



Recent Trends in Live Feeds for Marine Larviculture: A Mini Review

Yen-Ju Pan^{1,2*}, Hans-Uwe Dahms^{3,4,5}, Jiang-Shiou Hwang^{2,6,7} and Sami Souissi⁸

¹ Department of Aquaculture, National Taiwan Ocean University, Keelung, Taiwan, ² Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung, Taiwan, ³ Department of Biomedical Science and Environmental Biology, Kaohsiung Medical University, Kaohsiung, Taiwan, ⁴ Department of Marine Biotechnology and Resources, National Sun Yat-sen University, Kaohsiung, Taiwan, ⁵ Research Center for Environmental Medicine, Kaohsiung Medical University, Kaohsiung, Taiwan, ⁶ Institute of Marine Biology, National Taiwan Ocean University, Keelung, Taiwan, ⁷ Center of Excellence for Ocean Engineering, National Taiwan Ocean University, Keelung, Taiwan, ⁸ Université de Lille, CNRS, Université du Littoral Côte d'Opale, IRD, UMR 8187 LOG, Laboratoire d'Océanologie et de Géosciences, Station Marine de Wimereux, Lille, France

In marine larviculture, farmed larvae mainly rely on the alimentation of a group of smallsized phytoplankton and zooplankton referred to as live feed. Under the diversifying demands of human consumption and ornamental aquarium industry, new species of live feed and their innovative production methods are essential focuses for sustainable larviculture of many emerging fish and invertebrate species. The selection of proper live feed for larval feeding is based on several parameters, such as size, morphology, nutritional value, stock density, and growth rate. This review aims to highlight the biological characteristics, production approach, common larviculture applications as well as recent innovations in the aquaculture technology of live feed organisms (microalgae, ciliated protists, rotifer, *Artemia*, copepod, and others).

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***Correspondence:** Yen-Ju Pan panyj@mail.ntou.edu.tw

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INTRODUCTION

The percentage of world aquaculture production over the total fishery resource has increased from 14.6% in 1986 to 46% in 2018 (FAO, 2020). Although aquaculture is a fast-growing industry, one of the bottlenecks is proper rearing of the early life stages of many farmed fish and invertebrate species (Hu et al., 2018; Gallardo et al., 2022). The significant difficulty is the first feeding at larval weaning stage. When larvae deplete yolk reserves and experience transition from endogenous to exogenous feeding, they do not benefit from a well-developed gastrointestinal tract to efficiently digest the formulated diets (Infante and Cahu, 2001; Yúfera and Darias, 2007). The young larvae have limited capacity of predation (detection and capture) due to its immature jaw, muscle, and optical developments (Hu et al., 2018). Moreover, the specific larval feeding behaviors and nutritional requirements should be considered when selecting suitable first feeding ingredients to achieve a successful larviculture production (Rønnestad et al., 2013; Mejri et al., 2021). Contrary to formulated diets, motile and viable phytoplankton and zooplankton provide more bioavailable nutrients and trigger higher predatory responses, and have been recognized as promising exogenous nutrients for marine larvae (Conceição et al., 2010; Nielsen et al., 2017; Kandathil Radhakrishnan et al., 2020). These dietary planktons could live with the farmed larvae in the rearing system, and be ingested by the larvae whenever desire, are thus referred as live feeds.

Most emerging species in marine aquaculture and aquarium industries have a sensitive and small-mouthed larval stage, and their larviculture are very challenging due to a lack of appropriate first feeding protocols. It is of a crucial interest to enhance diversification and innovation within live

feed production programs to advance the fast-growing marine larviculture industry. Consequently, the aquaculture technologies of live feed productions are a focus point worldwide (Hansen and Møller, 2021). Here we review recent trends of live feed production at laboratory and industrial scales and discuss challenges and perspectives of its applications.

MICROALGAE

Microalgae plays a fundamental role in aquatic food webs by converting solar energy into bioavailable organic compounds and trophic resources. These micro-sized autotrophs are sustainable food item for aquaculture (Hemaiswarya et al., 2011), and are used as live feeds for several marine organisms such as bivalves (Tahir and Ransangan, 2021; Hassan et al., 2022), zooplankton (Pan et al., 2018; Dayras et al., 2021), larvae of crustacean (Sharawy et al., 2020; Sandeep et al., 2021), and echinoderm (Militz et al., 2018; Gomes et al., 2021). In marine hatcheries, the usage of microalgae could be categorized in three scenarios: (i) direct diet to provide nutrients to early developmental stages (Camus et al., 2021; Dayras et al., 2021); (ii) natural enrichment ingredients to zooplankton live feed organisms (Fu et al., 2021); (iii) water conditioners: microalgae are added to create "green water" which conditions water quality, reduces bacterial loads, increases visual contrast, and prey detection (Basford et al., 2021). Based on a variety of microalgal characteristics (Table 1) several aspects should be considered in applications: (i) cell size: that should be compatible to the ingestion capacities of the larvae; (ii) cell structure: property of cell walls or skeletons (e.g., cellulose, SiO₂, or CaCO₃) could affect the efficiency of ingestion and digestion; (iii) nutritional profile: content (actual amount) and composition (percentage) of various bioactive nutrients should be taken into account according to the nutritional requirements of their consumers (Borowitzka, 2013; Pan et al., 2018; Dayras et al., 2021). In general, the production of marine microalgal Chlorophytes (e.g., Nannochloropsis sp. and Tetraselmis sp.) can easily be sustained at high cell concentration and wide environmental conditions. Nevertheless, the thick cellulose cell wall and nutritional deficiency [i.e., low docosahexaenoic acid (DHA), 22: 6n-3, DHA or eicosapentaenoic acid (EPA), 20: 5n-3, EPA] hinder their applicability as live feed for some phytoplankton feeders (Pan et al., 2014). On the contrary, haptophyte and cryptophyte species (e.g., Isochrysis sp., Tisochrysis sp., and Rhodomonas sp.) provide superior nutritional values and higher digestibility due to their balanced polyunsaturated fatty acid (PUFA) profiles and soft cell structures (Latsos et al., 2020; Mai et al., 2021). Unfortunately, those microalgal species are relatively fragile and sensitive toward environmental stressors (e.g., temperature, salinity, and pH variations), and require more time and experienced labor to achieve successful productions. Recent studies focused on how to technically enhance their cell densities by manipulating the culture environments at automated regulations. In the past decade, photobioreactors (PBR) have been developed to produce microalgal biomass for biodiesel production (Peter et al., 2022). Currently many programs of biomass production are used to

extract bioactive compounds with an increasing use of diverse systems such as mesh ultra-thin layer, tubular glass, plastic bag, and flat-plate PBRs (Sandmann et al., 2021; Tayebati et al., 2021; Wurm and Sandmann, 2021). Although the PBR might increase production cost, these well programmed systems could realize extremely high cell density for aquaculture purposes (Vu et al., 2019; Tibbetts et al., 2020; Leal et al., 2021). Biotechnology has opened new avenues for microalgal applications, where strain selection including non-genetic as well as genetic modifications facilitate beneficial bioactive compounds (e.g., anti-pathogenic, anti-oxidant, etc.) for farmed aquatic larvae (Kiataramgul et al., 2020). Yet the biosecurity of transgenic microalgae should be carefully evaluated before their large-scale utilization.

CILIATED PROTISTS

Ciliates are a group of single-celled protist, which commonly exist in marine environments worldwide. Some ciliate species are pathogenic for fish, because they experience partially or completely their life cycle in or on the host (Jahangiri et al., 2021). Another group of ciliates appear to be planktonic and they have a potential as live feed in marine hatcheries (Wan-Mohtar et al., 2021). Culture techniques for Euplotes sp. and Fabre sp. have been developed in recent studies (Table 1). Ciliates could rapidly increase their populations by fission when fed on baker's yeast, fermented fish meal, and photosynthetic bacteria (de Freitas Côrtes et al., 2013; Balamuralir, 2020; Teiba et al., 2020). The production of these fast-growing protists does not necessarily rely on a microalgal diet, which greatly enhance the feasibility and convenience for culture maintenance. Most importantly, ciliates are known for their tiny cell size (20-60 μ m), which is particularly favorable for small-mouthed larvae (Hill et al., 2020). Indeed, ciliate-based diets have been acknowledged to successfully sustain larvae rearing of several marine ornamental or edible fish species (Nagano et al., 2000; Rhodes and Phelps, 2008; Madhu and Madhu, 2014; Leu et al., 2015). On the other hand, the use of bacteriovorous ciliates for pathogen removal has recently emerged. Lin et al. (2020) noted the remarkable increase of survival rate (approx. 60%) in pathogen challenge trials of grouper larvae when the water containing rich Vibrio campbellii was prefiltered by the ciliate Strombidium sp.

ROTIFERS

Rotifers are a group of multicellular microorganisms making up a phylum Rotifera. Since the 1970s, species and strains of the genus *Brachionus* have been used as live feed for the first feeding of marine larvae during 3–10 days post hatching (dph) (Lubzens et al., 2001). Although the taxonomy of *Brachionus plicatilis* and *Brachionus rotundiformis* complex remains inconclusive, they are normally referred as SS, S, and L type rotifer based on their size. Rotifers are highly demanded in the current larviculture industry due to the following reasons: (1) reasonable size spectrum (100– 250 μ m) and slow cruising swimming pattern for first feeding of commercially important fish species (e.g., sea bream and sea

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		Size range as live feed	General culture conditions	Common nutrient/diet	Applications as live feeds	Key nutritional advantages (% total FA or AA)	References
	<i>lsochrysis</i> sp.	3–6 µm	15–30°C, SNS			1–9% EPA; 8.1–12.5% DHA	Pan et al., 2018; Balakrishnan and Shanmugam, 2021; Shekarabi et al., 2021
	Tisochrysis sp.	3–7.5 μm	18–30°C, SNS			0.6–0.8% EPA; 10–11% DHA	Tato and Beiras, 2019; Dayras et al., 2021; Mai et al., 2021
Microalgae	<i>Pavlova</i> sp.	4–6 μm	23–20°C, SNS	Walne's, f/2 medium, agricultural fertilizers	Diet for copepod, rotifer, larvae of bivalves, echinoderms, and phytoplanktivorous fish	17.8–33.9% EPA; 3.6–10.2% DHA	Rehberg-Haas et al., 2015; Yang et al., 2020; Dayras et al., 2021; Hassan et al., 2022
	Nannochloropsis sp.	2–4 μm	26-30°C, SNS			26.2-35.2% EPA; 0-0.52% DHA	Pan et al., 2018; Yang et al., 2020
	Tetraselmis sp.	13–15 μm	26-30°C, SNS			4.2-5.2% EPA; 23.6-27.9% ALA	Pan et al., 2018; Lee et al., 2021
	Rhodomonas sp.	7–14 μm	15–25°C, SNS			8-15.8% EPA; 6-8.8% DHA	Latsos et al., 2020; Oostlander et al., 2020; Dayras et al., 2021
	Brachionus sp.	90–320 μm	25°C, 15–35 ppt				Snell et al., 2019
Rotifer	Colurella sp.	48–99 μm	22–28°C, 15–34 ppt	Microalgae (fresh cells, lipolyzed powder or concentrated paste)	First-feeding (2–10 dph) of larval fish and crustacean	Nutritional profile could be manipulated by enrichment	Chigbu and Suchar, 2006; Madhu et al., 2016
	Proales sp.	$82.7\pm10.9\mu\text{m}$	25°C, 2–25 ppt				Wullur et al., 2011; Hagiwara et al., 2014
Ciliated Protist	Euplotes sp.	60–110 μm	25–32°C, 20–30 ppt	Baker yeast, fermented fish diet, and microalgae	First-feeding (2–10 dph) of small-mouthed larval fish	Nutritional profile could be manipulated by enrichment	Tarangkoon et al., 2018; da Annunciação et al., 2020
	Metacylis sp.	37–50 μm	30°C, 33 ppt				Lee and Choi, 2016
Artemia	<i>Artemia</i> sp.	Newly-hatched: 400–500 μm; Enriched: 500–700 μm	28°C, 25–33 ppt	No feeding: nauplii used after hatch or enrichment (fish oil, fish soluble emulsions)	Fish or crustacean larvae at second-stage feeding (> 10 dph)	Nutritional profile could be manipulated by enrichment	Figueiredo et al., 2009
	Pseudodiaptomus annandalei/ P. inopinus	150–1,100 μm/ 200–800 μm	25–30°C, 15–20 ppt/20°C, 17 ppt	Live microalgae cell (Isochrysis, Rhodomonas/Phaeodactylum, Pavlova, Tisochrysis, and Chlorella)		2.9–12.8% EPA, 12.6–57% DHA/ 0.6–24.4% EPA, 1.3–12.7% DHA	Golez et al., 2004; Rayner et al., 2015; Matsui et al., 2021; Nielsen et al., 2021
	Acartia bilobata/ A. tonsa	100–1,100 μm/ 100–1,200 μm	25–30°C, 15–20 ppt/ 17–23°C, 27–34 ppt	Live microalgae cell (Isochrysis/Rhodomonas)		ND/ 16.5% EPA, 7.9% EPA	Drillet et al., 2008; Pan et al., 2014; Chi et al., 2018; Torres et al., 2022
	Apocyclops royi	100–1,000 μm	25–30°C, 15–20 ppt	Live microalgae (<i>Isochrysis</i> , <i>Rhodomonas</i> , and <i>Dunaliella</i>), baker yeast		1.8–13.4% EPA; 4–35.3% DHA	Chang and Lei, 1993; Pan et al., 2018; Nielsen et al., 2021
Copepod Other live feeds	Parvocalanus crassirostris	60–400 μm	21–27°C, 20–36 ppt	Live microalgae (Tisochrysis, Isochrysis, Rhodomonas, Tetraselmis, and Heterocapsa)	Several developmental stages (size range: 60–1,200 μm) for larval fish and crustaceans at	2.8-5.4% EPA; 6.1-22.3% DHA	McKinnon et al., 2003; Alajmi, 2015; Kline and Laidley, 2015; Jackson and Lenz, 2016
	Paracyclopina nana	70–600 μm	18°C, 15 ppt	Live microalgae (<i>Tisochrysis, Rhodomonas,</i> and <i>Pavlova</i>)	different feeding stages	2.3–5.5% EPA; 8.9–13.3% DHA	Lee et al., 2006; Dayras et al., 2021
	Bestiolina similis/ B. amoyensis	70–560 μm/ <100–<1,000 μm	26–28°C, 29–31 ppt/ 24–26°C, 28 ppt	Live microalgae (Isochrysis, Pavlova, Rhodomonas, and Tetraselmis/Isochrysis)		0.6% EPA; 2.5% DHA/ ND	McKinnon et al., 2003; Lian et al., 2018; Camus et al., 2021
	Moon jellyfish <i>Aurelia aurita</i>	$5\pm1~\text{cm}$	22°C, NS	Artemia nauplii/wild-captured	Lobster phyllosoma larvae.	9.88–17.5% EPA; 1.3–1.8% DHA, 0.8–14.5% glycine	Liu et al., 2015; Wakabayashi et al., 2016b
	Flame jellyfish Rhopilema esculentum	$2\pm0.5~\text{cm}$	22°C, NS	zooplankton	Juveniles of silver pomfret, and threadsail filefish	7.8% EPA; 1.36% glycine	Liu et al., 2015
	Fungal-like protists Schizochytrium sp.	9–14 μm	30°C, FW	Glucose solution	Diet or enrichment products for copepod, rotifer, and Artemia	40-54% DHA	Ramos-Vega et al., 2018; Guo et al., 2020
	Oyster fertilized egg or trochophore	50-70 μm	27.5-29°C, 35 ppt	No feeding: trochophore used after fertilization	First-feeding (2–10 dph) of small-mouthed larval fish	2.2-5.4% EPA; 2-3.3% DHA	Hur et al., 2008; Basford et al., 2019

FA, fatty acid; AA, amino acid; SNS, sterilized natural seawater; NS, natural seawater; FW, fresh water; EPA, eicosapentaenoic acid (20: 5n3); DHA, docosahexaenoic acid (22: 6n3); ALA, α-Linolenic acid; dph, days post hatching; ND, no data.

bass) (Conceição et al., 2010); (2) parthenogenetic reproduction facilitates high duplication rates (Fu et al., 2021); (3) capacity of tolerating high population densities and environmental variation (Suantika et al., 2003); (4) vector of nutrients or medicine delivery for fish larvae (Eryalcin, 2018; Fu et al., 2021; Safiin et al., 2021). In common batch culture systems, the density of Brachionus rotifer peaks during 4-7 day-post-inoculation, then the partial harvest and water exchange are carried out until subsequent inoculation (Sales et al., 2019). A semi-continuous recirculating aquaculture systems (RAS) has been developed to sustain superintensive rotifer cultures (>5,000 ind./mL) for periodic harvest (Suantika et al., 2000; Suantika et al., 2003). The maintenance of superintensive culture, however, increase the cost of rotifer production due to the equipment requirements of a recirculating aquaculture system (Suantika et al., 2003). Besides environmental control, antioxidants could be fed to rotifers to further improve their stress resistance in high density cultures with deteriorating water quality (Gao et al., 2021). The nutritional enrichment of rotifers is necessary due to the lack of many essential fatty acids for fish larvae at the first feeding stage (Ferreira et al., 2018; Ghaderpour and Estevez, 2020). Several enrichment products and protocols have been developed and evaluated to enhance larval growth and survival by improving ω 3 highly unsaturated fatty acid (HUFA) content, and a high DHA/EPA ratio in rotifers (Abu-Rezq et al., 2002). Recently, cultures of very tiny rotifer species ($<100 \ \mu$ m), such as *Proales* similis and Colurella adriatica, have been established (Table 1) and used particularly for the first feeding of small-mouthed larvae of marine ornamental species (Hagiwara et al., 2014; Madhu et al., 2016; Rebolledo et al., 2021).

ARTEMIA

Artemia is a genus of aquatic crustaceans in the class Branchiopoda, which dominates in hypersaline habitats (e.g., inland salt lakes). During dry seasons, Artemia starts to produce floating resting eggs (aka cysts) due to extreme hypersaline stress. The cysts are collected and processed (purification and dehydration), then canned in dark and cold conditions for further storage and distribution. Although Artemia are not naturally accessible food items for most marine or brackish larvae, they are extensively used in larviculture industry due to the following reasons: (i) durable cysts and manipulable hatching: obtain nauplii at desirable timepoints for larval feeding; (ii) size suitability: first naupliar stage of various Artemia species is ranging 400–500 μ m offering preferable size for second-staged larval feeding (7-14 dph); (iii) vector of nutrients or medicine delivery systems (enrichment needed before use) (Eryalcin, 2018). Artemia franciscana (Table 1) is one of the most utilized species due to its smaller body size and first-ranked annual production (1,000–2,000 tons) from the Great Salt Lake of Utah, United States. Whereas the production from hypersaline lakes in West Siberia, Russia and Kazakhstan, and salt works at Bohai Bay, China are ranked second or third cyst production areas of Artemia parthenogenetica and A. franciscana, respectively (Litvinenko et al., 2015). Other production areas, such as Brazil

(Camara, 2020), Vietnam (Le et al., 2019), Iran (Manaffar et al., 2020), and Tunisia (Sellami et al., 2020), also contribute certain amounts of cyst production. Due to the high market demand, Artemia Reference Centers have been established at Ghent University, Belgium in 1978, and at Tianjin University of Science and Technology, China in 2018 to promote applications of Artemia globally. Climate change and pollution have significant impacts on the harvest yield of cysts and consequently the price (Guong and Hoa, 2012; Santos et al., 2018; Van Stappen et al., 2020). Proper managements of culture conditions in salt work production (especially in Bohai Bay, China and Mekong Delta, Vietnam) should be addressed to stabilize both cyst and salt production, which might encourage a better socio-economic perspective for Artemia farming and their global supply (Manaffar et al., 2020).

COPEPODS

Planktonic copepods are naturally accessible and preferable live feeds for fish or invertebrate larvae in the marine environment and are used as live feeds in aquaculture hatcheries (Drillet et al., 2011; Santhanam et al., 2019; Fernández-Ojeda et al., 2021). Species from the orders Calanoida, Cyclopoida, and Harpacticoida are commonly selected and cultivated for larval feedings. Copepods provide wide windows of prey size (60-1,500 µm) due to their species diversity and 12 developmental stages (six nauplii, five copepodites, and adult). Their jerky swimming pattern attracts a higher predatory response of fish larvae (Burbano et al., 2020). Remarkably, the nutritional advantages (great contents of ω 3 HUFA) make these zooplankters favorable for larviculture even without an additional enrichment process (Matsui et al., 2021). In Taiwan and Vietnam, copepods are commonly harvested from outdoor earthen ponds after fertilization (Su et al., 2005; Blanda et al., 2015; GrØnning et al., 2019). Outdoor combined-species cultures might be feasible and cost effective, but the concerns of unstable production, species composition, and risks in pathogenic transmission have hindered the applications of copepods (Chang et al., 2011; Blanda et al., 2017). On the other hand, mono-species indoor copepod cultures of various species were established at either laboratory or intensive scales (Table 1), which facilitate copepod biomass of economic feasibility and biosecurity for larviculture industry (Abate et al., 2016; Santhosh et al., 2018). Particularly, the success in "micro-sized" copepod production (i.e., adult < 1 mm and nauplii $< 80 \ \mu$ m, such as in Parvocalanus sp., Bestiolina sp., and Paracyclopina sp.) have opened bright avenues for the larviculture of marine ornamental fish (Kline and Laidley, 2015; Callan et al., 2018; Zeng et al., 2018; Dayras et al., 2021; Wang L. et al., 2021), which are considered as challenging but necessary for trade and conservation demands. Instead of maintaining the culture, resting eggs and cryopreservation are alternative approaches to obtain alive copepods (Kaviyarasan and Santhanam, 2019; Pan et al., 2020; Wilson et al., 2021). Although the cold stored production of a specific copepod species (Acartia tonsa) seems to be applicable and commercialized, induction and storage protocol of various dormant copepod species and stages

should be further optimized to universally apply their novelties by the industry.

OTHER LIVE FEEDS

Heterotrophic Schizochytrium sp., Halophytophthora sp., and Salispina sp. (Table 1) are a group of unicell or filamentous microorganisms containing great amounts of PUFAs (Estudillodel Castillo et al., 2009; Su et al., 2021). The spray-dried powder of these microorganisms implicates great potential as alternative or supplementary diets to microalgae for the feeding and enrichment of zooplanktonic live feeds (Eryalçın, 2019). Besides holoplankton, some sessile marine organisms could be used as live feeds at their early developmental stages of planktonic life forms. Fertilized eggs and trochophore of bivalves, such as oyster (Crassostrea sp.) and blue mussel (Mytilus sp.), could be obtained by strip spawning (Scarpa, 2002; Turan and Kling, 2018). They are of a suitable size (40-60 μ m) and great ω 3 HUFAs contents, thus particularly supportive for the first-feeding of small-mouthed fish such as grouper and other reef species (Liao et al., 2001; Basford et al., 2019). Planktonic barnacle nauplii (100-150 µm) are also considered as potential live feeds (López et al., 2010; Basford et al., 2019). Cladocera species (e.g., Daphnia sp., Moina sp., and Ceriodaphnia sp.) could be cultivated with low cost using aquaculture biofloc technology and fermented animal wastes (da Silva Campos et al., 2020; Rasdi et al., 2020; Turcihan et al., 2022), and serve as live feeds for many freshwater fish larvae such as tilapia (Herawati et al., 2015), catfish (Vu and Huynh, 2020), and ornamentals like Betta fish (Kwon et al., 2013) and freshwater angelfish (Farhadian et al., 2014). Notably, studies have also indicated the feasibility of using water flea as live feed in marine larviculture of fish (Kamrunnahar et al., 2019) and shrimp (Mona et al., 2017). Jellyfish are used as live feed for the phyllosoma larvae of lobster (Palinuridae and Scyllaridae) (Goldstein and Nelson, 2011; Wakabayashi et al., 2012, 2016a), Threadsail filefish (Miyajima et al., 2011), and silver pomfret juveniles (Wang Q. et al., 2021).

DISCUSSION AND FUTURE PERSPECTIVES

Despite their wide applications in marine larviculture, the widely used live feeds (*Brachionus* rotifers and *Artemia*) show several

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limitations. The diversification and establishment of new live feed culture (especially micro-sized copepod and rotifer species) is promoting research programs and industrial applications. Production of dormant live feed (e.g., copepod resting eggs) is an ongoing program, and this is expected to pave the road for the marine larviculture industry. Future programs should target both indoor and outdoor aquaculture systems using appropriate RAS techniques with artificial intelligence (AI) technology to optimize both prey and larval culture performances. Developing technology and management of both virus free and bacterial free live feed for larviculture. Transferring scientific technology of live feed from academic achievements to stakeholders such as the aquaculture industry and farmers. Both scientists and farmers should work closely together to ensure the upscaling of pilot studies and maintain a required feedback cycle between industrial needs and their declination as scientific research challenges.

AUTHOR CONTRIBUTIONS

Y-JP wrote the first draft of the manuscript. H-UD, J-SH, and SS contributed to manuscript revision with Y-JP. All authors contributed to conception, design of the mini review, and approved the submitted version.

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