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Utilization of live feeds in fish larviculture: A review

Christopher Teye-Gaga[1,2*] – Péter István Molnár[1] – Elshafia Ali Hamid Mohammed[2,3] – Péter Bársony[3]

[1]University of Debrecen, Faculty of Agricultural and Food Sciences and Environmental Management, Institute of Animal Science, Biotechnology and Nature, Department of Animal Science, University of Debrecen, 138 Böszörményi street, 4032 Debrecen, Hungary
[2]University of Debrecen, Doctoral School of Animal Science
[3]University of Debrecen, Faculty of Agricultural and Food Sciences and Environmental Management, Institute of Animal Science, Biotechnology and Nature, Department of Nutrition Physiology, 138 Böszörményi street, 4032 Debrecen, Hungary
[*]Corresponding author: christopher.teye.gaga@agr.unideb.hu

SUMMARY

This review examines the significance of live feeds in commercial aquaculture industry for production of fish and shrimp larvae, along with various challenges and prospects. Live feeds are an essential food source in larviculture, especially for marine fish, which depend on them for nutrition during the initial days of exogenous feeding. They are palatable, highly digestible, and their movement stimulates natural hunting and foraging instincts, promoting better development, lowering captivity stress, and increasing survival rates. Artemia is the most commonly used live feed in larviculture; however, it has low levels of omega-3 HUFA. Copepods are the most nutritionally rich live feed, containing high levels of DHA and EPA. Despite these benefits, they are less frequently used in larviculture due to technical challenges associated with large-scale cultivation at high densities. The use of live feed is labour-intensive and costly. The feeding period for fish larvae can be shortened using a co-feeding strategy. Microalgae rich in DHA have been utilized to enrich live feeds. Further research is needed to determine the most effective approach to significantly reduce the weaning time of fish larvae from live feed. This will lead to gradual and eventual complete replacement of life feed in the near future.

Keywords: *Live feed; fish larvae; Artemia nauplii; exogenous feeding; enrichment*

INTRODUCTION

Fish is a crucial source of protein for humanity, accounting for at least 17% of animal protein consumed by people globally (FAO, 2020). As the human population grows, the demand for fish meat is rising. To meet this demand, it is necessary to increase fish production through intensification of aquaculture. Producing healthy, high-quality and cost-effective fish for human consumption depends on the ability to produce a large number of healthy larval fish reliably and efficiently (Herath and Atapaththu, 2013; Mozanzadeh et al., 2021). A major challenge in the industrial upscaling of fish and shellfish production is the initial feeding of early larval stages, due to their dependence on live feed (Abate et al., 2016).

Fish at early life stages instinctively ingest moving feed (Rayner et al., 2015; Jaseera et al., 2021). In larviculture, the movement of live feed in the culture tank could activate their natural hunting and foraging impulses. This may help reduce captivity stress, increase survival rate and foster better growth and development (Conceição et al., 2010; Radhakrishnan et al., 2019). According to Kolkovski (2001), live feed is regarded as the most suitable and efficient source of sustenance for these larvae due to their natural composition and biological qualities.

These feeds supply essential nutrients, including protein with high amino acid content, highly unsaturated fatty acids, vitamins, and minerals, which support the development of the nervous system, immune system, as well as overall health of larvae (Jobling, 2016). They are palatable, making it readily acceptable; they contain only about 10% dry matter (Kolkovski, 2001; Rønnestad et al., 2013; Ljubobratovic et al., 2020), which facilitates better digestion. The small size of most live feeds (about 50–150 µm) is considered appropriate for the fish larvae's mouths. One major benefit of live feed, such as rotifers, *Artemia* and copepods, is that they can be enriched to meet the specific nutritional needs of different fish and shrimp species (Radhakrishnan et al., 2019). On the other hand, formulated diets, which typically contain fishmeal and soybean, have high dry matter content (about 60–90%) and lower amounts of soluble protein, which creates difficulty for fish larvae to fully break down and digest the proteins present in diets due to low levels of proteolytic enzymes (Kolkovski, 2001).

Notwithstanding the benefits of live feed in the successful raising of finfish and shrimp, producing and maintaining live prey can be expensive. This process is labour-intensive and often requires specialized skilled personnel. Additionally, it may necessitate extra infrastructure and equipment (Rønnestad et al., 2013; Ljubobratovic et al., 2020). The nutritional quality of live feed is influenced by the diet of the organism and the culture environment. This variability could result in inconsistencies in the quality and nutritional composition of the live feed fed to fish larvae, which may have a substantial impact on the growth and development of fish larvae (Radhakrishnan et al., 2019). Furthermore, the availability of live feed can fluctuate periodically, leading to a limited regular supply (Kolkovski, 2001; Ljubobratovic et al., 2020). For instance, during certain harvesting seasons in the Great Salt Lake, UT, USA, there have been low harvests of *Artemia* cysts due to disruptions caused by 'El-Nino' climatic conditions (Kolkovski, 2001; Sorgeloos et al., 2001; Abate et al., 2016). The use of live feed presents a risk of transmitting diseases to the

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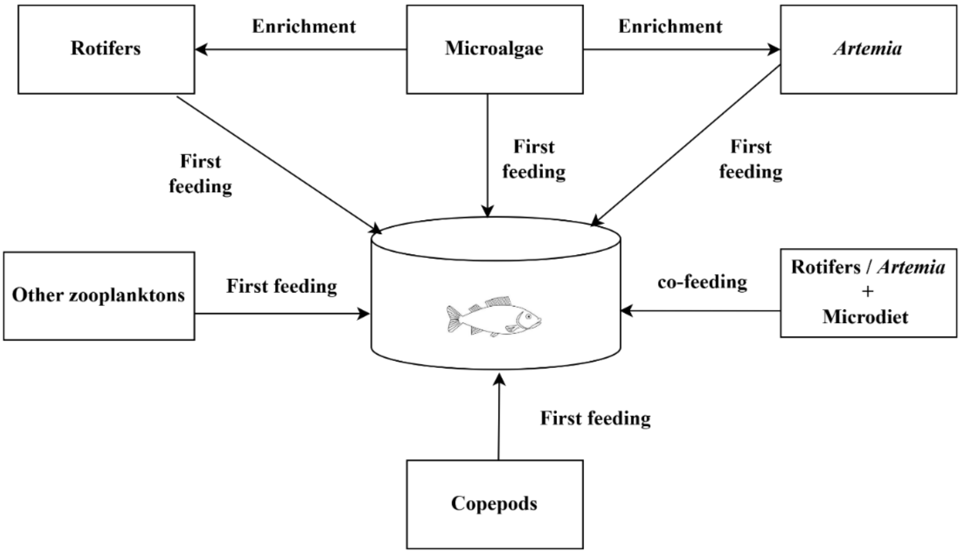
aquaculture system if not managed properly. These organisms can serve as vectors for parasites or harmful bacteria, which can endanger the health and survival of fish larvae (Hamre et al., 2019).

This review examines the importance of live feed in the commercial aquaculture industry for the production of fish and shrimp larvae, along with the challenges and prospects. We also examine the nutritional values and deficiencies of these feeds, as well as their enrichment to meet the nutritional requirements of fish larvae (*Figure 1*). Additionally, we discussed co-feeding and its relevance in the success of larviculture.

Figure 1. **Schematic diagram of fish larval feeding**



NUTRITIONAL REQUIREMENTS OF FISH LARVAE

The nutritional requirements of fish vary significantly depending on the species, their developmental stage, and environmental conditions. Fish larvae undergo rapid physiological and morphological growth, accumulating muscle and developing internal organs; their digestive anatomy and function differ from those of juveniles and adults. Moreover, there are considerable differences in ontogeny and feeding physiology in these life stages (Zambonino-Infante and Cahu, 2010; Hamre et al., 2013). Fish larvae have specialized dietary needs that differ both qualitatively and quantitatively from those of juveniles and adults (Kolkovski, 2001; Zambonino-Infante and Cahu, 2010; Hamre et al., 2013). Nutritional deficiencies during this critical stage can be catastrophic for their survival (Cahu and Zambonino-Infante, 2001; Zambonino-Infante and Cahu, 2010; Hamre et al., 2013). Nevertheless, in general, fish in their early stages require higher-quality diets than juveniles and adults (Henry et al., 2015). They need higher protein, lipids, vitamins and minerals for healthy growth and survival. However, carbohydrate is needed in lower levels since they can obtain sufficient energy from lipids and protein for metabolic activities **(**Zambonino-Infante and Cahu, 2010).

Protein functions as the primary structural component of tissues and muscles in the body (Moughan and Hendriks, 2018). Fish require high-quality proteins for growth, maintenance, tissue repair, reproduction and metabolic functions. As fish age, the proportion of protein required in their diet tends to decrease (Lim and Webster, 2008; Mjoun et al., 2010; NRC, 2011; Henry et al., 2015). The quality of protein in a fish diet is determined by a proper balance of the essential amino acids (Davis et al., 2009; Mjoun et al., 2010). Fish require ten essential amino acids (EAA), which cannot be synthesized de novo and must instead be obtained through their diet. EAA are crucial for protein synthesis in fish, so it is important to consider not just the protein content but also the amino acid profile of the diet for fish larvae. Also, it is imperative to provide the right balance of HUFA and EAA in the diet to ensure their healthy growth (Rajkumar and Vasagam, 2006; Glencross et al., 2014; Nunes, 2014). Carnivorous fish larvae have higher demands for animal-based protein (about 50–60%) than omnivorous and herbivorous fish. In intensive aquaculture, fishmeal is the primary source of protein with the highest amino acid profile that meets the requirements of fish (Zambonino-Infante and Cahu, 2010; Glencross et al., 2020; Kundu et al., 2021).

Dietary lipids, particularly phospholipids, are a rich source of highly digestible energy and essential fatty acids that are necessary for various physiological activities, including reproduction and immune function (Lim and Webster, 2008; Mjoun et al., 2010). For a variety of reasons, highly unsaturated fatty acids (HUFA), particularly eicosapentaenoic acid (EPA, 20:5n-3), docosahexaenoic acid (DHA, 22:6n-3) and arachidonic acid (ARA: 20:4n-6), are regarded as most important for larval fish (Watanabe et al., 1983; Evjemo et al., 2003; Mazorra et al., 2003; Hamre et al., 2013, 2019). They contribute to preserving the structure and function of cell membranes, which is

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necessary for a variety of physiological activities (Hamre, 2013; Hauville et al., 2014). HUFA are essential for the development and proper functioning of the brain, neural, visual systems and immune system in fish, which is critical for larvae's ability to sense and respond to their surroundings (Hauville et al., 2014). As a result, they are better equipped to withstand stress, which increases their survivability, particularly since they are more vulnerable to environmental stressors (Watanabe et al., 1997; Hamre et al., 2013; Mozanzadeh et al., 2021).

It has been established that the early life stages of carnivorous marine fish species require a significant amount of omega-3 HUFA. However, because fish larvae are inefficient at synthesizing HUFA, they must obtain this nutrient from their diet (Watanabe et al., 1983; Cahu and Zambonino-Infante, 2001; Evjemo et al., 2003; Ljubobratovic et al., 2020; Samat et al., 2020). It is important to consider the dietary ratio of DHA to EPA. For marine fish species, a dietary ratio of DHA/EPA of at least 2:1 is considered to be adequate for fish larvae since the yolk of many wild marine fish eggs typically contains a DHA/EPA ratio of approximately 2 (Kjørsvik et al., 2003; Ohs et al., 2009; Hamre et al., 2013). Vitamins, including water-soluble vitamins (B vitamins and vitamin C) and fat-soluble vitamins (A, D, E, and K), are required in small quantities for healthy growth, maintenance and many physiological processes (Lim and Webster, 2008). Vitamins C and E serve as antioxidants, assisting in protecting fish larvae from oxidative stress induced by metabolic processes and environmental variables.

Essential minerals, including calcium, phosphorus and magnesium, are required in small quantities for bone and tissue formation. In addition, trace minerals like iron, zinc, and copper are also necessary in trace amounts for various functions, including enzyme activity, osmoregulation, acid-base balance, skeletal development, and proper functioning of muscles and nerves (Sorgeloos et al., 2001; Lim and Webster, 2008; Mjoun et al., 2010). While fish in semi-intensive systems (e.g., fertilized ponds) are likely to meet their vitamin and mineral needs through natural food consumption, in an intensive system where natural food is limited, it is important to supplement the diet with vitamin/mineral premix to prevent structural deformities, ensure normal growth and maintain good health (Lim and Webster, 2008; Mjoun et al., 2010).

It is important to take into consideration the size and texture of feed (either live feed or microparticulate diet) since fish larvae are small and delicate; appropriate size and texture are essential to facilitate ingestion and digestion (Cahu and Zambonino-Infante, 2001; Imentai et al., 2020). Other factors, such as feeding frequency, feeding rate, and water quality management, are crucial for the proper development and health of fish larvae.

Rotifers

Rotifers (Brachionus species) are small aquatic invertebrates whose sizes range from 50 to 200 μm, depending on the strain and age (Dhert et al., 2014; Steenfeldt, 2015; Imentai et al., 2020). Rotifers are a vital source of live feed in the production of marine and freshwater finfish and crustacean larvae in most regions of the world. Their small size makes them appropriate for the mouth gape of many larvae. Additionally, their ability to remain suspended in water column, along with their sluggish swimming speeds, makes it easier for fish larvae to capture them. Furthermore, they have acceptable nutritional value and energy content (*Table 1*) and can be altered by dietary manipulation (Radhakrishnan et al., 2019; Imentai et al., 2020). *Brachionus plicatilis* and *Brachionus rotundiformis* are the two most widely used species of rotifers (Branchionidae: Rotifera) in marine larviculture, serving as a first-feed for the rearing of Atlantic cod (*Gadus morhua*), European turbot (*Psetta maxima*) and haddock (*Melanogrammus aeglefinus*) (Lim et al., 2003; Olsen et al., 2004).

Table 1. **Chemical composition (%) of live feed**

Live feed	**Nutrients**				**Reference**
	Protein	**Lipids**	**Carbohydrate**	**Ash**	
Artemia nauplii	43–61	14–23	10–20	5–14	Sorgeloos et al., 1986
Artemia adult	51–62	7–17	8–17	11–24	Sorgeloos et al., 1986
Enriched *Artemia*	52–68	10–19	11–17	8–14	Mourente &Tocher, 1992
Decapsulated cyst	50–57	13–14	6–7	5–6	Garcia-Ortega et al., 1998
Rotifers	28–63	928	10.5–27	–	Øie et al., 2011
Copepods	52–61	8–13	–	9–12	van der Meeren et al., 2008
Moina	66.33	10.82	19.83	–	Gladyshev et al., 2016
Daphnia	39.68	24.99	–	28.15	Cheban et al., 2017
Zooplankton	36.63	14.3	–	15.3	van der Meeren et al., 2008

Rotifers are also commonly used as first-feed in the cultivation of snappers, basses, rabbitfish, and groupers (Bengtson, 2003) and pike-perch *Sander lucioperca* larvae (Yanes-Roca et al., 2018; Imentai et al., 2020), zebrafish *Danio rerio* (Martins et al., 2019). These authors found that its use significantly reduced skeletal deformities, enhanced the growth and survival rate of fish larvae. The nutritional composition of rotifers (*Table 1*) depends on the size or age and the diet quality they are fed. Rotifers have high crude protein content

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(28–63% DW) (Øie et al., 2011), with approximately 50.6% of the crude protein being soluble protein (Srivastava et al., 2006).

However, studies have shown that the amino acid profile is unbalanced for several fish species, which may negatively impact larval growth and health (Srivastava et al., 2006; Abate et al., 2016). The lipid content ranges from 9–28%, with high phospholipid content, which accounts for 34–43% of their total lipids and 20–55% of triacylglycerol (van der Meeren et al., 2008). Rotifers contain high levels of vitamins B1, B2, C and E (Hamre et al., 2008; Jobling, 2016). However, they lack certain essential minerals such as copper, iodine, zinc, manganese, selenium and taurine, which may raise concern (Hamre et al., 2008; Mæhre et al., 2012; Hawkyard et al., 2014; Jobling, 2016).

Artemia spp

Artemia (brine shrimp) (Branchiopoda) is another important live-feed organism, which constitutes the most widely used species in commercial aquaculture industry due to its nutritional value and ease of culture. It is a significant food source for finfish, molluscs, and crustaceans (Hoffmann et al., 2021; Jaseera et al, 2021). The *Artemia* genus comprises eight species and over 50 geographical strains (Hou et al., 2006). *Artemia salina* and *Artemia franciscana* are utilized more widely in larviculture (Santhosh et al., 2018). The adult *Artemia* (about 8–12 mm in length) produces latent cysts that remain metabolically inactive when kept dry (Olsen, 2004). In aquaculture, these dormant cysts are employed as a convenient and nutritious off-the-shelf food supply for fish larvae (Gapasin and Duray, 2001). *Artemia* cysts of various species and strains can be obtained worldwide, particularly along the shorelines of hypersaline lakes, solar saltworks and coastal lagoons. The Great Salt Lake (GSL), Utah, and San Francisco Bay, California (both in the United States), Chaplin Lake, Canada, Macau, Brazil, Bohai Bay, China and Urmia Lake, Iran are some areas where Artemia cysts are harvested in commercial quantity (Laven and Sorgeloos, 1996; Nielsen et al., 2017).

Newly hatched *Artemia* nauplii (instar I) are between 400–500 µm long and dark brown-orange coloured. After about 8–10 hours of hatching, the organism undergoes a moult and enters the metanauplius I (instar II) stage, at which point it begins to feed. Just like rotifers, *Artemia* metanauplii are non-selective filter-feeders of minute particles (about 16.0 µm) such as microalgae, organic detritus and bacteria. Under optimal conditions, the larva goes through 15 moulting stages into adulthood between 12–14 d (Conceição et al., 2010). *Artemia* has been used in mass culture of various fish species including sea bream *Sparus aurata*, sea bass *Dicentrarchus labrax* (Cahu and Zambonino-Infante, 1994), Atlantic cod, *Gadus morhua* (Baskerville-Bridges and Kling, 2000), Atlantic halibut *Hippoglossus hippoglossus* (Hamre et al., 2019), turbot *Scophthalmus maximus* (Bromley and Howell, 1983), jade perch *Scortum barcoo* (Hoestenberghe et al., 2015), milkfish (Gapasin and Duray, 2001) and commercially important crustaceans such as giant freshwater prawn (*Macrobrachium rosenbergii*) and tiger shrimp (*Penaeus monodon*) (Gapasin and Duray, 2001) and African catfish, *Clarias gariepinus*.

The nutritional value of *Artemia* largely reflects the food they feed on. The nutritional status could also differ depending on the species, life stages, geographical strain and seasonality. While the range of protein content appears to be adequate for fish larvae, *Artemia* nauplii have been reported to have an unbalanced amino acid composition for many marine species with a deficiency in histidine, methionine, phenylalanine and threonine (Wanatabe et al., 1983; Zambonino-Infante and Cahu, 2010; Abate et al, 2016; Radhakrishnana et al., 2019). This imbalance has been linked to reduced nitrogen utilization, skeletal deformities and higher mortality in fish larvae (Martins et al., 2019; Zambonino-Infante and Cahu, 2010; Cavrois-Rogacki et al., 2021). However, *Artemia* contains significant levels of canthaxanthin, a pigment similar to astaxanthin found in copepods. Canthaxanthin acts as an antioxidant and a source of vitamin A, which is required for various physiological processes in fish larvae (van der Meeren et al., 2008). *Artemia* is rich in vitamins C, E, B1, and B2, which are essential for the general well-being of fish larvae. It also contains a high concentration of the most essential minerals required by fish larvae, except iodine and zinc (van der Meeren et al., 2008; Hamre et al., 2013). Iodine is essential for synthesizing thyroid hormones, which play a vital role in the metamorphosis of fish larvae, particularly flatfish larvae. Iodine deficiency in *Artemia* could lead to malpigmentation and other issues during metamorphosis, impairing fish larvae's growth (van der Meeren et al., 2008). Zinc is vital for the development of the skeletal system. Hence, its supplementation is necessary in the diet of fish during the early growing stage to prevent structural deformities (Nguyen et al., 2008; Fehér et al., 2013).

One of the major drawbacks of utilizing *Artemia* as live feed is its inherent deficiency in HUFA. It has low levels of ARA, EPA and a negligible amount of DHA and consequently poor DHA/EPA ratio (Hamre et al., 2013; Mozanzadeh et al., 2021), making it a suboptimal food source for fish larvae. While EPA is thought to correspond with a high survival rate, DHA is crucial for improving larval growth and quality as well as for brain and visual development; the lack of which significantly affects larvae's capacity to catch feed and respond to their environment (Conceição et al., 2010; Hauville et al., 2014). But most importantly, an optimal level of DHA/EPA ratio (2 or higher) is essential in promoting growth, stress resistance and pigmentation (Mourente et al., 1993; Conceição et al., 2010; Mozanzadeh et al., 2021).

Brine shrimp are rich in alpha-linolenic acid (LNA; 18:3n-3) and contain some moderate levels of linoleic acid (LA; 18:2n-6). These short-chain PUFA exist as phospholipids and are essential components of cell membranes, contributing to the overall well-being of fish larvae (Cahu and Zambonino-Infante, 2003; Kjørsvik et al., 2009). However, they are insufficient to

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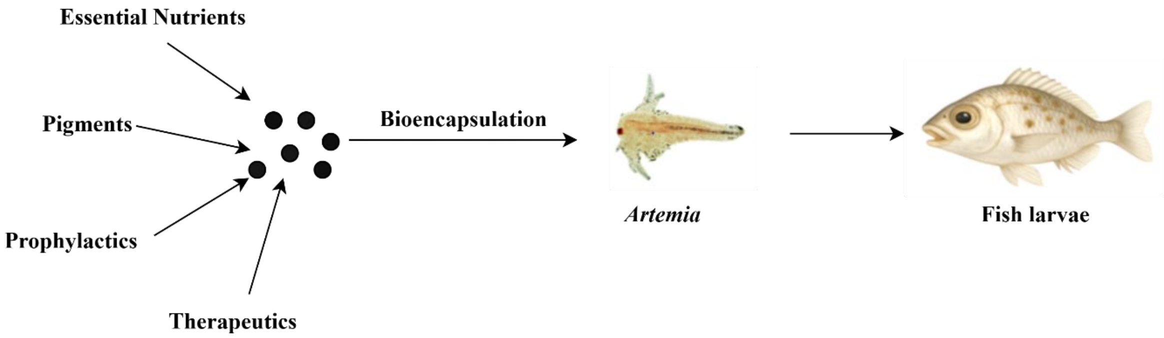
fully compensate for DHA, EPA, and ARA deficiencies.

While fish larvae can bioconvert LNA ingested in their diet into EPA and subsequently DHA in their cellular structure, this natural bioconversion process is often inadequate to meet their DHA requirement (Ohs et al., 2009). As a result, *Artemia* brine shrimp may not provide sufficient nutrition to the organisms that consume them. To address these challenges, *Artemia* is usually enriched using DHA-rich microalgae such as *Schizochytrium sp.* and *C. cohnii*, emulsified lipid diets, marine fish oil, tuna orbital, oil extracts and other commercial products (Kjørsvik et al., 2009; Jobling, 2016). For *Artemia*, the enrichment process typically involves immersing freshly hatched nauplii in a nutrient-rich solution of essential fatty acids, vitamins or minerals for 24 h. As the nauplii moult to metanauplii, they begin to feed and accumulate these nutrients into their biomass.

Bioencapsulation

Because *Artemia* metanauplii are continuous, nonselective, obligate phagotrophic filter-feeders capable of filtering particles smaller than 25µm regardless of particle type, these unique traits laid the groundwork for bioencapsulation, which involves embedding or suspending specific nutrients or compounds such as antibiotics, probiotics, therapeutics, prophylactics, pigments, and essential nutrients (e.g., fatty acids, vitamins, minerals), in small fat droplets (*Figure 2*).

Figure 2. **Schematic outline of the bioencapsulation technique using *Artemia***



Adapted from Léger et al. (1987)

These droplets are then fed to *Artemia* metanauplii, which are subsequently given to fish larvae (Léger et al., 1987; Roiha and Analytiq, 2015). Fish larvae greatly benefit from this delivery method, as *Artemia* acts as a 'living pill'. These nutrients and compounds enhance nutrient absorption, gut health, disease resistance, and reduce oxidative stress, making this an effective approach to supporting the healthy growth and development of fish and shrimp larvae (Sorgeloos et al., 2001; Rogers, 2009).

Copepods

Copepods are found in all aquatic ecosystems (freshwater, brackish and marine waters) of the world. In marine environments, they form the most abundant type of zooplankton. It is estimated that over 11,500 species exist (Evjemo et al., 2003; Drillet et al., 2011; Hamre et al., 2013; Alajmi et al., 2014). They constitute the main natural diets of fish larvae in the wild, a vital link between primary producers to consumers (Drillet et al., 2011; Alajmi and Zeng, 2014). Their size ranges from 0.3 mm (nauplii) to 2.5 mm (adult), making them highly beneficial for animals that require relatively small feed during their early feeding stages, such as groupers. Their unique swimming pattern, characterized by a hop-and-sink motion, has been found to effectively trigger feeding responses in fish larvae (Alajmi and Zeng, 2014; Abate et al., 2016). Copepods are capable of producing diapause and resting eggs that can be obtained and stored for days or months. Dormant eggs can be artificially hatched to produce new nauplii for fish larvae in hatcheries (Santhosh et al., 2018).

Copepods are categorized into three orders: Calanoida, Harpacticoida, and Cyclopoida (Støttrup, 2003). Among these, calanoid copepods, such as *Acartia spp*. and *Eurytemora affinis*, *Pseudodiaptomus annandalei* and *Oithona similis*, are most commonly used in aquaculture for marine fish larvae due to their high nutritional value compared to the other taxa (Evjemo et al., 2003; Rayner et al., 2015).

Nutritional value of copepod

It is generally acknowledged that copepods are the most nutritious live feed and may serve as a nutritional benchmark for fish larvae due to their biochemical composition (Ajiboye et al., 2011; Alajmi et al., 2014; Zeng et al., 2018). They are excellent sources of protein and essential amino acids, phospholipids and omega-3 fatty acids (Conceição et al., 2010), vitamins, and microminerals, which are crucial for larval growth performance, energy expenditure, stress tolerance, survival rate, pigmentation and successful metamorphosis. Copepods are therefore an important part of fish diets in both natural habitats and aquaculture, as they supply crucial nutrients for fish

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growth and overall health (van der Meeren et al., 2008; NRC, 2011; Zeng et al., 2018; Samat et al., 2020). Unlike other live feeds, copepods (especially calanoids) do not need to be enriched before being given to fish larvae (Abate et al., 2016).

The nutritional value of copepods can vary depending on the species, the geographical location, environmental conditions and food availability (Hamre et al., 2013). Nevertheless, in general, they have high protein content (52.4–57.6% DW) (Evjemo et al., 2003; Conceição et al., 2010) and also contain free amino acids (56–86 µg/mg DW) (Øie et al., 2011). This is particularly beneficial for fish larvae, which struggle to efficiently break down protein to obtain specific amino acids (Hamre et al., 2013; Rayner et al., 2015). The availability of free amino acids in copepods enhances protein utilization and growth in fish larvae (Rønnestad et al., 1999; Rayner et al., 2015). Copepods contain high levels of HUFA (particularly EPA and DHA), which account for about 60% of total fatty acids (Evjemo et al., 2003; van der Meeren et al., 2008). This percentage is significantly higher than even enriched rotifers and *Artemia* (Zeng, 2014; Alajmi and Zeng et al., 2018).

Moreover, in copepods, HUFA are mainly found in the polar fraction, which primarily consists of phospholipids, whereas in *Artemia*, they are mainly found in the neutral lipid fraction, predominantly made up of triacylglycerols. HUFA in phospholipids are easily digestible, hence more bioavailable in copepods (Evjemo et al., 2003; Jobling, 2016; Román-Padilla et al., 2017), making them an essential energy source for the fast-growing fish larvae. The DHA/EPA ratios are often greater than 2, which is considered optimal for larval growth (Rayner et al., 2015).

Although being present in lower quantities in copepods relative to *Artemia* or rotifers, ARA is nutritionally significant due to its role as a precursor for the synthesis of cell-signalling molecules, including eicosanoids, which play a critical role in osmoregulation, cardiovascular functions, neural control and reproduction (Gapasin and Duray, 2001; Mazorra et al., 2003; Hauville et al., 2014; Rayner et al., 2015).

Copepods are a rich source of astaxanthin, a vital antioxidant and precursor to vitamin A. They are also rich in essential vitamins such as C, E, B1, and B2, which are necessary for the overall health of fish larvae (Conceição et al., 2010). When compared to *Artemia*, copepods contain significantly higher levels of iodine, which is essential for the production of thyroid hormones (Jobling, 2016). A deficiency of iodine in *Artemia* can lead to malpigmentation and other metamorphic difficulties in flatfish larvae (van der Meeren et al., 2008). Studies have shown that using copepods as the main feed or complementary feed produces remarkably superior outcomes compared to using rotifers and/or *Artemia* (Alajmi and Zeng, 2014; Zeng et al., 2018). This is particularly true for species like Atlantic halibut (*Hippoglossus hippoglossus*) and Atlantic cod larvae (*Gadus morhua*), turbot (*Scophthalmus maximus*), yellow tail flounder (*Pleuronectes ferruginea*) and Senegalese sole (*Solea senegalensis*) (Evjemo et al., 2003), spotted rose snapper *Lutjanus guttatus* (Burbano et al., 2020). Utilizing copepods in aquaculture has proven to provide better outcomes in terms of healthy growth and development, survival rate and pigmentation than other zooplanktons (Dhert and Sorgeloos, 1995; Øie et al., 2011).

Despite these aforementioned benefits, copepods are not routinely used in the aquaculture industry. Although a recent study demonstrates the feasibility of producing and supplying copepods in commercial quantities, the lack of a well-established protocol for mass cultivation technology remains a significant impediment (Abate et al., 2016; Santhosh et al., 2018). As a result, developing a protocol for large-scale cultivation appears to be a promising direction for future research (Santhosh et al., 2018).

OTHER ZOOPLANKTONS

Cladocera

Cladocerans, commonly known as water fleas, are freshwater zooplankton with a high reproductive rate and the ability to tolerate a wide range of temperatures. They serve as a significant food source for freshwater fish. *Moina* and *Daphnia* are the two main genera of cladocerans used in larviculture (Leung, 2009; Radhakrishnan et al., 2019). They can be mass-cultured at high densities and are also an economical food source for raising ornamental freshwater fish (Malla and Banik, 2015). *Moina* is often employed as a substitute feed for *Artemia* in larviculture (Rasdi et al., 2020) and has been utilized in the culture of several fish species, including rainbow trout, Atlantic salmon, striped bass, Asian sea bass (*Lates calcarifer*), African catfish (*Heteroclarias*), and *Macrobrachium* spp (Dhert and Sorgerloos, 1995; Okunsebor and Ayuma, 2011; Rasdi et al., 2020). Although cladocerans are high in protein (*Table 1*), *Moina* and *Daphnia* possess a low content of essential fatty acids, particularly omega-3 HUFA. However, their nutritional value is greatly influenced by their food source. As a result, these organisms can be enriched to fulfil the specific nutritional needs of fish larvae (Dhert and Sorgeloos, 1995; Radhakrishnan et al., 2019). *Daphnia* contains a range of digestive enzymes such as amylase, proteinase, peptidases, and cellulase, which can act as exo-enzymes in the gut of fish larvae (Kumar et al., 2005; Malla and Banik, 2015).

Paramecium spp

Paramecium spp are a type of ciliate protozoan that serves as a vital food source for fish and shrimp larvae in their natural habitat due to their abundance in aquatic (freshwater, brackish and marine) environments. *Paramecium caudatum* and *Paramecium bursaria* are commonly used in larviculture as starter feed for fish and shrimp larvae due to their small size (50–300 µm). Their slow swimming ability also makes it easier for fish larvae to capture.. These protozoans have high nutritional content, and their soft body facilitates easy digestion. Nevertheless, these organisms do not meet the nutritional requirements of fish and need to be

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enriched (Wan-Mohtar et al., 2021; Lahnsteiner et al, 2023). *Paramecium* spp are relatively easy to culture under laboratory conditions. They are mostly cultured on bacteria, e.g., *Bacillus subtilis*. They reproduce rapidly under favourable conditions, providing a stable food supply for fish and shrimp during their larval stage. *P. caudatum* has been successfully used as a first feeding for zebrafish *Danio rerio* (Borla et al., 2002). Lahsteiner and Kletzl (2018) observed a high survival rate (90% at 10–18 dph) in larvae of perch *Perca fluviatilis* fed on *P. caudatum.* Similarly, Lahsteiner et al. (2023) reported positive effects on the growth performance of pikeperch (*Sander lucioperca*) and burbot (*Lota lota*) when fed *P. bursaria* as starter feed for 10 days.

CO-FEEDING STRATEGY IN LARVICULTURE

In their natural settings, fish larvae instinctively feed on live feed (Hoffmann et al., 2021). However, in hatcheries, a co-feeding strategy is employed to facilitate the weaning process onto wholly artificial diets. This technique typically involved feeding fish with a combination of live feed organisms (such as rotifers, *Artemia* nauplii, copepods and microalgae), along with microdiets that provide essential nutrients (Mai et al., 2009; Herath and Atapaththu, 2013; Merrifield and Ringø, 2014; Radhakrishnan et al., 2019) for some days, to progressively enhance the acceptability of dry feed (Rosenlund et al., 1997; Ljubobratović et al., 2015; Karakatsouli et al., 2021). As the digestive system develops anatomically and functionally, live feed is gradually replaced with inert foods until the weaning process is complete (Cahu and Zambonino-Infante, 2001; Karakatsouli et al., 2021). This approach appears to prepare and precondition the larvae’s gut to ingest and assimilate inert food. It also helps to rectify and complement potential nutrient deficiencies in live feed

Since the 1980s, co-feeding strategy has been employed to reduce mortality rate and improve healthy growth of fish and shrimp larvae (Rosenlund et al., 1997; Parma et al., 2013; Hauville et al., 2014). Kolkovski (2001), Kumar et al. (2005) suggested that feeding fish larvae with a combination of live feed and a formulated diet results in better growth and nutritional assimilation. This is because live feed contains certain hormones or neurotransmitter factors that can stimulate digestive enzyme secretions in fish larvae, thereby improving their digestive activity and ability to digest a dry diet (Hauville et al., 2014; Khoa et al., 2020). Although freshwater fish can be fed microdiets from the onset of exogenous feeding with a certain level of success, in hatcheries, most marine fish typically require live feed for a few days before transitioning to wholly formulated diets (Baskerville-Bridges and Kling, 2000; Cahu and Zambonino-Infante, 2001).

The duration for weaning differs among species; therefore, applying a co-feeding strategy should be tailored to the specific species (Mozanzadeh et al., 2021). Nevertheless, co-feeding typically begins when the larvae reach a particular size and developmental stage just before the start of gastric digestion (Baskerville-Bridges and Kling, 2000; Karakatsouli et al., 2021). In a study conducted by Ljubobratović et al. (2015), a seven-day (from 15 to 22 dph) co-feeding weaning strategy was recommended for optimal growth and high survival rate of pikeperch larviculture. In a similar experiment, Hoestenberghe et al. (2015) concluded that the jade perch (*Scortum barcoo*) larvae required a minimum of 10 dph for the start of co-feeding.

Studies demonstrate that fish larvae grow effectively in co-feeding conditions when the substitution of live feed is not excessive (Rosenlund et al., 1997; Hauville et al., 2014). Co-feeding strategy is also utilized to reduce production costs by promoting early weaning and shortening reliance on expensive live feed (Rosenlund et al., 1997; Fosse et al., 2018). This is important because, besides the high production cost, prolonged reliance on live feed can hinder the ability of fish larvae to effectively transition to formulated feed (Rosenlund et al., 1997; Parma et al., 2013; Ljubobratović et al., 2015; Fosse et al., 2018; Mozanzadeh et al., 2021). Co-feeding trials using commercial microdiets along with rotifer or *Artemia* have shown enhanced growth and a better survival rate of Atlantic halibut (Hamre et al., 2019), sea bass, gilthead seabream and turbot (Rosenlund et al., 1997), common carp (Fosse et al., 2018), pike-perch *Sander lucioperca* (Ljubobratovic et al., 2015; 2020) when compared to those fed solely enriched *Artemia* or a completely inert diet (Parma et al., 2013).

Overall, co-feeding is an essential strategy in aquaculture larviculture that acknowledges the complexity of nutrition needed for aquatic organisms to develop successfully during their early stages. Developing varied and balanced diets can help improve the general health and growth of fish larvae, leading to cost-effectiveness in larval production. (Rosenlund et al., 1997; Parma et al., 2013; Fosse et al., 2018).

Microalgae

Microalgae are primary producers in the aquatic food chain and serve as a natural source of nutrition for aquatic animals, including finfish and shellfish. They are an essential component in fish larval production in hatcheries, where they are used to enrich live feed or provided directly as food for fish larvae (*Figure 1*) (Shield and Lupatsch, 2012; Jaseera et al., 2021). Fish species such as Atlantic cod, halibut and turbot rely on microalgae for nourishment from the onset of first feeding (Dhert and Sorgeloos, 1995; Øie et al., 2011). Molluscs and crustaceans (penaeid shrimps) consume microalgae directly (Shield and Lupatsch, 2012; Pacheco-Vega et al., 2018). Microalgae can be grown in hatcheries or purchased as concentrate or paste. They are often supplied to the larval tank alongside live feed, a practice known as "green water technique" (Øie et al., 2011; Merrified and Ringø, 2014; Jobling, 2016).

Incorporating microalgae into the fish-rearing tank could have multiple benefits. These include conditioning the water by removing harmful nitrogenous substances; altering the light milieu, which creates shaded conditions that reduce excessive light

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exposure; maintaining a balanced nutrient cycle while providing a source of food for fish; improve visual contrast between feed and the tank background thereby enhancing feed capture rate; stimulate feeding behaviour and promoting production of digestive enzymes in larval fish (Dhert and Sorgeloos, 1995; Shield and Lupatsch, 2012).

The selection of microalgae for direct food or for feed enrichment in larviculture is based on several factors, including, availability, physical characteristics of the cell and optimal cell size (12–15 µm) that satisfies the requirements of consumer organisms, sufficient nutritional value, high digestibility, absence of toxins, ease of culture at high densities, short life cycle, reproducibility in captivity, and tolerance to different environmental conditions (Patil et al., 2005; Shield and Lupatsch, 2012; Pacheco-Vega et al., 2018; Glencross et al., 2020). When different microalgae species are combined, it usually enhances animal growth as they compensate for each other's nutrient deficiencies (Øie et al., 2011). Although there are over 60 microalgae species, only a few are routinely cultured for aquaculture hatcheries (*Table 2*).

Table 2. **Groups, genera and species of microalgae most commonly used in aquaculture nutrition**

Group (Class)	Genera	Species	Application
Cyanophyceae	*Arthrospira (spirulina)*	*platensis*	FFI
Chlorophyceae	*Chlorella*	*sp., vulgaris, grossii,*	R, FFI
		virginica, minutissima	R, FFI
	Dunaliella	*sp., tertiolecta, salina*	R, FFI
	Haematococcus	*pluvialis*	R, FFI
Eustigmatophyceae	*Nannochloropsis*	*sp., oculata, gaditana*	R, FFI, GW
Prymnesiophyceae	*Isochrysis*	*galbana*	B, FFI, GW
	Pavlova	*lutheri*	B, FFI
Thraustochytriaceae	*Schizochytrium*	*sp.*	RAD, FFI
Bascillariophyceae (diatoms)	*Chaetocerous*	*calcitrans, gracilis*	B, CL, FFI
	Skeletonema	*costatum*	B, CL
	Navicula	*gregaria*	B, CL, FFI
Dinophyceae (dinoflagellate)	*Crypthecodinium*	*cohnii*	RAD

Key: FFI = formulated feed ingredient; B = bivalve molluscs (larvae/post larvae/broodstock), CL = crustacean larvae (shrimp, lobster); R = rotifer live feed; RAD = rotifer and *Artemia* live feed (dry product form); GW = "green water" for finfish larvae.
Source: adapted from Shield and Lupatsch (2012).

Nutritional value of microalgae

In recent years, extensive research has been conducted to determine the suitability of different microalgae strains for aquafeed, primarily relating to their nutritional content. The focus has been finding sources of long-chain polyunsaturated fatty acids (PUFA), such as eicosapentaenoic acid (20:5n–3, EPA), docosahexaenoic acid (22:6n–3, DHA) and arachidonic acid (ARA) as these nutrients which are particularly important for various marine animals are found in some microalgae species (Patil et al., 2005; Shield and Lupatsch, 2012; Glencross et al., 2020).

The chemical composition of microalgae (*Table 3*) can vary considerably depending on factors such as species, growth conditions and the processing method. Most microalgal species contain moderate to high levels of EPA (7-34%). *Nannochloropsis spp.* and diatoms have the highest levels of ARA (up to 4%). Species of class Haptophyceae, such as *Isochrysis galbana* and *Pavlova lutherin* are rich in DHA. Also, the family Thraustochytridae, particularly *Schizochytrium sp.*, have high lipid content, constituting up to 70% with DHA content of up to 35% (Conceição et al., 2010). Crude protein content can be as high as 60% in certain species like *Chlorella* spp and *Spirulina platensis* (Fadl et al., 2017; Glencross et al., 2020). However, the average chemical composition of major microalgae species used in aquaculture includes protein (12–40%), lipids (7–23%) and carbohydrates (5–23%) (Patil et al., 2005; Pacheco-Vega et al., 2018).

Microalgae also contain essential minerals (such as Mg, Zn, Se, Ca, Fe), vitamins (such as ascorbic acid, folic acid, α-tocopherol, biotin and pantothenic acid) (Abdelghany et al., 2020**).** Some species of microalgae, such as *Schizochytrium platenesis* and *Chlorella vulgaris*, have high concentrations of bioactive compounds, ß-1,3-glucan, which may function as an immunostimulant and antioxidant in fish; vital for disease resistance, larval growth and survival (Patil et al., 2005; Glencross et al., 2020; Sherif et al., 2020; Jaseera et al., 2021).

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Table 3. **Protein, lipid and carbohydrate content of some microalgae used in Aquaculture**

Genus	Protein	Lipid	Carbohydrate	References
Chlorolla sp	52	7.5	24.3	Shield and Lupatsch, 2012
Chlorolla vulgaris	51–58	14–22	12–17	Becker, 2007
Schzochytrium sp	11.9	54.1	–	Sarker et al., 2016
Spirirula sp	61.3	55	–	Sarker et al., 2016
Isochrysis galbana	36.6	26	34.5	He et al., 2018
Arthrospira plantensis	50–65	4–9	8–14	Becker, 1994
Nannochloropsis sp	30.3	21.8	9.6	Kent et al., 2015
Nannochloropsis oculata	42.2	5.6	–	Chen et al., 2013
Nannochloropsis salina	35	28	28	Chen et al., 2013
Dunaliena sp	34.2	14.4	14.6	Kent et al., 2015
Dunaliena salina	55	11	30	Chen et al., 2013
Schizochytrium sp	40.2.	12.5	38.9	Shield and Lupatsch, 2012

PROSPECTS

Wild zooplankton serve as a food source for a variety of finfish and shellfish in different stages of development. These organisms can be harvested from water bodies and used as supplemental feed in larviculture. However, their use increases the risk of disease transmission, which can lead to high mortality rates. Furthermore, the availability of wild zooplankton is limited. Their abundance varies depending on seasonality and location, posing a challenge to the continual reliance on them as a food supply in larviculture. As previously stated, producing live feed is a labour-intensive and expensive process. Except for calanoid copepods, all live feeds, including *Artemia* and rotifers, have to be enriched to enhance their nutritional content. Brine shrimp, the most used live feed globally, may not always be available and affordable since its reproduction is highly influenced by cyclical weather patterns such as El Niño. Due to a lack of appropriate technology for its intensive culture at high density, the use of calanoid copepods, which are arguably the most nutritionally appropriate live feed, is limited. Therefore, there is a need to replace live feed with alternative feeds such as biofloc technology and processed terrestrial insects.

Microdiets could completely replace live feed in larviculture. This will help reduce labour and cost and ensure a reliable food source. Research has demonstrated that some marine fish larvae could be fed on microdiets from the start of exogenous feeding. Although feed processing technology has advanced to produce homogeneous small-size feed to meet nutritional needs and larval mouth size, these microdiets lack the visual stimuli that live feed induces in fish larvae. More research is needed to determine the best approach to significantly reduce the weaning time of fish larvae off live feed. This will lead to the gradual and eventual complete replacement of life feed in the near future.

CONCLUSIONS

The first 4 to 5 weeks of exogenous feeding are critical for larval recruitment. It is important to provide adequate and optimal nutrition, coupled with good environmental conditions and excellent hatchery management practices, to ensure healthy growth and survival. Despite advancements in fish nutrition and feeding technology, live feed remained an integral food source for larviculture, especially for altricial marine fishes of high commercial value. It is important to gain a deeper understanding of the nutritional requirements of fish larvae to optimize diets and feeding protocols that improve larval quality. It has been established that the rising demand for seafood products could be met through the intensification of aquaculture. The starting point towards meeting global demand for fish is to ensure the production of healthy, high-quality quality and cost-effective larvae in an ecologically sustainable manner.

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List of Abbreviations:

ARA = Arachidonic acid
DHA = Docosahexaenoic acid
DPH = Day post-hatching
EAA = Essential amino acids
EPA = Eicosapentaenoic acid
FAO = Food and Agriculture Organisation
HUFA = highly unsaturated fatty acids
LA = Linoleic acid
LNA = Alpha linolenic acid
MOFA = Monounsaturated fatty acids
NEAA = Non-essential amino acids
NRC = National Research Council
PUFA = polyunsaturated fatty acids
SFA = Saturated fatty acids