States dollars in 2020. The prognostication anticipates a yearly expansion rate of 7.4% for KM, projecting an approximate valuation of 148 million United States dollars by 2027 (Cappell et al., 2022).

The aquaculture industry stands as the fastest-growing food-producing sector and is a primary consumer of fishmeal derived from forage fish, a resource with finite availability, that would rapidly approach its capture limits (Cottrell et al., 2020; FAO, 2022; Froehlich et al., 2018; Naylor et al., 2021). Efforts to replace fishmeal in aquafeed with alternative protein sources have gained traction over recent decades. Various substitutes, including poultry by-products (Galkanda-Arachchige et al., 2020), insect meals (Tran et al., 2022), fermented plant proteins (Mugwanya et al., 2023), single-cell proteins (Couture et al., 2019), among others, have been integrated into aquafeed formulas.

Krill meal has gained interest as a protein source in aquaculture diets due to its promising nutrient composition (Burri and Nunes, 2016; Leonardi et al., 2023). This shrimp-like meal contains significant amounts of protein, amino acids, and poly-unsaturated fatty acids – notably the n-3 constituent, a rich array of trace minerals, chitin, and natural astaxanthin. Additionally, KM is highly palatable and is a natural dietary component for numerous marine fish species (Albrektsen et al., 2022; Xie et al., 2017, 2019). These attributes position KM as an attractive component for aquaculture feed formulations, especially in addressing nutrient deficiencies in low fishmeal diets.

Exploration into the impact of dietary KM on animal growth performance has yielded varied outcomes. Studies on salmonids, for example, depict conflicting results. Olsen et al. (2006) observed no alterations in the specific growth rate (SGR) of Atlantic salmon when fed dietary KM. Conversely, salmon subjected to graded levels of KM as a fishmeal substitute exhibited a significant increase in SGR (Hatlen et al., 2017). Notably, a comprehensive regression model linking the explanatory variable (dietary KM) with growth performance indices remains elusive. Such a model, once established with pertinent metadata, could serve as a predictive tool for assessing animal growth variations at different KM inclusion levels.

Meta-analysis proves to be a valuable approach in consolidating and extracting information from diverse studies (Hua, 2021), mainly through the computation of Hedges'g (g) value effect size. Additionally, meta-regression aids in identifying the optimal correlation between effect size and KM levels, thus showing the most effective inclusion levels. Furthermore, meta-analysis allows for exploring various factors influencing animal growth performance when fed dietary KM, presenting invaluable insights for future KM-based feed formulations.

Aquaculture primarily relies on marine-derived fishmeal as a key feed input, particularly in shrimp, salmon, and various marine fish taxa (Cottrell et al., 2020; Naylor et al., 2021). Reducing this dependence through alternative feed ingredients could significantly diminish the need for fishmeal and fish oil in aquafeed. This reduction can be quantified using the economic fish-in fish-out (eFIFO) principle, which operates on the premise of economic allocation (Kok et al., 2020). Employing a comprehensive analysis of multiple publications and their metadata could furnish robust insights into the current status of this ratio, prompting efforts toward more efficient utilization of marine resources.

Recent attention has been directed toward the food-feed competition inherent in aquafeed formulations (Sandström et al., 2022; van Riel et al., 2023). Feed formulations for certain fish species heavily rely on ingredients that could otherwise serve as human food sources (Aas et al., 2022; Sandström et al., 2022; Tran et al., 2024). Using KM from the feed-grade category could alleviate this conflict by diverting many edible resources away from animal feed, thereby preserving them for human consumption.

This review undertook a meta-analytic approach to quantify the overall impact of dietary KM on growth performance indices - specifically, the specific growth rate, feed conversion ratio, protein efficiency ratio, and survival rate - of aquaculture species. Furthermore, the study explored the relationship between these growth indices and varying levels of KM inclusion. Meta-regression was employed to elucidate the correlation between dietary KM and both the eFIFO and food-competing feedstuff use. This work shed light on the potential challenges and outlooks for incorporating KM into aquafeeds in the forthcoming decades.

2. Methods

2.1. Data collection

The literature search was conducted following the Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA) guidelines (Moher et al., 2009). Between September 15th and 30th, 2023, we searched relevant records in three online databases: Web of Science (http://www.webofknowledge.com), SCOPUS (https://www.scopus.com), and PubMed (https://pubmed.ncbi.nlm.nih.gov) for studies that evaluate effects of dietary KM (*E. superba*) on growth performance of aquatic animals. The keywords and search procedures are presented in Table S1.

2.2. Study selection

Publications were screened and eligible records were compiled based on the following criteria: (1) KM as replacement for fishmeal; (2) focused on aquatic animals; (3) one of the growth performance parameters was presented: specific growth rate (SGR, %/d), feed conversion ratio (FCR), protein efficiency ratio (PER, %), and survival rate (SR); (4) sufficient information on mean value, sample size, treatment error (standard deviation, standard error). Studies investigating the combination of KM with other protein sources as a replacement for fishmeal were not eligible for the database. In addition, to avoid bias, using refined forms of KM, such as hydrolysate or fermentation, other than raw KM was not considered.

2.3. Data extraction

We retrieved the means, number of replications, and treatment error (standard deviation, standard error, or confidence intervals) for each eligible study. The information extracted from the articles also included fishmeal level, fish oil level, trophic level (retrieved from FishBase (https://www.fishbase.se/), experimental duration, temperature, nutritional composition of experimental diets, year of publication, and the study country.

2.4. Statistical analysis

Hedges'g value effect size with a 95% confidence interval and a *P*-value were calculated as previously described (Guo et al., 2020). A positive *g* value, with a 95% confidence interval that did not overlap with zero, indicated a significant increase in the growth performance of organisms fed KM-containing diets relative to KM-free diets.

The correlation between the moderator and *g* value was performed with multiple linear regression under the Analysis of Covariance (ANCOVA) framework.

Heterogeneity in effect sizes was evaluated using the heterogeneity (I^2) index (Thompson and Sharp, 1999), which was categorized as low (0 to 25%), moderate (26% to 75%) or substantial (76% to 100%).

The publication bias among studies was checked using Egger's test (Matthias et al., 1997). *P*-value < 0.05 indicated statistically significant evidence of publication bias. The potential outliers greater than two times the average effect size were removed. We found that removing these data did not change the conclusions in most cases. In addition, the trim-and-fill method was employed to impute artificial effect sizes that were missing due to the influence of publication bias on the literature search results. Subsequently, corrected effect sizes were calculated (Duval and Tweedie, 2000).

All statistical analyses were performed in the R statistical package (RStudio, 2023.03.1 Build 446 © 2009-2023 Posit Software, PBC), using the "meta" and "metafor" packages (Viechtbauer, 2010). All figures were prepared by "ggplot2"and "ggsankey" package.

3. Results

3.1. Overview of compiled literature

A total of 55 studies were identified following a search based on selected keywords, of which 22 were eligible for inclusion in this meta-analysis. The compiled dataset covered a total of 14 aquatic species, the majority from the marine environment, with Atlantic salmon (*Salmo salar*) mainly being investigated (7 from 22 studies), followed by rainbow trout (*Oncorhynchus mykiss*) (3 studies), Atlantic halibut (*Hippoglossus hippoglossus*), Atlantic cod (*Gadus morhua*) white-leg shrimp (*LitoPenaeus vannamei*) and yellow crocker (*Larimichthys crocea*), each of which shared 2 from 22 publications. All compiled studies were conducted in six countries, where Norway ($n = 9$) and China ($n = 9$) accounted for most of the studies during the period from 2006 to 2022 (Fig. S1; Tables S1 and S2).

Such literature allows us to conduct a meta-analysis and subsequently, a systematic review, thus elucidating significant conclusions on using KM in aquatic animal diets.

3.2. Nutritional composition of krill meal (E. superba)

Compared to conventional aquafeed protein sources (fishmeal and soybean meal) and to novel counterparts (insect meal such as black soldier fly [*Hermetia illucens*]), KM showed similar nutritional properties to fishmeal, an ideal protein source for many carnivorous and omnivorous fish species. In addition, KM contains chitin, which is also present in insect meal (Fig. S2).

The amino acid profile of KM is considerably variable and generally rich in essential amino acids. When visualized by Principal Component Analysis, KM showed an amino acid profile similar to fishmeal but different from those of soybean and insect meal (Fig. S3).

The fatty acid composition of KM is characterized by the balance among saturated, mono-unsaturated, and highly unsaturated, which is similar to that of fishmeal. In contrast, insect and soybean meals exhibit a high content of saturated and considerably lower content of highly poly-unsaturated fatty acids (Fig. S4).

Owing to these significant properties, including KM in aquatic animal diets could result in comparable performance to fishmeal-based diets. Furthermore, other components, such as chitin, astaxanthin, carotenoid, and fluorine, contained in KM, may offer additional benefits to fed aquatic organisms.

3.3. Meta-analysis on Hedges'g value effect size of specific growth rate (SGR), feed conversion ratio (FCR), protein efficiency ratio (PER), and survival rate (SR)

Dietary KM significantly increased the growth performance of investigated aquatic species through SGR ($g = 1.92$ and 95% confidential interval [CI]: 0.73 to 3.10) ($P = 0.001$). Spotted halibut (*Verasper variegatus*); Danube sturgeon (*Acipenser gueldenstaedtii*); European seabass (*Dicentrarchus labrax*); Atlantic cod (*G. morhua*); and gilthead seabream (*Sparus aurata*) had positive responses associated with SGR to dietary KM ($P < 0.05$), while the *g* value of other feed animals did not differ from fishmeal-based diets ($P > 0.05$) (Fig. 1, Table S3).

A similar phenomenon was observed for FCR, with a significantly negative *g* value (−2.42, CI: −3.69 to −1.16) ($P < 0.001$), denoting that dietary KM significantly reduced FCR in organisms compared to the control. While this was observed for the majority of aquatic species, Atlantic salmon and sharpsnout seabream (*Diplodus puntazzo*) had significantly positive *g* value for FCR while fed KM-containing diets ($P < 0.05$) (Fig. 2, Table S4).

PER of tested organisms was not affected by dietary KM, as illustrated by *g* value (1.52, CI: −1.04 to 4.07) ($P = 0.25$), with the exception of Atlantic cod, which had an increased *g* for PER (2.79, CI: 1.51 to 4.06) when fed KM-containing diets compared to the control ($P \leq 0.001$) (Fig. 3, Table S5).

Our meta-analysis indicated that dietary KM did not significantly affect SR ($g = 0.08$, CI: −0.63 to 0.79) ($P = 0.208$) (Fig. 4, Table S6).

3.4. Meta-regression analysis

Hedges'g value effect size of investigated parameters calculated from meta-analysis was employed to elucidate the correlation with dietary KM. The meta-regression models are presented in Fig. 5 and Tables S3–S6.

Dietary KM significantly correlated with SGR *g* value for rainbow trout, as demonstrated by the positive linear model ($P = 0.022$, adjusted R-square = 0.67).

Regarding FCR, fed organisms had a contrasting relationship with dietary KM. While *g* value for FCR significantly reduced with increased dietary KM for Atlantic cod ($P = 0.011$, adjusted R-square = 0.96) and Danube sturgeon ($P = 0.023$, adjusted R-square = 0.99) respectively, Atlantic salmon fed KM exhibited increased FCR effect size ($P = 0.012$ adjusted R-square = 0.51).

PER effect size was positively correlated with dietary KM for Atlantic cod ($P = 0.021$ adjusted R-square = 0.95). There was no significant relationship between *g* value for SR and dietary KM for aquatic species.

3.5. Heterogeneity and publication bias

Our study revealed significant inter-study heterogeneity (as indicated by I^2 values) for SGR effect size ($I^2 = 99.91\%$), FCR ($I^2 = 99.75\%$), PER ($I^2 = 99.79\%$), and SR ($I^2 = 99.49\%$).

Analysis of covariance (ANCOVA) highlighted that growth performance *g* value were significantly affected by several explanatory

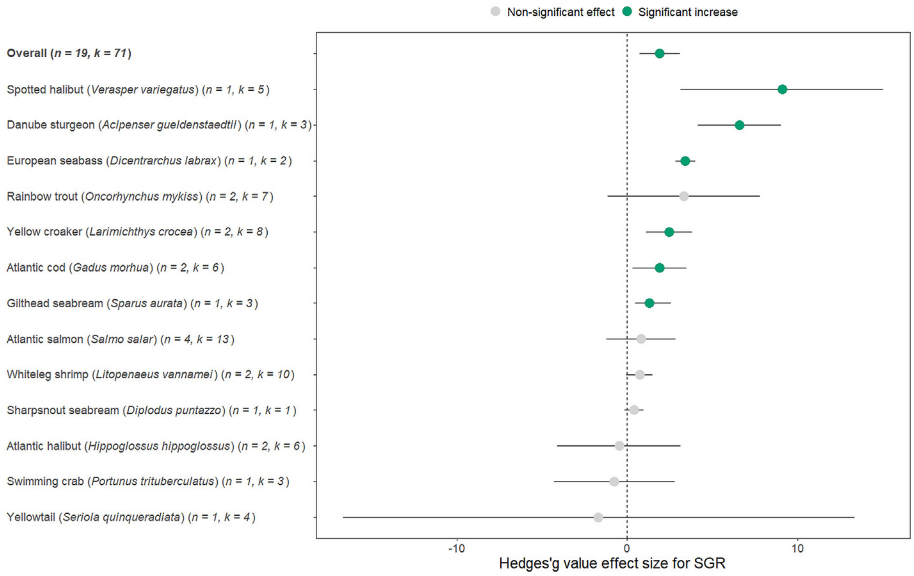

Fig. 1. Forest plot for specific growth rate (SGR). The data is presented as mean of Hedges'g value effect size (fill dots) and 95% confidential interval (error bars). *n* indicates the number of studies; *k* indicates the number of comparisons (treatment vs. control group).

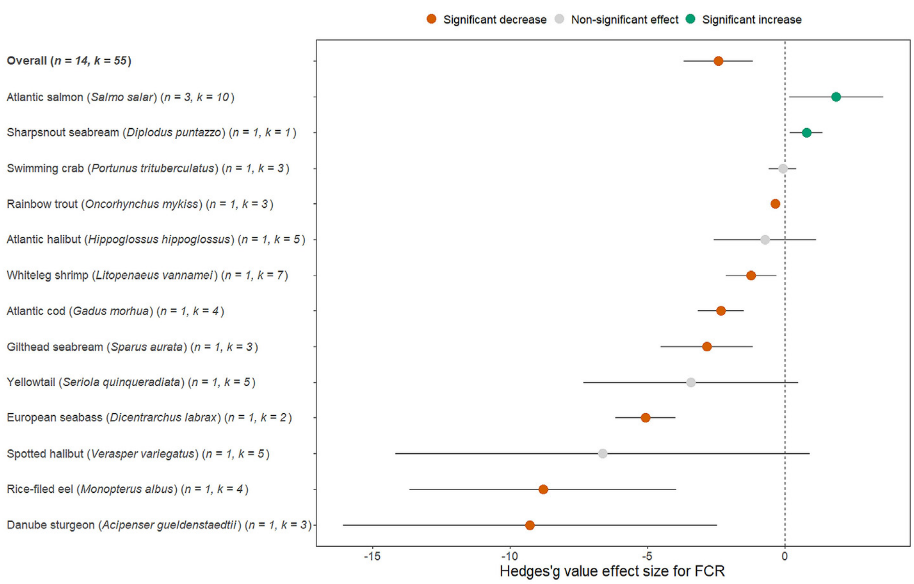

Fig. 2. Forest plot for feed conversion ratio (FCR). The data is presented as mean of Hedges'g value effect size (fill dots) and 95% confidential interval (error bars). *n* indicates the number of studies; *k* indicates the number of comparisons (treatment vs. control group).

variables, including the nutritional composition of diets, trophic level, experimental duration, temperature, and dietary KM (Figs. S5–S7).

Publication bias (Egger's test, $P < 0.01$) was confirmed for all tested growth performance indices (Figs. S8–S11). Following the removal of outliers, the *g* value remained unchanged from primary meta-analysis outputs (Tables S3–S6), indicating that publication bias in the present meta-analysis did not interfere with the conclusion.

3.6. Economic fish-in fish-out: forage fish used to produce one unit of live aquatic animal products

Since the aquafeed industry significantly impacts forage fish from marine resources, we explored if dietary KM may play a function in reducing this impact by investigating the eFIFO. Our analysis revealed that including KM in diets for different taxa significantly reduced eFIFO, as illustrated by negative models (Fig. 6):

For marine fish, generalized additive model (GAM), $P = 0.001$, adjusted R-square = 0.52, deviance explained = 62.9, generalized cross validation (GCV) = 0.34. For salmon, GAM, $P < 0.001$, adjusted R-square = 0.48, deviance explained = 52.6, GCV = 0.48. For shrimp, Linear model, $P < 0.001$, adjusted R-square = 0.99. For trout, GAM, $P < 0.001$, adjusted R-square = 0.80, deviance explained = 82.5, GCV = 0.14.

The upper-panel density plot visualized the distribution of data points. In general, most studies focus on including KM at less than 40% (Fig. 6).

Overall, dietary KM could mitigate the dependence of the aquafeed industry on wild forage fish, but shift the reliance on

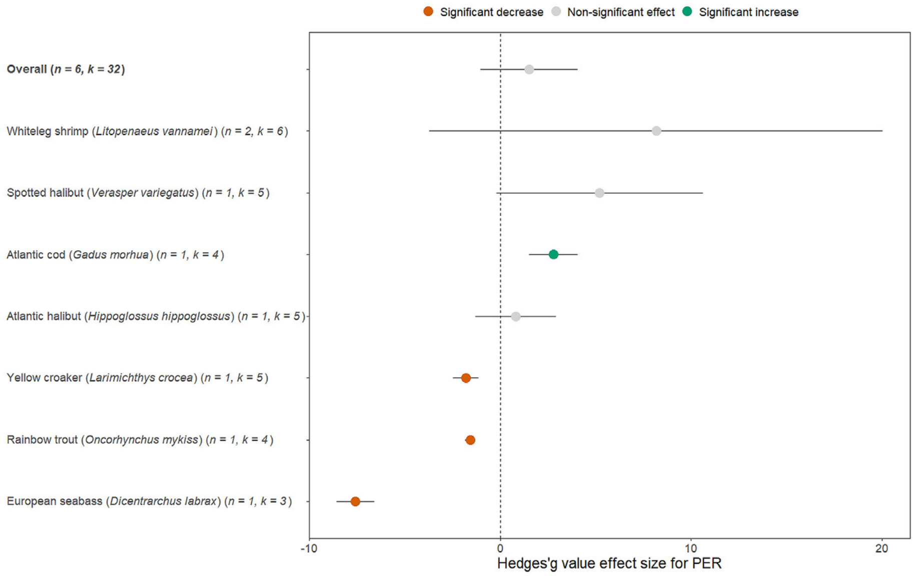

Fig. 3. Forest plot for protein efficiency ratio (PER). The data is presented as mean of Hedges'g value effect size (fill dots) and 95% confidential interval (error bars). *n* indicates the number of studies; *k* indicates the number of comparisons (treatment vs. control group).

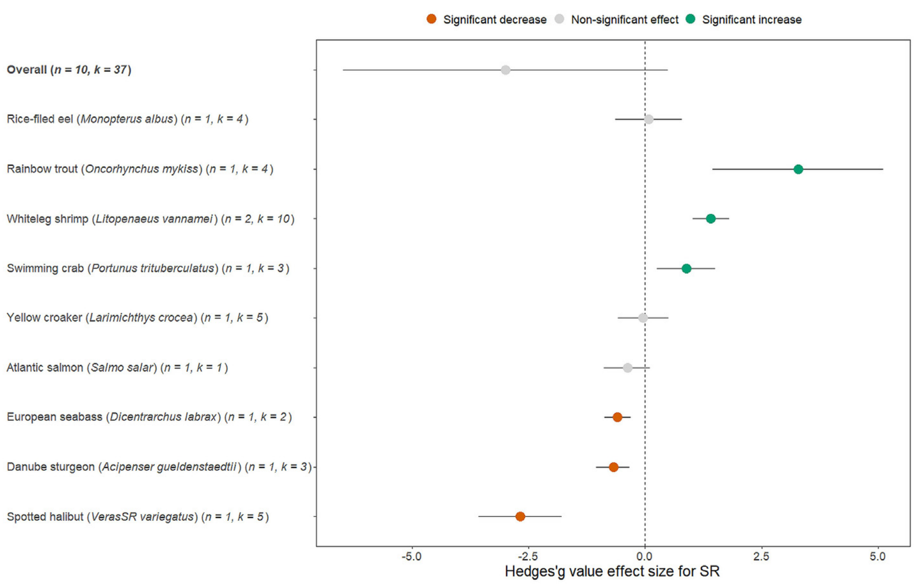

Fig. 4. Forest plot for survival rate (SR). The data is presented as mean of Hedges'g value effect size (fill dots) and 95% confidential interval (error bars). *n* indicates the number of studies; *k* indicates the number of comparisons (treatment vs. control group).

another marine wild resource — such as crustaceans, which requires further elucidation and sustainable use.

3.7. Food-feed competition associated with the use of krill meal in aquafeed

Concerning the use of edible human food in aquafeed, we investigated the current use of food-competing feedstuff (FCF) in feed for farmed fish species and the role of dietary KM — a non-food competing feedstuff in addressing this conflict. In most farmed species, increased dietary KM significantly reduced the percentage of FCF in diets (Fig. 7, lower panel). Specifically, the percentage of FCF negatively correlated with dietary KM as illustrated by negative models: for eel, linear, $P < 0.001$, adjusted R-square = 0.99; for freshwater crustacean, linear, $P < 0.001$, adjusted R-square = 0.99; for marine fish, GAM, $P < 0.001$, adjusted R-square = 0.49, deviance explained = 50.5, GCV = 0.187; for salmon, GAM, $P < 0.001$, adjusted R-square = 0.87, deviance explained = 88.3, GCV = 55.92; for shrimps, GAM, $P < 0.001$, adjusted R-square = 0.77, deviance explained = 80.1, GCV = 51.5; for sturgeon, linear, $P < 0.001$, adjusted R-square = 0.99; for rainbow trout, linear, $P < 0.001$, adjusted R-square = 0.98.

It is worth noting that more than 50% of the current dietary components of many farmed species is based on FCF, except for freshwater crustacean and shrimp diets, which contain less than 25% and 45% of FCF, respectively (Fig. 7, upper panel).

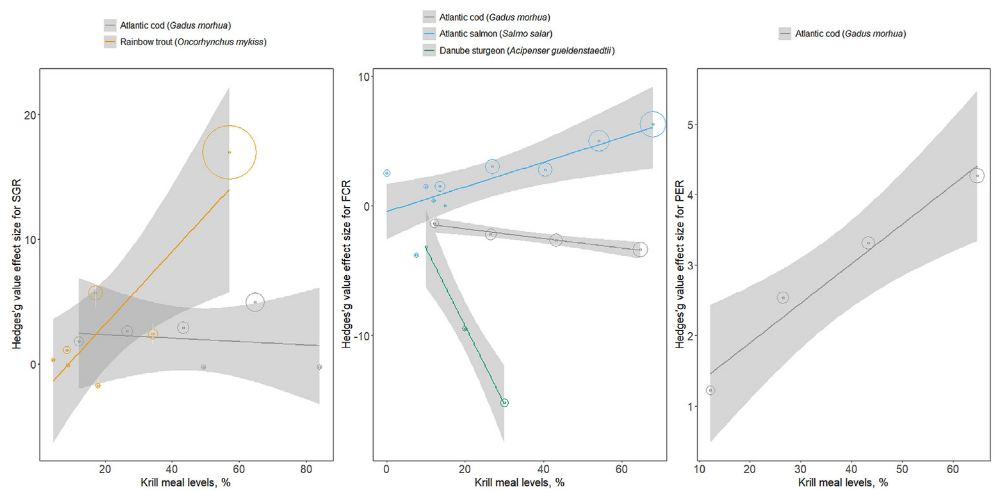

Fig. 5. Meta-regression analysis between dietary krill meal and effect size of specific growth rate (SGR), feed conversion ratio (FCR) and protein efficiency ratio (PER). The colored filled dots and diameters represent mean and 95% CI of the effect size.

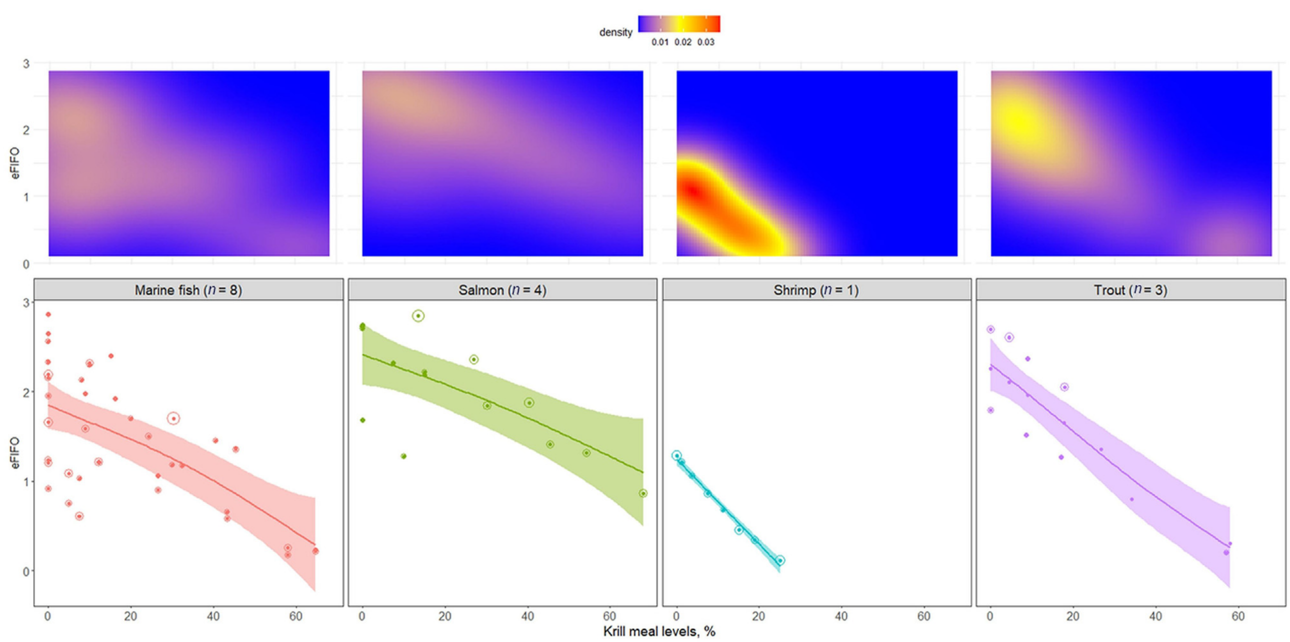

Fig. 6. Economic fish-in fish-out (eFIFO) for four aquatic taxa. The upper panel depicts density of eFIFO value. The lower panel elucidates meta-regression model between dietary krill meal and eFIFO of different taxa. The colored filled dots and diameters represent mean and 95% CI of the effect size.

4. Discussion

Our study, encompassing 19 publications spanning from 2006 to 2022, assessed the overall impact of dietary krill meal (*E. superba*) (KM) on the growth performance indices of aquaculture species. We evaluated the specific growth rate (SGR), feed conversion ratio (FCR), protein efficiency ratio (PER), and survival rate (SR) across aquaculture species. Our findings underscored the favorable acceptance of KM in aquaculture diets, evidenced by a significant positive effect on SGR depicted by *g* value. Moreover, including KM reduced FCR, but had no impact on survival rate of most fish species (Figs. 1–4). The findings emphasize the pivotal role of KM in future aquafeeds, particularly in addressing the pressing issue associated with the scarcity of marine wild fish. Incorporating KM into diets could reduce the demand of wild fish populations, minimizing their exploitation for fishmeal in aquafeed. Additionally, the utilization of feed-grade KM, devoid of food competition, offers a viable solution to eliminate food-feed competition — a critical consideration in an era marked by limited natural resources and a growing population.

4.1. Nutritional composition of krill meal

Numerous studies have highlighted the superior nutritional properties of KM, positioning this crustacean as a viable substitute for fishmeal in diets of various fish species (Burri and Nunes, 2016; Kaur et al., 2022). Our study, employing principal component analysis, showed a similarity in amino acid profiles between KM and fishmeal (Fig. S2). Unlike alternative protein sources derived from terrestrial origins, which often lack essential amino acids like

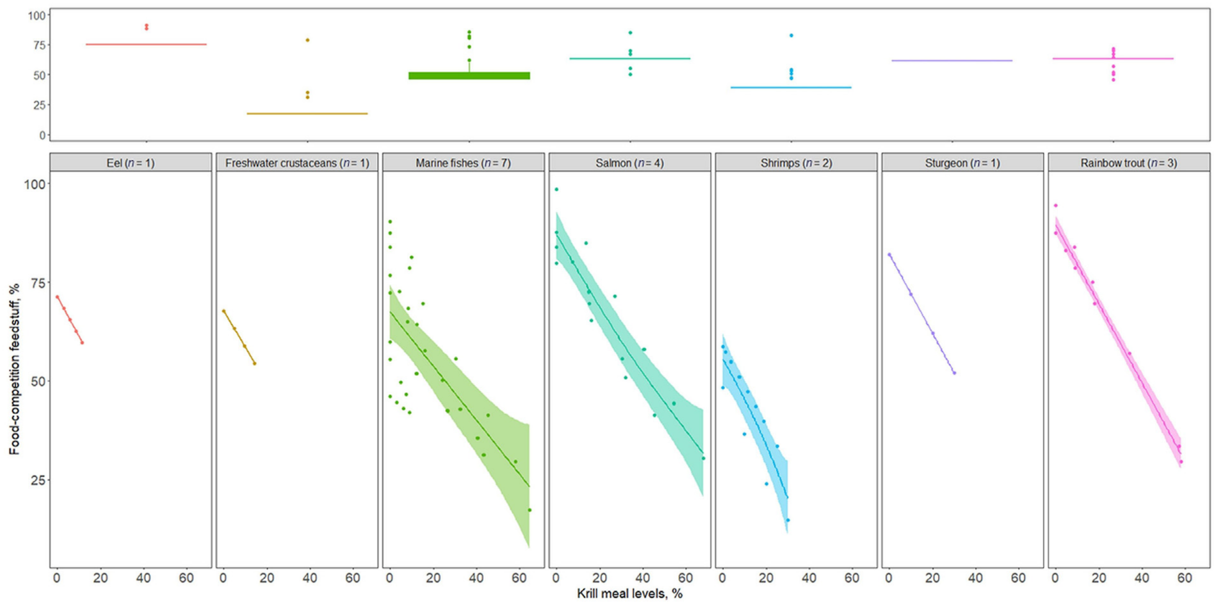

Fig. 7. Food-feed competition aspect of using krill meal in diets for seven aquatic groups. The boxplots from upper panel represent the current use of food-competition feedstuff (%) in different species. The meta-regression between dietary krill meal and edible food materials is illustrated in the lower panel. The dots denote the observed data. The data for upper panel was retrieved from Sandström et al. (2022).

methionine and lysine (Hua, 2021; IAFFD, 2023; Sales, 2009), KM typically serves as a rich source of these components. Most publications compiled in this study did not supplement essential amino acids in high KM diets, particularly for taxa with high nutritional requirements, such as white-leg shrimp, marine fish, and Atlantic salmon (Saleh et al., 2018; Shan et al., 2019; Torrecillas et al., 2021; Wei et al., 2022). For instance, Atlantic cod exhibited significantly higher SGR when fed KM-containing diets than did KM-free diets without supplementation of amino acids (Tibbetts et al., 2011). It's worth noting that the amino acid composition of KM exhibits considerable variation contingent upon harvesting season, storage, and processing methods (Chen et al., 2009; Jiang et al., 2016; Wang et al., 2015).

KM contains components superior to fishmeal, notably chitin and astaxanthin (Suontama et al., 2007b; Tibbetts et al., 2011; Wei et al., 2019b, 2022; Yoshitomi et al., 2007). Even in relatively low levels, chitin has been observed to support the growth performance of certain marine fish species (Tran et al., 2022). Chitin fragments smaller than 40 μm have demonstrated the ability to stimulate macrophage IL-10 production (Lee et al., 2008). Additionally, chitin undergoes fermentation in the fish gut by microbes, producing short-chain fatty acids that enhance host immunity (Terova et al., 2019). In addition to chitin, astaxanthin found in KM enhances the coloration of salmonid fish fillets (Kaur et al., 2022; Roncarati et al., 2011) and offers various physiological benefits (Lim et al., 2018).

It's widely acknowledged that KM contains significantly higher levels of fluorine and copper compared to fishmeal (Hansen et al., 2010; Shi et al., 2021; Wei et al., 2019a, 2019b). Fluorine, primarily found in the krill exoskeleton, varies between 870 and 1120 mg/kg on a dry matter basis in whole KM, whereas fishmeal typically ranges between 15.91 and 66.47 mg/kg (Shi et al., 2021; Wei et al., 2019b, 2022; Yoshitomi et al., 2007). On the other hand, copper concentrations in KM surpass those in fishmeal (Hansen et al., 2010), as krill's use of copper in hemocyanin for oxygen transportation instead of iron as observed in vertebrate hemoglobin (van Holde and Miller, 1995). Copper, an essential trace element, serves various bodily functions, but excessive levels can lead to toxicity concerns (Krogdahl et al., 2015).

As KM increasingly replaces fishmeal in feed formulations, there's an elevation in fluorine and copper concentrations in feed. However, studies have not yet found any adverse effects on fish fed KM-containing diets compared to KM-free diets (Shi et al., 2021; Wei et al., 2019a, 2022; Yoshitomi et al., 2007). Reports indicate that dietary fluorine from krill did not accumulate in the muscle of several fish species, yellowtail (*Seriola quinqueradiata*), Atlantic salmon, Atlantic cod, rainbow trout, and Atlantic halibut (Moren et al., 2007), but was elevated in the vertebral bone of yellowtail. Moreover, dietary fluorine did not cause histopathological changes in yellowtail (Yoshitomi and Nagano, 2012). While these elements did not compromise fish growth, attention should be paid to the limited fluorine and copper concentrations allowed in European fish diets, which are set at 3000 mg/kg for fluorine (Regulation, 2008) and 25 mg/kg for copper (Regulation, 2003).

4.2. Growth of aquaculture species fed dietary krill meal

The meta-analysis indicated that dietary KM enhances the growth performance of organisms, as evidenced by a high effect size of SGR (*g* value = 1.73) (Fig. 1). It's important to note that this tool quantifies the proportional change in fish growth indices between KM-containing diets and control diets. While some fish species showed a positive response to dietary KM, others did not exhibit significant differences, as indicated by the *g* value, suggesting that replacing fishmeal with KM either improved or did not compromise fish performance. The majority of marine fish display positive responses to dietary KM, signifying its potential as a viable protein source for these species in the future while sustaining fish growth. This could alleviate the pressure on wild forage fish, considering marine fish taxa are among the leading users of fishmeal in aquaculture species (Naylor et al., 2021).

In contrast, Atlantic salmon, a prominent consumer in global fishmeal production, presents varying outcomes when incorporating KM into diets. Hatlen et al. (2017) observed significantly higher SGR in salmon fed dietary KM compared to the control diet, despite a lower protein digestibility in the KM-containing diets. Similarly, Suontama et al. (2007a) observed elevated SGR in the KM group compared to the control. Conversely, Olsen et al. (2006) highlighted that dietary KM had no adverse effects on protein digestibility or fish growth, which is in agreement with previous findings (Rungruangsak-Torrissen, 2007). In light of these divergent findings, our meta-analysis, encompassing data from these studies, concluded that dietary KM did not compromise growth of Atlantic salmon (g value = 0.82). Additionally, our study highlighted various factors influencing fish growth responses, including feed composition and water temperature (Figs. S1–S3).

Incorporating KM into aquatic animal diets notably reduced FCR, without adverse effects on PER and SR (Figs. 2–4). This implies that no severe health issues were induced by dietary KM which aligns with earlier confirmations (Benitez-Santana et al., 2020; Yoshitomi and Nagano, 2012). This also suggests that nutrients in KM-containing diets are effectively utilized by aquatic organisms, as demonstrated by highly digestible organic matter, protein, and energy in Atlantic cod and halibut (Tibbetts et al., 2011). Previous studies have affirmed the high palatability of KM for many fish species, with higher feed intake compared to fishmeal diets observed in walleye pollock (*Gadus chalcogrammus*) (Choi et al., 2020), yellow croaker (*L. crocea*) (Wei et al., 2019b), and halibut (Tibbetts et al., 2011). Consequently, the combination of high feed intake and the excellent digestibility of nutrients in KM diets may significantly enhance the growth performance of tested animals from a metadata standpoint. This phenomenon is species-specific; while dietary KM did not compromise growth in Atlantic salmon, it affected nutrient digestibility, notably reducing lipid and starch digestibility compared to control diets (Hansen et al., 2010; Olsen et al., 2006). This inefficiency might be attributed to the presence of chitin in KM, which has shown to adversely impact protein digestibility and growth performance in Atlantic salmon (Karlsen et al., 2017). Our meta-regression model supported this, showing a positive correlation between dietary KM and FCR in Atlantic salmon (Fig. 5). The results highlighted increased SGR in rainbow trout with higher KM levels, aligning with previous studies (Wei et al., 2019a). Atlantic cod responded positively to dietary KM, displaying increased SGR, PER, apparent net protein accretion, nitrogen intake, nitrogen gain, and nitrogen retention efficiency (Tibbetts et al., 2011), reinforcing the robustness of our correlation models (Fig. 5).

The present meta-analysis demonstrates both high inter-study heterogeneity and publication bias. Notably, heterogeneity emerged across the investigated indices as illustrated by I^2 value (>54.9, Tables S3–S6). From data extracted across 22 publications, various factors encompassing biological, biotic, abiotic, and dietary influences were identified, impacting the effect size of growth performance (Figs. S5–S7). However, certain factors, including chitin, fluorine, nutrient digestibility, and intake, were excluded from the meta-analysis due to limited available data in the literature. Nonetheless, the strength of our model and meta-analysis outcomes finds solid support in previously published works, underscoring the rigor and robustness of our findings. Furthermore, our study revealed evidence of publication bias in the effect sizes of growth performance as indicated by Egger test (Tables S3–S6). It's worth noting that publication bias is a common occurrence in laboratory animal experiments (Briel et al., 2013; Korevaar et al., 2011). Upon the removal of strong outliers from the dataset, the conclusions drawn from the meta-analysis retained their rigor (Tables S3–S6).

4.3. Dietary krill meal reduces pressure on marine forage fish

Our meta-regression analysis, depicted in Fig. 6, underscores the potential for incorporating KM into diets for aquaculture species. This integration not only alleviates pressure on marine ecology but also yields a comparable amount of fed fish biomass. The eFIFO metric developed by Kok et al. (2020) offers a comprehensive assessment, considering forage fish utilization and co-products (derived from fisheries and aquaculture) for live seafood production. Our dataset encompassed 14 species, categorized into four taxa, revealing a negative correlation between dietary KM and eFIFO.

Across all taxa, the inclusion of moderate to substantial amounts of KM demonstrated the potential to reduce eFIFO to below 1, with the exception of the salmon group, which remained close to 1, especially at KM levels exceeding 60%. In a global standpoint, the eFIFO of four taxa reported in our study has consistently remained below 1 since 2020 (Marine fish: 0.94, salmon: 0.98, shrimp: 0.52, and trout: 0.98) (Kok et al., 2020). The relatively high eFIFO in the salmon group may be attributed to the notably high inclusion level of fishmeal in control diets. For instance, Olsen et al. (2006) formulated salmon diets with almost 60% fishmeal, twice the actual inclusion in commercial diets (30% in 2006) (Tacon and Metian, 2008).

The majority of aquaculture species serve as net producers, necessitating lower forage fish input to sustain biomass output. However, salmon and trout maintain a net neutral status, with fish input yielding equal fed fish output (Kok et al., 2020). Our model suggests that substantial inclusion of KM in diets for such taxa could significantly reduce eFIFO to levels lower than the current norm. However, achieving this would require significant efforts, including addressing issues related to the availability of krill.

Krill meal is being incorporated into diets for various species at relatively low levels, ranging from 0.03% to 8.37% for shrimp and 0.13% to 5.49% for salmon (Sandström et al., 2022). Aas et al. (2022) highlighted that Norwegian Atlantic salmon utilized 8155 tonnes of KM out of 1,976,709 tonnes of feed ingredients, accounting for 0.4% in 2020. Our analysis emphasizes the necessity for either significantly increasing KM inclusion to achieve an eFIFO below one or complementing KM inclusion with more protein-rich materials. The latter approach seems more strategic due to the limited global availability of feed-grade krill (totalling 51,200 tonnes in 2020, with minimal annual growth of 7.4% (Cappell et al., 2022)). This accounted for merely 2% of the total feed ingredients used in Norwegian salmon aquaculture (Aas et al., 2022). Therefore, future solutions may involve optimizing the complementary use of feed ingredients.

Globally, the majority of current aquafeed materials originate from plant sources; the proportion of fishmeal and fish oil derived from forage fish only account for less than 12% in current aquafeed formulation for some species (marine fish 11%, salmon 12%, shrimp 7%, and trout 11%) (Aas et al., 2022; Froehlich et al., 2018). Aquafeed contains recycled products from fisheries and aquaculture side streams serving as potential protein sources to meet future demands (Hua et al., 2019). Notably, approximately 50% of fishmeal used in global shrimp and salmon feed is sourced from such by-products (Naylor et al., 2021). Additionally, novel proteins, such as insect meal (Gasco et al., 2020), single-cell protein (Agboola et al., 2021), and microalgae (Chen et al., 2021), have been proposed and developed for inclusion in aquafeed, although their current utilization in Norwegian salmon feed stands at 0.4% (Aas et al., 2022).

Simply reducing fishmeal in feeds may not efficiently decrease the demand for forage fish in the coming decades compared to reducing fish oil across salmonids, shrimps, and marine fishes. Substituting fish oil significantly lowers forage fish use, projecting a demand of 18 million tonnes by 2030, whereas solely replacing fishmeal would require approximately 20 million tonnes — a seven million-tonne increase from the 2017 demand (Cottrell et al., 2020; Naylor et al., 2021). Notably, aiming for the highest plausible thresholds of fishmeal and oil replacement substantially diminishes global aquaculture's forage fish demand to around 8 million tonnes by 2030 (Cottrell et al., 2020). Moreover, focusing on replacing fishmeal and fish oil for top forage fish consumers like salmon and shrimp could result in substantial forage fish savings for aquaculture by 2030, as these two taxa accounted for over 50% of total forage fish consumption in 2017 (Naylor et al., 2021).

Suggestions for sustainable aquaculture growth highlight the potential of sparing fish oil from aquafeed (Cottrell et al., 2020; Hua et al., 2019). While krill oil is considered an alternative, its high price, US$103/kg in 2021 (Cappell et al., 2022), compared to fish oil, US$1.9/kg in 2021 (Kok et al., 2020) in 2021 and limited production volume, 1481 tonnes of liquid for the pet per animal sector in 2020 (Cappell et al., 2022) vs. 620,000 tonnes fish oil demand in 2017, calculated from Naylor et al. (2021), pose significant challenges. Similar constraints affect microalgae oil, despite its potential as a substitute for fish oil in aquafeed (Chauton et al., 2015; Vigani et al., 2015). Notably, a canola-derived long-chain omega-3 fatty acids source, rich in DHA and comparable to fish oil, has emerged as a recent development (MacIntosh et al., 2021). While novel alternatives are being developed, fish cut-offs continue to supply valuable lipid sources to aquafeed (Aas et al., 2022).

KM and krill oil could play a part in mitigating forage fish demand, potentially alleviating pressure on marine ecology and preserving biodiversity in the future. Challenges, including production volume, product costs, and capture limitations regulated by the Conservation of Antarctic Marine Living Resources (CAMMLR), may impede the widespread use of this feedstuff. The strategic use of krill is crucial to prevent shifting the aquafeed pressure from forage fish to other marine resources. Combining KM with other protein-rich materials to reduce fishmeal and exploring fish oil alternatives could be beneficial. Considering krill as an additive rather than a primary protein source in aquafeed might be advantageous, given its potential as a palatability enhancer, pigment source, and immunostimulant (Albrektsen et al., 2022; Ambasankar et al., 2022).

4.4. Mitigating food-feed competition through dietary krill meal in aquafeed

Taking KM into account as a non-food competition feedstuff (Sandström et al., 2022; van Riel et al., 2023), our simulations indicate a significant reduction in food-feed competition within aquaculture. This is achieved by diminishing the proportion of food-competing feedstuff (FCF) while elevating non-feed competing feedstuff (NFCF), ultimately preserving a substantial amount of edible food for human consumption (Fig. 7). Referring to current levels of FCF component in aquafeeds (Fig. 7, upper panel), our model forecasts a reduction in FCF across all taxa, notably in marine fish, salmon, and shrimp, with dietary KM.

Present aquafeed practices heavily rely on protein-rich resources from both marine and crop origins, such as forage fish and soy, diverting valuable food resources from human consumption. This situation raises environmental and food security concerns (Couture et al., 2019; Froehlich et al., 2018; van Riel et al., 2023). Our study highlights that most taxa consume over 50% of FCF in their diets, with the exception of freshwater crustaceans (21% FCF) and shrimp (41%) (Fig. 7, upper panel). Among these taxa, shrimp is a major aquafeed consumer (7.5 million tonnes), followed by marine fish (4.3 million tonnes) and salmon (3.4 million tonnes) in 2017 (Tacon, 2020). Our simulations suggest that dietary KM could substantially reduce FCF, potentially sparing several million tonnes of edible food for human consumption.

Presently, several materials categorized as NFCF have been developed and integrated into aquafeeds, encompassing animal and crop by-products, black soldier fly, and microbial ingredients (Aas et al., 2022; Sandström et al., 2022). Some of these materials operate under the circular bioeconomy principle, such as methanotroph bacterial protein (*Methylococcus capsulatus*) (Ruiz et al., 2023), filamentous fungi (*Paecilomyces variotii*) (Bergman et al., 2024). These advancements not only contribute to reducing the food-feed conflict but also offer environmental benefits. Due to the limited volume of krill and catch restrictions, incorporating KM alone to reduce FCF in aquafeed might encounter challenges. The complementary use of KM with other NFCF materials presents a more comprehensive solution, balancing nutritional properties, achieving environmental advantages, supplying protein inputs for aquafeeds, and preserving more edible food for human consumption. Tran et al. (2024) found that a blend of insect meal and animal by-products in diets for European perch (*Perca fluviatilis*) significantly reduced the use of human-edible feedstuff as sources of essential nutrients. Implementing NFCF combinations requires careful consideration of material availability, costs, market dynamics, regulations, and nutritional composition (Sandström et al., 2022; van Riel et al., 2023). It's crucial to note that some of these materials may have low-density energy and antinutrient factors, which could hinder nutrient utilization in fed animals, potentially compromising fish production performance and leading to increased waste, particularly phosphorus and nitrogen (Colombo et al., 2023).

5. Conclusion

Krill meal, recognized for its valuable nutritional composition rich in protein, amino acids, highly unsaturated fatty acids, chitin, and astaxanthin, is increasingly considered an alternative protein source for fishmeal in aquatic animal diets. A comprehensive meta-analysis underscored the significant positive impact of dietary krill meal on growth indices, particularly in specific growth rate and feed conversion ratio across 14 aquaculture species. Notably, the findings revealed that incorporating krill meal did not compromise the survival rate of the organisms, especially showcasing positive responses in marine fish species across all growth indices.

Beyond enhancing growth metrics, the incorporation of krill meal in aquafeed has substantial additional benefits, addressing the demand for forage fish in producing fed fish biomass, as illustrated by eFIFO, and food-feed competition. Its inclusion significantly lowered the eFIFO metric across all animal taxa, effectively alleviating pressure on marine forage fish. Moreover, the utilization of krill meal in aquafeed could reduce the use of human-edible food, thus conserving more food for direct human consumption.

While krill meal presents a favorable nutritional value, it's crucial to note its relatively high concentration of fluorine and copper. Adhering to regulatory limits, feed formulation should meticulously consider the concentration of those elements within permissible regulations.

For future aquafeed development, incorporating krill meal should aim to avoid transferring pressure from marine wild fish to other marine resources, such as Antarctic krill. Strategies could involve considering krill meal as functional additives at lower inclusion rates, channeling krill meal to marine fish species, integrating it with other novel circular materials, and reducing reliance on both fishmeal and fish oil in diet formulations.

In the coming decades, aquaculture - under pressure to produce blue food in an era of growing populations, limited natural resources, and environmental concerns - should source feed ingredients, in addition to krill meal, that offer minimal or no food competition and possess a low ecological footprint. Emphasis should be placed on feed formulation that complies with existing regulations, prioritizes animal welfare, and minimizes waste output while maximizing nutrient reusability or recycling.

CRediT authorship contribution statement

Hung Quang Tran: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Tram Thi Nguyen:** Formal analysis, Data curation. **Markéta Dvořáková Prokešová:** Writing – review & editing, Data curation. **Margareth Øverland:** Writing – review & editing. **Laura Gasco:** Writing – review & editing. **Vikas Kumar:** Writing – review & editing. **Hien Van Doan:** Writing – review & editing. **Vlastimil Stejskal:** Writing – review & editing, Supervision, Investigation.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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Appendix A. Supplementary data

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