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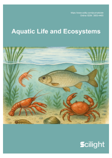

Review

Ecological Basis and Aquaculture Use of Copepods as Live Feed with Emphasis on Nutritional Value, Production Constraints, and Future Directions

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Abstract: Copepods are a good live feed for aquaculture because they feed a variety of fish and crustacean larvae. Their roles in larviculture are explained by their ecological role in the transfer of energy from primary producers to higher trophic levels. Copepods exhibit higher levels of protein, amino acid profiles, digestive enzymes, and essential fatty acids, such as docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), which are critical for larval growth, neural development, stress resilience, and survival, when compared to conventional live feeds like rotifers and Artemia nauplii. Despite all of these advantages, copepod use is constrained by significant production constraints. Complex life cycles, sensitivity to environmental changes, changes in the nutritional makeup of algal diets, and difficulties achieving reliable high-density production are some of the difficulties that mass culture faces. The persistent obstacles continue to restrict their widespread commercial use. This review summarizes what is currently known about the ecological importance of copepods, assesses their nutritional value and production limitations, and suggests important lines of inquiry to improve their widespread use as sustainable live feed in aquaculture.

Keywords: copepods; aquaculture; growth; fisheries; ecology

1. Introduction

Copepods are small crustaceans that live in both freshwater and marine environments. They are used as live prey [1], are essential to marine ecosystems, serve as the trophic link between phytoplankton and higher trophic levels, and are a vital food source for many marine fish and crustacean larvae [2]. Its sizes range from 50–500 µm during the nauplius stage to 1–2 mm during the adult stage. Its active swimming behavior facilitates the larvae's efficient uptake during the rearing period [3].

Copepods have shown improved growth and development in a variety of commercial and ornamental fish larvae species when compared to Artemia nauplii and rotifers. Their higher nutritional value, especially in vital nutrients like docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), which are critical for fish larvae development [4]. Despite their remarkable nutritional status, copepods' functions can be significantly impacted by their diet and culture. Therefore, controlled feeding of copepods with nutrient-rich microalgae or prepared diets, which are subsequently fed to the target aquaculture species, is typically used in enrichment protocols to improve copepod biochemical profiles [5]. Enrichment can raise the nutritional value of copepods and align them with the dietary needs of larvae by increasing the concentrations of essential fatty acids.

However, the creation of economical mass production techniques remains a major obstacle. Due to copepods' dietary selectivity and their ability to bioaccumulate high concentrations of polyunsaturated fatty acids and carotenoids from phytoplankton through the food chain, one of the main challenges is the uneven availability of suitable prey [6]. Therefore, this review examines the current understanding of the ecological significance of copepods, evaluates their nutritional value and production constraints, and identifies important research avenues to enhance their widespread use as sustainable live feed in aquaculture.

2. Functional Diversity of Copepods

Copepods fulfil trophic roles, including herbivory, omnivory, and carnivory, and their feeding behaviours impose significant top-down regulation on phytoplankton communities via size-selective and taxon-specific grazing [7]. This selective predation can modify phytoplankton size composition, competitive dynamics, and eventually influence the initiation and cessation of algal blooms. They significantly contribute to the biological carbon pump by encapsulating consumed substances into rapidly descending faecal pellets, therefore augmenting the vertical export of particulate organic carbon [7]. Feeding selectivity is significantly affected by prey size distribution, mobility, and taxonomic makeup, hence connecting copepod trophic strategies to phytoplankton community structure [8]. For instance, omnivorous copepod taxa frequently target larger phytoplankton or microzooplankton, resulting in a shift in their trophic position based on community composition [7]. Copepods often act as omnivores, consuming both phytoplankton and microzooplankton. This feeding strategy can suppress protist grazing, resulting in indirect top-down effects that enhance net phytoplankton growth in both freshwater and marine ecosystems [9].

Furthermore, in addition to grazing, copepods exert key bacteriostatic/bactericidal interactions with the bacterial communities in the water. They can defecate and feed indiscriminately, potentially contributing nutrients for bacterial sustenance [10]. Copepods influence marine bacterial communities via two complementary mechanisms. Initially, through the excretion of dissolved nitrogen and excretion of dissolved nitrogen and phosphorus compounds and through inefficient feeding practices, copepods enhance the nutrient concentration in their immediate environment. This process promotes the proliferation of rapidly growing bacteria, including Vibrionaceae, Oceanospirillales and Rhodobacteraceae [11].

They consistently host species bacterial taxa, particularly Flavobacteriaceae and Pseudoalteromonadaceae, on or within their bodies, thereby effectively "farming" these microbes and releasing them into the surrounding seawater. The combined effects and nutrient provisioning and microbiome exchange position copepods as a critical, yet frequently underestimated, factor in the organisation of both attached and free-living bacterial communities, thereby closely associating microbial processes with carbon and nutrient dynamics in planktonic food webs [11].

Copepods are essential to the biological carbon pump, in addition to their role in trophic regulation. Their consumption of particulate organic matter and the subsequent formation of rapidly sinking faecal pellets facilitate the vertical transfer of carbon from the euphotic zone to deeper layers, thus exporting dissolved and particulate organic carbon to the deep ocean [8]. Carcasses of copepods, moulted exoskeletons, and particles associated with feeding play a significant role in the enhancement of particulate organic carbon export. Additionally, numerous copepods engage in diel vertical migrations, facilitating the transport of carbon and nutrients between surface and deeper layers, thereby improving sequestration efficiency.

This biogeochemical contribution is dependent on traits, larger copepods and those with efficient pellet production tend to exert disproportionate effects on carbon export relative to their biomass, whereas small omnivorous forms may recycle more organic matter within the surface microbial loop [12].

3. Copepod Nutritional Value and Performance as Live Feed to Aquaculture Species

3.1. Nutritional Value of Copepod

Copepods are recognised for their nutritional advantages as live feeds for the early stages of marine fish, due to their elevated essential fatty acid content and biochemical profiles when compared to Artemia nauplii and rotifers [4]. According to recent research, copepods, especially Apocyclops royi, have higher concentrations of long-chain highly unsaturated fatty acids (HUFAs), such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), than unenriched Artemia nauplii [13]. The growth, survival, and physiological development of larvae depend on these fatty acids.

A recent study on *Mesocyclops leuckarti* confirmed that copepods can attain approximately 52% protein (dry weight) and significant lipid content when suitably enriched, with measurable DHA and EPA fractions. This indicates their potential as protein-rich, HUFA-rich live feeds for aquaculture species [14]. Even when Artemia is enriched, comparative feeding trials show that copepod-based diets, which are distinguished by high HUFA levels and DHA:EPA ratios, typically promote better survival and growth outcomes in early larval stages when compared to conventional live feeds. The biochemical requirements of larvae are met by copepods' high HUFA content, which promotes improved tissue accretion and reduces deformities [13].

3.2. Copepod Performance as Live Feed to Fisheries and Aquaculture Species

Aquaculture species derive a significant portion of their dietary nutrient needs from naturally occurring zooplankton. They provide a crucial source of essential nutrients, such as amino acids, proteins, lipids, fatty acids, enzymes, and vitamins [15]. Zooplankton play a significant role in the diet of freshwater fish larvae and crustaceans [16]. A balanced diet is crucial for meeting the nutritional needs of fish larvae, which in turn improves their survival and growth [17]. The population dynamics of copepods have an impact on the overall productivity of fishery and the survival of fish larvae in the wild environment because numerous species of fish larvae rely on copepods for growth and survival [18].

Fish larval survival could decrease if copepod numbers reduced, making fish harvest less economic and fisheries unsustainable. Copepod population size and their responses to the environment manipulation have to be monitored to enhance the fishery management [19]. The highest growth of different fish species such as sea bream [20] or cod [21] depends on the copepod component in their first life stages. It has important applications to fisheries sustainability and productivity, and is fundamental to the functioning of the trophic dynamics of marine systems. Their impact and interaction with upper and lower trophic levels underline the need for management and the conservation of these fisheries. Copepods play a critical role in enhancing the production of fish and to conserve marine aquatic biodiversity, as part of a global trend towards bio-ecological sustainability in aquaculture and fisheries [18]. Figure 1 shows the ecological and aquaculture importance of copepods.

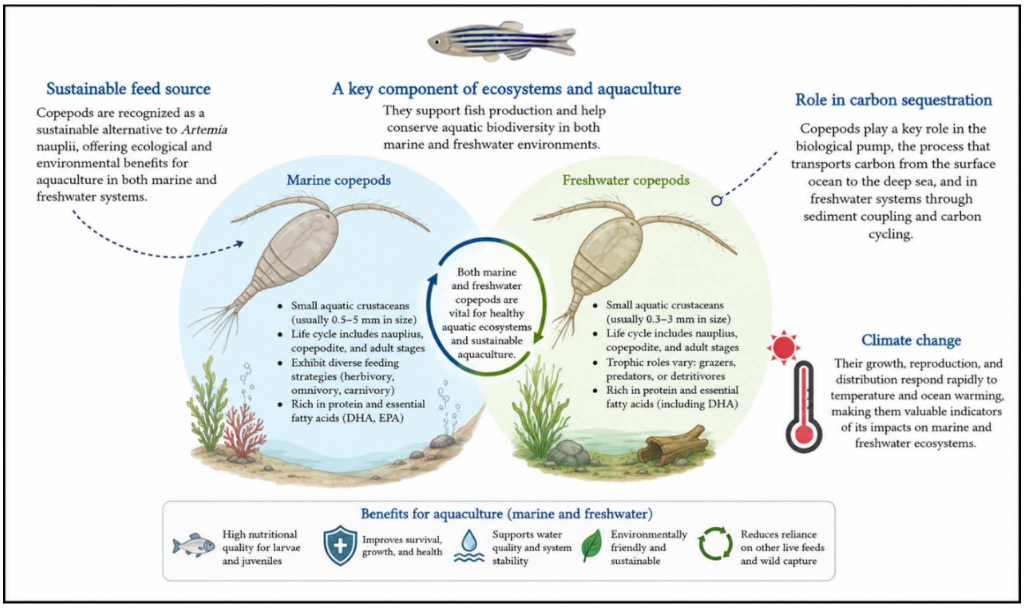

Figure 1. Ecological and aquaculture importance of copepods.

Additionally, there are ongoing studies on the production of aquaculture feed, where the live feeds such as copepods and cladocerans are cultured in controlled environments, either indoor in tanks or outdoor systems. Copepods have been studied and utilised as live diets in many aquaculture species including Atlantic cod larvae [21], gilthead sea bream [20], mud crab [1], and angelfish [22]. DHA and EPA from the copepods had been found to decrease larval mortality and increase larval growth.

During the initial 10 days of a culture cycle, the survival, growth, and colouration of larvae fed varying densities of copepods (*Parvocalanus crassirostris*) and rotifers (*Brachionus rotundiformis*) were examined. The inclusion of 2 copepods ml^{-1} in rotifer co-feeding enhances developmental progress, and improved colouration, when compared to the use of rotifers alone during the 10-day larval rearing of *G. brasiliensis* [22]. Copepods resemble the natural diet of turbot larvae, resulting in enhanced survival and growth rates when turbot larvae are fed copepods compared to *Artemia*. The consumption of copepods enhances skeletal development and swim bladder inflation in turbot, leading to improved quality [23]. Copepods also resemble the natural prey of many marine fish larvae and stimulate stronger feeding responses. Because of their suitable size, swimming behaviour, and balanced nutrients, copepod feeding can enhance skeletal development, swim bladder inflation, and overall larval quality. Therefore, incorporating copepods into larval feeding regimes, either alone or together with rotifers, can significantly improve larval performance in aquaculture systems [1,3].

Copepods in their natural condition increase coloration [24], which is desirable in commercial tilapia. Studies show that larvae fed copepods have not only an enhanced growth but also immune response and survival compared to those that are fed other live feeds such as rotifers or Artemia. In the case of lobster larvae, nutrient rich diets are necessary for adequate development. Copepods add to carapace growth while also promoting post larval settlement. Yuslan et al. [1] exhibit that rearing mud crab larvae on copepods is more efficient. The patterns in the data from this study indicated that larval survival was significantly higher on copepod-rich diets compared to diets enriched with nauplii of the same species, moulting success was higher and carapace development more advanced

4. Production, Enrichment, and Scaling Constraints

4.1. Production and Enrichment of Copepod

Zooplankton enrichment enhances the nutritional quality of fish larvae. This technique is applied in hatchery to improve the nutritional quality of live food on a large scale, particularly in terms of protein and other nutrient compositions for host consumption [25]. Common methods for enriching zooplankton involve the use of microalgae, organic waste and even probiotics which may enhance the growth and survival of the copepods. Table 1 shows the enrichment of copepods and its application in larviculture.

Table 1. Enrichment of copepod and its application in larviculture.

Species	Treatments	Findings	References
Apocyclops royi	*Chloroidium saccharophilum*	Seabass larvae exhibit higher levels of essential fatty acids, including EPA and DHA, when provided with live food sources such as copepods.	[13]
Copepod	Ginger, mint and spadeleaf	Spadeleaf serves as an effective enrichment source, markedly increasing protein and lipid content in copepods, which enhances the essential nutritional profile necessary for *Litopenaeus vannamei* post-larvae, indicating its potential as a dietary supplement in aquaculture.	[26]
Cyclops sp. and *Diaptomus* sp.	Live *Monoraphidium littorale* and powdered *M. littorale*	Live copepods enriched with *Monoraphidium littorale* demonstrated enhanced growth and survival rates in *O. niloticus* larvae, establishing them as a promising live food source due to their improved nutritional profile.	[27]
Harpaticoid copepod	*Halamphora* sp.	Harpacticoid copepod enriched with diatoms *Halamphora* sp. enhanced the growth of black tiger shrimp postlarvae.	[28]
Mesocyclops leuckarti	Rice bran, soybean meal, *Chlorella* sp., and *Spirulina* sp.	Rice bran exhibited a higher population density (53.3 ind/mL) and survival rate (97.4%) compared to other dietary conditions after 16 days of cultivation.	[14]
Oithona rigida	Rice bran, *Nannochloropsis oceanica* and mix diet	Rice bran and *Nannochloropsis oceanica* are recommended diets that enhance growth and reproduction in copepods, whether provided individually or in combination.	[29]
Copepod	*Chlorella* sp., capsicum, mixed vegetable (carrot and spinach), yeast and rice bran	Copepods enriched with rice bran exhibited increased levels of protein and lipid.	[30]
Copepod	Yeast, rice bran, *Chlorella sp.* and palm kernel cake (PKC)	Copepods that are fed rice bran demonstrate beneficial effects on the growth rate, survival rate, and colouration of fish larvae, contingent upon the organic nutritional content provided to the copepods.	[31]
Copepod	*Tetraselmis* sp., *Nannochloropsis* sp., mixed algae (*Tetraselmis* sp. and *Nannochloropsis* sp.), yeast (*Saccharomyces cerevisiae*) and micro-pallet	Copepods that are fed microalgae exhibit positive outcomes in growth, reproduction, and biochemical composition, which are influenced by the nutritional content of the algae provided to them.	[32]
Cyclopoid copepod	Carrot, water spinach, lettuce and *Tetraselmis* sp.	To increase the nutrient content of copepods, water spinach (*Ipomoea aquatica*) can be used in place of microalgae as an enrichment. *Penaeus monodon* fed copepod-enriched *Tetraselmis* sp. had the best survival rate (91.67 ± 0.29%).	[33]
Cyclopina kasignete	*Nannochloropsis oculata*, *Tisochrysis lutea,* dry *Melosira* sp. and mix diets	Copepods demonstrated enhanced growth, survival, and productivity when provided with fresh *T. lutea*, dry *Melosira* sp., and a combination of both species, in comparison to alternative dietary treatments.	[34]

In copepod enhancement, microalgae are a good enrichment diet as they contain a feeding profile that can stimulate growth, survival and life table parameters of most aquatic organisms [35]. The success of copepod mass culture is directly associated with the microalgae quality and availability provided to the aquatic animals. Dietary microalgal content has direct effects on copepod growth, reproduction, and survival. Integral propagation methods of microalgae such as the adjustment of light and nutrients and culture conditions are important for better performance of copepod culture [35].

The application of probiotic treatment in fish and crustacean larvae through live feeds has emerged as an innovative strategy aimed at enhancing fish larvae growth performance, survival rates, and disease resistance [36]. Probiotics have been delivered to the target species through enrichment and bio-encapsulation in some cases [37]. During bio-encapsulation, a suite of nutrients is encapsulated into live organisms to improve their nutritional and physiological characteristics. Researchers have recognized the contribution of zooplankton by fermentation feed with the addition of probiotics [38].

This method aims to enhance plankton development and promote sustainable aquaculture practices through the utilisation of organic matter derived from agricultural by-products, including crop residues, manure, and other waste materials. Recent work showed that diverse feeding regimes such as swiftlet waste, rice bran and soybean meal were suggested for copepods, *Oithona rigida* as an enrichment food and showed effective growth and survival of fish [1].

4.2. Copepods Scaling Constraints

Extensive copepod production imposes significant costs. The 18 L canisters of concentrated *Chlorella* sp. (density approximately 20 billion cell/mL) utilised as feed cost between US $140 and $150 [39]. Scaling up continues to be a constraint because of the vulnerability to egg cannibalism and culture collapse in batch and semi batch-systems. This necessitating considerable labour, and algal production equipment, in contrast to automated, standardised RAS designs that have not yet achieved commercialisation. Studies indicate that inadequate production ($<10{,}000$ eggs L^{-1}), heightened sensitivity of egg vialability to ammonia (NH_3), and productivity declines beyond peak density suggesting non-linear scale effects [40].

Seasonal field methods, such as Taiwanese earth-pond copepod farms utilising inorganic fertilisation at around 700 µg N/L and 100 µg P/L, decrease expenses by 50% relative to pond fed by algae [2]. Nevertheless, they lack year-round uniformity and necessitate continuous nutrient management. Consequently, techno-economic research indicate that research should priorities automatic continuous feeding (to decrease labour), modular recirculating aquaculture system (RAS) design, selective breeding for enhance fecundity, integration with recirculating aquaculture or multitrophic systems. Table 2 discusses constraints and suggested research and development directions of copepods

Table 2. Constraints and priority research and development directions of copepod culture.

Constraint	Underlying Cause	Research and Development Directions
Culture instability and population collapse	High incidence of egg and nauplii cannibalism under high-density conditions, coupled with pronounced sensitivity of early developmental stages to un-ionised ammonia (NH_3) accumulation and suboptimal waste removal efficiency	Selective breeding programmes aimed at enhancing fecundity and tolerance to ammonia stress, alongside the optimisation of biofiltration and water exchange strategies
High production cost	Heavy reliance on continuous production of high-quality live microalgae, which requires energy-intensive infrastructure, skilled labour, and strict environmental control	Development and validation of low-cost alternative diets, including formulated feeds, fermented products, and agro-industrial by-products
Limited scalability of culture systems	Lack of standardised, modular system designs tailored to copepod biological requirements	Engineering and validation of modular, scalable RAS designs for intensive copepod production
Labour-intensive operations	Absence of automated feeding, monitoring, and size-selective harvesting technologies specifically designed for copepod culture	Design and implementation of automated continuous feeding systems and mechanised harvesting technologies
Variable production output	Non-linear population dynamics driven by density-dependent effects, stage-specific mortality, and fluctuating food availability	Development of predictive population dynamic models and optimised harvesting schedules aligned with larval feeding windows

5. Environmental Change and Implications for Culture

Pelagic ecosystems have been significantly affected by climate change, particularly through the rise in ocean temperature, as well as through alterations in other significant environmental factors, including salinity, mixed-layer depth, and chlorophyll concentration [41]. Determining the suitable culture parameters for live feed organisms, such as copepods, is essential for comprehending their potential application in marine fish larviculture. Providing the appropriate environment for growth and reproduction is essential for producing a sufficient number of organisms to assess feeding efficacy across different species of marine fish larvae [42].

Generation time and reproduction are essential for calanoid copepods, influencing life-history traits and population dynamics. It exhibits significant variability in response to environmental conditions. Under optimal growth conditions, the majority of available energy is dedicated to reproduction, considering metabolic costs [43]. Establishing optimal culture conditions for copepods is essential for generating nutritionally uniform live feed. Marine fish larvae depend significantly on live food for first feeding because of their restricted digestive ability and substantial need for highly unsaturated fatty acids (HUFAs), especially docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA). Inadequate HUFA deficiency is a significant factor contributing to inadequate survival, aberrant development, and stunted growth in larval fish [44].

When metabolic demands are satisfied, assimilated energy is mainly used for reproduction under ideal environmental conditions, leading to high nauplii production and rapid population growth. However, inadequate salinity, temperature, or food conditions divert energy toward stress tolerance and maintenance, which slows development and decreases fecundity. These alterations may directly reduce copepod biomass production and jeopardize the availability of nutrients for larval rearing [43,45].

Larvae's dietary intake is indirectly influenced by environmental factors. Fish larvae's access to essential fatty acids will be impacted by dietary or cultural changes in copepods. Copepods raised on a high PUFA diet showed fatty acid profiles appropriate for larval rearing in a controlled feeding trial involving pikeperch (Sander lucioperca), with notable DHA/EPA ratios. This lends credence to the idea that careful culture design can raise or preserve targeted HUFA levels [46].

Production results are influenced by cultural and environmental strategies. Effective nutrient management can boost phytoplankton abundance, which in turn promotes copepod production, according to studies on cultural inputs, specifically the inorganic fertilization of copepod culture systems [2]. Environmental enrichment stabilizes culture conditions by controlling food supply, oxygen dynamics, and pH—all of which are known stressors for copepods—instead of directly changing temperature or salinity. Copepods' nutritional output is subsequently impacted by these factors [47].

This has a crucial strategic implication for aquaculture: environmental variability affects copepod abundance as well as their biochemical quality and, eventually, the performance of larval fish. Therefore, future climate-related changes may have an impact on hatchery productivity by changing the cost, stability, and efficiency of copepod culture. Sustainable marine fish larviculture should prioritize the development of robust culture protocols that sustain high reproductive output and consistent HUFA profiles under variable conditions.

6. Future Research Directions

Despite extensive experimental protocols over several decades, the commercial-scale intensive culture of copepods is still less developed than that of rotifers and Artemia. This is primarily attributed to variability in production yield, high labour demands, and challenges in maintaining water quality. System-level innovations, including automated recirculating culture systems, dynamic nutrient dosing, and mechanised harvesting, require systematic testing to enhance biomass output and economic viability [42]. The design and validation of standardised, replicable methods for industrial-scale copepod production are crucial for transitioning from experimental systems to established hatchery industry standards [48].

The nutritional composition of copepods, specifically the concentrations of essential fatty acids (EPA, DHA) and amino acids, is influenced by algal diet and culture conditions [45]; however, existing enrichment strategies remain insufficiently investigated. Research must quantify the effects of diet manipulation, algal strain selection, and microalgal enrichment on the biochemical quality of copepods and the subsequent growth performance of larvae, aiming to develop customised feeding protocols that optimise in situ nutrient transfer to fish larvae.

Copepod production systems demonstrate variability in biomass and developmental stage composition across seasons and time periods [24,49]. Research must concentrate on developing predictive models of cultural dynamics alongside optimised harvesting schedules to synchronise copepod life stages with fish larval feeding periods, thereby minimising waste and improving feed utilisation efficiency. This may encompass integrated environmental monitoring and modelling of abiotic factors such as temperature and salinity.

7. Conclusions

Copepods serve as a nutritionally superior live feed for larval fish when compared to traditional options like rotifers and Artemia. This superiority is attributed to their high protein content and favourable fatty acid profiles, including EPA and DHA, which align closely with the dietary needs of marine fish larvae. Their biochemical quality frequently exceeds that of enriched Artemia, diminishing the necessity for post-harvest enrichment protocols and improving larval survival, growth, and developmental outcomes when integrated into early feeding regimes. Despite these benefits, production limitations continue to pose a significant obstacle to broad implementation. Intensive culture methods for copepods remain less advanced compared to those for rotifers and Artemia, primarily due to variable yields, insufficient understanding of optimal diets and culture systems, and operational costs that impede scalable production in commercial hatcheries. Furthermore, extensive and semi-intensive systems provide accessible culture methods; however, they pose risks related to disease transmission, nutrient variability, and restricted control over copepod nutritional composition, elements that may undermine culture stability and larval feeding efficacy. To fully harness the potential of copepods in aquaculture, it is essential to implement integrated strategies that encompass enhanced culture protocols, species-specific nutritional optimisation, and analyses of economic feasibility. Addressing these challenges is essential for transitioning copepods from a supplementary feed to a dependable, commercially scalable live feed option that improves larval rearing success and promotes sustainable aquaculture growth.

Author Contributions

N.W.R.: includes conceptualization, methodology, literature review, writing—including preparing the first draft—supervision, project management, and obtaining funding; A.A.: writing—preparing the first draft, data curation, and literature review; N.A.H.: writing—review and editing, validation, and visualization; H.J.L.: writing, editing, and validation; S.R.Y.: Research, verification, writing, editing, and review; H.K.A.: stands for investigation, validation, writing, editing, and review; E.R.: stands for conceptualization, supervision, writing, editing, and review. All authors have read and agreed to the published version of the manuscript.

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The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

During the preparation of this work, the authors used ChatGPT (OpenAI) to assist with language refinement and improvement of grammar and readability. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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