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Perspective

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Domesticating rotifer as animal feed using natural phytoplankton from eutrophic waters

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Rotifer biomass may be amplified with natural phytoplankton while rotifer seeds can be raised with auto- and hetero-trophically cultured microorganisms. Centralizing the seed raising but decentralizing the biomass amplification should make scaling rotifer domestication up convenient. We configure here a conceptional system with which rotifer are domesticated with natural phytoplankton and harvested as animal feed, which may achieve simultaneously animal feed production and environmental governance.

The world population is predicted to reach 9.7 billion in 2050, and 1250 million tons of meat and dairy must be produced annually to meet the global demand for animal-derived protein at the current consumption level until 2050[1]. Such demand should amplify further the need of the feed protein[2]. Researchers and manufacturers have never ceased to exploit new sources of proteins. From plants and insects to microbes, diverse alternative proteins, *e.g*., cultured meat, mycoproteins, bacterial proteins among others, have been marketing[3]. Microalgal and insect proteins have received intensive attentions nowadays. Microalgae can produce 22–44 tons of protein per hectare per year on small production scales, and capture simultaneously carbon dioxide from air[4,5]. Insects are the human and animal diets for thousands of years and still are today, and the global market for edible insects is forecasted to reach US$ 8 billion by 2030[6]. As the alternative sources of proteins, the cost, sustainability, environment friendliness, scalability among others determine their production efficiency while the allergens, hormones, diverse additives among others associate with their applications[3]. To date, a system driven by different energies, integrating economic and environmental profits, being easily scalable and highly efficient is not available yet. Here, we tried to configure a conceptional system with which rotifer are domesticated with natural phytoplankton inhabiting either freshwater or brackish and seawater and harvested as animal feed (Fig. 1).

Rotifer biology

Rotifer, a group of multicellular animalcules, mainly inhabit freshwater, and some of them inhabit salt and brackish waters and even damp mosses and lichens. Rotifer live about two weeks, and are approximately 0.1 mm to 0.5 mm in body length. Some rotifer species are free swimming while others are worming or sessile. To date, about 2200 rotifer species have been documented in phylum Rotifera which consists of classes Seisonidea, Bdelloidea and Monogononta. Rotifer species cultured as the live feed of aquacultured animals belong to class Monogononta, which reproduce both sexually and asexually. Rotifer feed on microalgae, bacteria, protozoa and organic detritus up to 10 micrometers large, and are preyed upon by shrimp, crabs among others[7].

The representative freshwater monogonont rotifer *Brachionus calyciflorus* is a species complex containing *B. calyciflorus sensu stricto* and other three, which success at temperatures varying between 19 °C and 37 °C[8,9]. The salt water or brackish rotifer *B. plicatilis* is also a species complex which contains *B. plicatilis sensu stricto* with larger body and genome size, *B. ibericus* with medium body and genome size and *B. rotundiformis* with small body and genome size as the representatives[10,11].

Up to date, cross-mating is the only method tried to develop new rotifer strains[12]. The CRISPR methodology has been developed in *B. manjavacas* by microinjecting Cas9-sgRNA ribonucleoprotein into the vitellaria of young amictic females. A developmental gene (*vasa*) and a DNA mismatch repair gene (*mlh3*) have been CRISPRed out and in, respectively[13]. A horizontally acquired and overexpressed gene encoding a specific DNA ligase mediates the extreme tolerance of *Bdelloid* rotifer to radiation. Their heterologous expression in human cell lines significantly improves their radio-tolerance[14]. Comparatively less genetic improvement has been carried out for rotifer, and almost all cultured rotifer species/stains are the isolates from natural environment. In such scenario, we prefer to use "domesticate" rather than "culture/cultivate" to describe their growth in artificial environments.

Historical knowledge of domesticating rotifer as live feed

The rapid growth of aquaculture depends on the steady supply of animal seeds while the live feed for their larvae is critical for seed raising. Diverse techniques have been developed to produce rotifer as the best live feed of larvae, which include batch, continuous and semi-continuous and high-density domestications[15]. The live rotifer feed is non-substitutable; they may donate their digestive enzymes, gut neuropeptides and nutritional growth factors essential for the feed digestion of the larvae[16].

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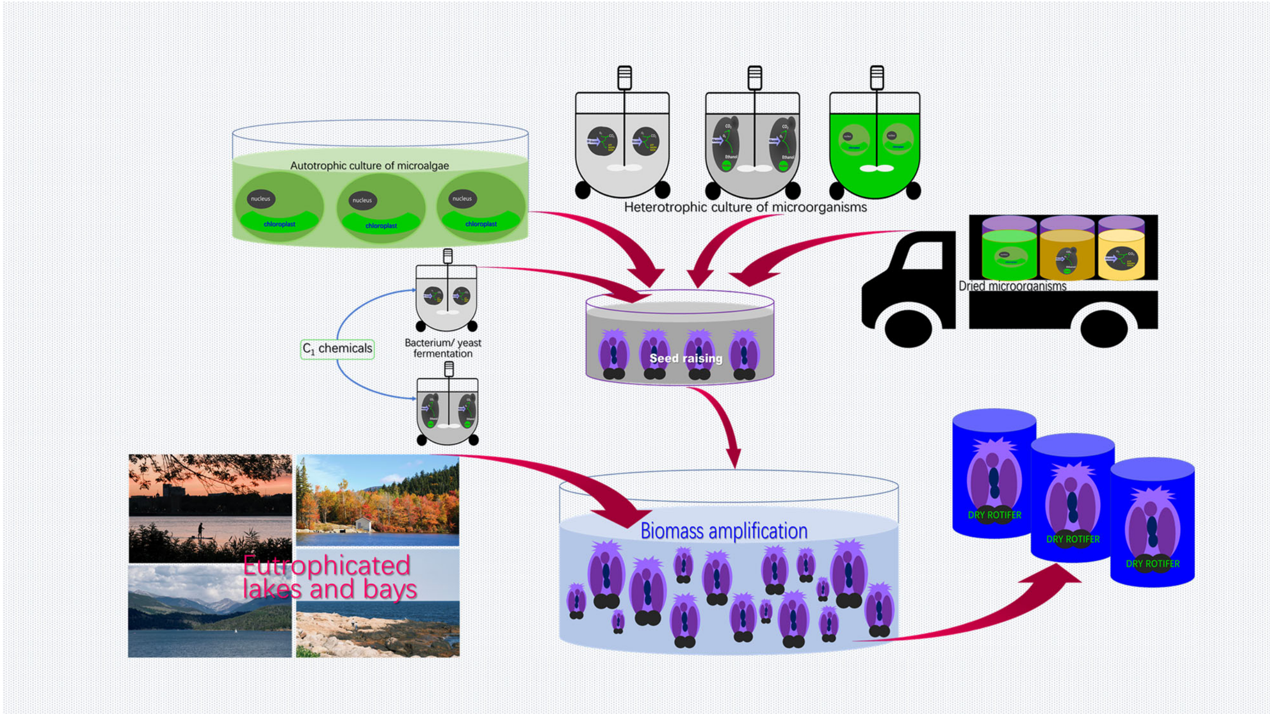

Fig. 1 | The rotifer seeds are raised with either dried microorganisms including bacteria, yeasts and microalgae or heterotrophically cultured bacteria, yeasts and microalgae or autotrophically cultured microalgae. The bacteria and yeasts fermenting C_1 chemicals can also be used in rotifer seed raising. The biomass of rotifer can be amplified with the natural phytoplankton from eutrophicated lakes or bays, and harvested and dried as animal feed. The figure is created with Microsoft PowerPoint 2019.

B. calyciflorus and *B. rubens* are the most commonly mass-domesticated freshwater rotifer. They tolerate temperatures varying between 15 °C and 31 °C, and thrive in waters of various ionic composition. They have been successfully reared on the microalgae *Scenedesmus costatogranulatus*, *Kirchneriella contorta*, *Phacus pyrum*, *Ankistrodesmus convoluus* and *Chlorella* sp., yeast and artificial diets[17]. When the density increases, *B. calyciflorus* can aggregate linearly to form resting eggs[18]. When batch-domesticated with *Chlorella* and a supply of oxygen at 28 °C, *B. calyciflorus* reached the highest density, 19,200 ind. mL^{-1}. When domesticated with a supply of oxygen and at constant acidity pH7 and 32 °C, the maximum density reached 33,500 ind. mL^{-1}. The high-density domestication of *B. calyciflorus* can be realized under optimal conditions, dissolved oxygen > 5 mg L^{-1} and NH_3-N < 12.0 mg L^{-1}, under which, the density of freshwater *B. calyciflorus* reached the maximum 33,500 ind. mL^{-1} [19]. In Japan at commercial scales, stable high-density domestication of rotifer realized also densities of 20,000–30,000 ind. mL^{-1}, and even 160,000 ind. mL^{-1} [15].

B. plicatilis species complex is commonly used as the first feed of over 60 marine fish and 18 crustacean species[17,20]. When *B. plicatilis* at an initial density of 737 ± 80 ind. mL^{-1} was domesticated with 200 cells mL^{-1} of *Chlorella* sp., twice a day, in 100 L plastic cylindrical tanks and seawater renewed on every 5th day for 32 days, 1798 ± 25 ind. mL^{-1} was recorded on day 20, and > 1000 ind. mL^{-1} was sustained till day 32[21]. Continuously domesticating *B. plicatilis* under the optimal condition (dissolved oxygen ~8 mg L^{-1}, 26–27 °C, salinity 10–20) can reach a density >1,000 ind. mL^{-1} [22]. In an automatic continuous system, dark and continuously supplied diluted sea water (salinity 20) at 24 °C, and harvested from the same volume of the seawater transferred into a harvest tank, 1,100 to 2,200 ind. ml^{-1} of *B. plicatilis* and 3,000 to 6,000 ind. mL^{-1} of *B. rotundiformis* were maintained[23]. When continuously cultured with *Nannochloropsis oculata* concentrate, *B. plicatilis* can reach a density of 2,188 ind. mL^{-1} on day 85 and maintain a density >1,500 ind. mL^{-1} from day 60 to day 90 when harvested every other day, 16 times in total[24]. The density of rotifers in these systems depends on feed quality and quantity, salinity, temperature and acidity of the medium which should be optimizable further.

Addition of γ-aminobutyric acid, porcine growth hormone, serotonin and human chorionic gonadotropin is known to improve the health status of cultured rotifers. The density and egg/female ratio of marine rotifer *B. rotundiformis* batch domesticated with dried *N. oculata* and *Chlorella vulgaris* was enhanced by 50 mg L^{-1} of γ-aminobutyric acid[25]. With the aid of oxygen supply and supplementation of favorable chemicals, the density of domesticated marine rotifer is expected to reach that of freshwater rotifer. These historical knowledges provided a methodological basis and the goal of rotifer mass domestication with natural phytoplankton.

Learning from the traditional nutrition enrichment of rotifer

Vitamin B_{12} is essential to human and animals including rotifer. Its biosynthesis is confined to a few bacteria and archaea, and its production relies on the fermentation of a group of natural bacteria and engineered *E. coli*[26]. Vitamin B_{12}-producing bacteria have served as a nutritive complement for the domestication of *B. plicatilis*[27]. The vitamin B_{12} enriched *Chlorella vulgaris* completely supports and significantly improves the growth of *B. plicatilis*[28] and *B. calyciflorus*[29]. The vitamin B_{12} rich *Schizochytrium limacinum* greatly enhances the growth of rotifers[30]. Vitamin B_{12} production can be produced in methanol-utilizing bacteria[31] and engineered yeast[32].

Rotifer must be enriched with DHA, EPA, ARA among others essential for the development and survival of marine fish and shrimp larvae[33]. It is not clear if these long chain PUFAs are essential for the growth of rotifer themselves; however, live microalgae and microalgal paste rich in omega-3 fatty acids, carbohydrates, lipids and plant sterols are the most appropriate rotifer feeds and rotifer PUFA enrichment species. Engineering microorganisms offers the best solution to a stable, sustainable and affordable production of omega-3 fatty acids[34]. A variety of genetic engineering tools and novel metabolic engineering strategies make *Yarrowia lipolytica* a robust workhorse for the production of an array of value-added products including PUFAs[35,36]. In addition to microalgae like *Nannochloropsis* sp., oleaginous fungi like *Mortierella alpina* and *Thraustochytrids* synthesize also ARA, EPA and DHA[37]. A marine thraustochytrid strain, *Schizochytrium* sp. KH105, produces docosahexaenoic acid, docosapentaenoic acid, canthaxanthin and astaxanthin which can be incorporated into rotifer and Artemia nauplii, and finally aid to the growth of fish larvae[38]. *B. plicatilis* feeding *N. oculata* yields high biomass, egg production and egg-carrying females, and *N. oculata* is optimal for its long-term biomass production[39]. These findings indicate that vitamin B_{12} and PUFA rich feeds should benefit the growth performance of rotifer, which are applicable in rotifer domestication with natural phytoplankton as the auxiliary means.

Domesticating rotifer with autotrophically cultured microalgae

Microalgae are rich in vitamins, antioxidants, proteins and lipids but low in carbohydrates, therefore, they are believed to be healthy food compounds[40]. Microalgae have been massively cultured for the production of diverse products including single cell proteins, animal feed, human food components, drug components, PUFA source, hot debated biofuel among others. However, culturing microalgae as an alternative protein source is limited by cost-ineffectiveness and downstream processing techniques including biomass harvesting[41]. Microalgal biomass production is also challenged by the high cost, weak knowledge about harmful organisms and loss of active ingredients[42]. Gene engineered microalgae have been suggested for protein drug development and edible vaccine production[43], which may aid to mitigate these limitations and challenges. Feeding rotifer with the autotrophically cultured microalgae and using the harvested rotifer as animal feed may provide a way out of the dilemma; harvesting rotifer as animal feed detours at least the extremely energy-intensive microalgal harvest. The high cost of microalgal culture can be reduced further when the microalgae are used in raising rotifer as mass domestication seeds.

Domesticating rotifer with heterotrophically cultured microorganisms

The heterotrophically cultured microorganisms including microalgae, bacteria, yeast, dinoflagellate among others contain complete profiles of nutrients, which should support well the high-density domestication of rotifers in combination with auxiliary techniques like oxygen aeration and hormone supplementation. These heterotrophically cultured microorganisms themselves are the sources of single cell protein. Their values in rotifer domestication embodies in the stable and sustainable raising of rotifer seeds for biomass amplification.

The biomass of *Arthrospira platensis*, *Chlorella vulgaris* and *Dunaliella salina* has been used as the sources of food[44,45]. A group of microalgae can grow heterotrophically, yielding as much as 25-fold biomass of those grow autotrophically[46]. From glucose, an ultrahigh-cell-density of 286 g/L *Scenedesmus acuminatus* has been grown in 7.5 L bench-scale fermenters[47]. The heterotrophic and mixotrophic microalgae metabolizing volatile fatty acids have been isolated and tentatively cultured[48]. *Crypthecodinium cohnii*, a marine heterotrophic dinoflagellate, has been fermented to accumulate high amounts of omega-3 polyunsaturated fatty acids[49]. A marine thraustochytrid *Schizochytrium* sp. is known as an ideal producer of high levels of polyunsaturated fatty oils, in particular, docosahexaenoic acid[50]. Thraustochytrids can accumulate over 150 g/l biomass and contain up to 55% lipids. Their broad substrate utilization capacity, several effective key metabolic pathways and a well-developed suite of bioprocess engineering strategies all point toward their great promise for the future exploitation[51]. Thraustochytrids have been increasingly studied for their faster growth rate and high lipid content[52].

Saccharomyces cerevisiae is popular for alcohol fermentation from carbohydrates for thousands of years while its biomass is rich in proteins, vitamins and minerals, making it a valuable ingredient in animal feed and other food products. The fermentation can be orientated to shunt the sugar metabolism on to the oxidative pathway, creating more ATP and biomass[53]. Some strategies like glucose-limited feeding may aid to increasing yeast biomass production[54]. The engineered *Saccharomyces cerevisiae* Y294 simultaneously expresses α-amylase and glucoamylase genes and hydrolyzes raw starch[55,56].

In line with microalgae and yeast, bacteria have also been cultured as the single cell proteins[57]. Engineered *P. putida* may produce value added products for application in the food and feed from the substrates generated from renewable feedstocks, such as lignocellulose, oils and silage[58].

Rotifer seed raising

Both autotrophically and heterotrophically cultured microorganisms including microalgae, bacteria, yeasts, dinoflagellate among others can be used as the rotifer feed in raising rotifer seeds in the form of live individuals and resting eggs. These rotifer seeds may be amplified several orders of magnitude in biomass by feeding them with natural phytoplankton pumped into the rotifer domestication facilities from eutrophicated lakes and bays. The rotifer seeds may be expensive; however, they assure the stability, reliability, and sustainability of seed supply. Mass-produced rotifer individuals can be preserved at low temperature, and directly used as the seeds. However, for collection, transportation and storage, resting eggs and amictic eggs are recommended for starting new round of domestication[20].

Domesticating rotifer with natural phytoplankton

Phytoplankton refers to one or more of thousands of natural eukaryotic microalgae. In practice, phytoplankton cover also the cyanobacteria like spirulina/arthrospira. Here, we call phytoplankton inhabiting lakes, reservoirs, pools and seashore bays the natural phytoplankton. The rotifer seeds can be delivered to the sites with rich natural phytoplankton, for example eutrophicated lakes, and amplified there in biomass in facilities either luxuries or shabby. The natural phytoplankton are pumped into the domestication facilities, and the rotifer at the desirable density are simply intercepted using the nets like those for phytoplankton. We prefer to use "interception" instead of "filtration" to describe the rotifer harvest; the interception nets have much bigger meshes than filtration nets. Natural phytoplankton is almost costless while rotifer harvesting through interception should be cheap, which should yield both economic and environmental benefits, and reimburse rotifer seed raising. The harvested rotifer biomass can be sun-dried, which should reduce the production cost further. Once the supply chain of rotifer seeds is established, the rotifer biomass can even be amplified by individual farmers alongside the eutrophicated pools. With autotrophically cultured microalgae, the outdoor domestication of rotifer has been tried[59].

The dry weight of *B. calyciflorus* individuals varied between 0.06 and 0.47 μg[60], and we take the median 0.25 μg in calculating the rotifer yield. If the rotifer density can reach the high one touched under the optimal conditions, which varies between 20,000 and 30,000 ind. mL^{-1}, then 1000–1500 tons of dry rotifer can be produced in 10,000 m^2 waterbody (1 m in depth), *i.e.* one hectare, and in one year (20 times of harvest each). The natural phytoplankton inhabiting eutrophicated lakes, seashore bays among others seem to be inexhaustible. Removal of nutrients by domesticating rotifer with natural phytoplankton is also one of the most attractive imaginable biomanipulation strategies to our most knowledge. We do not clear if the density of marine rotifer can reach that of freshwater rotifer. The facility similar to that of freshwater rotifer domestication will yield one tenth of dry rotifer (100–150 tons) if 2000–3000 ind. mL^{-1} can be realized, which is worth trying.

Eutrophication and climate change catalyze dense and sometimes toxic cyanobacterial blooms which threaten ecosystem functioning and degrade water quality[61]. One of the most important grazers that aids to control cyanobacterial blooms is *Daphnia* although cyanobacterial toxins like microcystins stress it indeed. Cyanotoxins include microcystins, hepatotoxins, digestive inhibitors, neurotoxins and cytotoxins. Cladocera like *Daphnia* consume cyanobacteria although they are poor feeds[62]. With the aid of gut bacteria, copepods feed on phytoplankton mixture containing nodularin-producing cyanobacteria[63]. The non-rotifer micrograzers may dissipate cyanobacterial blooms first while rotifers survive well and thrive even the blooms and remove them later[64]. The cyanotoxins have negative effects on rotifer growth and reproduction; however, *Brachionus calyciflorus* changes its life strategy and grazing intensity in response to the toxic cyanobacterial blooms[65,66]. Marine copepods and rotifers like *B. plicatilis* survive the harmful *P. globose* blooms by adjusting their life history strategy[67]. Hydrogen peroxide is often used to reducing cyanobacterial abundance; cyanobacteria are more sensitive than other phytoplankton[68]. With the technical innovation and implementation, it is expected that the influence of cyanobacteria on rotifer growth and proliferation can be smoothed away. Actually, a simple barrier net ahead of water pumping should separate floating filamentous cyanobacteria from other phytoplankton. To these understanding, we believe that the cyanobacterial blooms may interrupt the continuous domestication of rotifer but should not terminate its domestication.

Powering rotifer domestication with non-solar energy

The methanotrophs growing in methane at 500 ppm and lower have been identified[69]. The synthetic methylotrophic bacteria and yeasts such as *E. coli*, *Corynebacterium glutamicum*, *Pseudomonas putida*, *Bacillus subtilis* and *S. cerevisiae* metabolize methane and methanol[70]. The biomass of these microorganisms contains major nutrients such as proteins, fatty acids among others, which may serve as the protein source of animal feed including rotifers[71]. Heterotrophically culturing microorganisms like bacteria and yeasts with C_1 carbon sources like methanol may extend rotifer domestication to a fossil energy supported process. Either autotrophically or heterotrophically microalgae may be combined with these bacteria and yeasts and used to raising rotifer seeds and raring them directly even.

The commonest *Daphnia* species are often arrested together with shrimp and crab eggs as the food of people living in Chaoshan area, Guangdong Province, China. Copepods have been recommended as human food very early[72,73]. The cladocera and copepods have also been cultured as the live feed of aquacultured animals. Comparatively, the studies on the biology and culturing methodology of copepods and cladocera are less intensive. In seeable future, industrializing rotifer domestication should prosper with every passing day. Currently, the price of fish meal on Chinese market varies between 1333 and 1666 US$ ton^{-1} (10,000–17,000 RMB ton^{-1}). If dry rotifer can replace fish meal, running a rotifer biomass amplification factory will be highly feasible and profitable. The rotifer seeds raised with the proposed strategy may be amplified also as the open feed of fish and crab larvae. The microorganisms fermented from one carbon materials may be integrated into rotifer domestication. Such trial will build a linkage between rotifer biomass production with fossil energy, providing a trade-off between eating and other exhaustions when our food supply is extremely short.

The technologies controlling the inherent predators in natural water

Using natural phytoplankton as the alternative feed of rotifer is highly risky; natural water body could be plenty of potential predators such as ciliates, other rotifers, pathogenic bacteria, predatory fungi among others. To control the rotifers in microalgal cultivation and break cells in microalgal processing, the technologies like high-voltage pulse electroshock[74], pulsed electric field[75], electroporation[76], high-pressure homogenization[77], ultrasonication[78,79], ionizing radiation[80,81] among others have been developed. The natural water body contains the phytoplankton in appropriate size as rotifer feed. Pretreating the water with these techniques will kill these predators and may break their cells completely. The organic materials released will be transformed into bacterial cells in a short-term fermentation (remaining in ponds, pools or tanks for couple of days before use), and then caught by rotifers as their feed. This pretreatment may completely transform phytoplankton into bacteria, making them the most appropriate feed source of rotifers. Within acceptable range, the harmfulness to ecology should not be obvious.

The destroyed include pathogens of rotifer in the natural water body, which will avoid their disease-causing risk. These pathogens may also be suppressed by the heavy population of rotifers inoculated. Breeding disease resistant or stress tolerant rotifer varieties will be the most effective way of shooting the disease trouble. Pathogens and hosts battle permanently, no final winner and no final loser. Crops and humans ourselves will never end the war between pathogens and hosts. We believe that we have the ability of controlling the pathogens to the level of "existing but harmless".

Data Availability

No datasets were generated or analysed during the current study.

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Author contributions

L.G. and H.L. collected literatures, and generalized the findings from them. G.Y. developed the main idea, designed the conceptional framework, and wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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