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A critical review of holistic parasite management in sustainable aquaculture, integrating conventional and emerging strategies

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ABSTRACT

Finfish aquaculture is expanding rapidly in freshwater and marine settings, and it is now catching up to capture fisheries worldwide. The introduction of new species also involves familiarising people with a range of parasites. In intensive systems, these parasites can grow extremely powerful, causing severe outbreaks and creating a risk of spreading to wild species. Chemotherapeutants are still often employed, but because of concerns about resistance, the environment, and food safety, alternatives such as mechanical removal, cleaner fish, vaccination, and selective breeding are gaining traction. However, parasite adaptability limits the effectiveness of single-method therapies. Integrated parasite control promotes sustainability and reduces reliance on chemicals by targeting the vulnerable stages of parasite life cycles. This study highlights the need for integrated control of protozoan and metazoan parasites in aquaculture to enhance prevention and foster sustainable sector growth. It also highlights the importance of understanding host interactions, parasite ecology, and environmental factors.

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1. Introduction

Finfish aquaculture continues to expand across both freshwater and marine environments worldwide (FAO, 2024). While mariculture holds documented potential for further growth (Knapp & Rubino, 2016), freshwater systems presently dominate global production, particularly in Asia, with China and Indonesia as key contributors. However, freshwater aquaculture is gaining grip in Europe and the Americas due to advancements in recirculating aquaculture systems (RAS), which are attracting growing investments. The sector now supplies fish for human consumption at levels comparable to capture fisheries (FAO, 2024).

As aquaculture of new finfish species progresses, a significant challenge remains the emergence and propagation of new pathogens (Baseggio et al., 2022). Even when disease-free stocks are introduced, infections may still arise due to exposure to water sources harboring pathogens or through contact with wild fish populations. This spill-over of parasites into cultured stocks often results in intensified disease outbreaks under confined culture conditions, compromising both health and productivity of fish (Jerônimo et al., 2022). Moreover, the back-spill of pathogens into fish culture raises ecological concerns and reinforces the need for robust disease management. Farmers commonly resort to chemotherapeutants and therapeutics treatments as primary responses; however, reliance on these methods poses risks of resistance, environmental impacts, and regulatory restrictions (Jerônimo et al., 2022). To mitigate these concerns, sustainable alternatives, including mechanical removal, biological control, immunoprophylactic approaches, and selective breeding for disease resistance, are increasingly encouraged (Jerônimo et al., 2022).

This review discusses available and emerging control strategies targeting key parasitic taxa, including oomycetes, protozoans, and metazoans. Drawing upon a range of peer-reviewed studies, this article evaluates the efficacy of various interventions including chemical treatments, biocides, herbal extracts, immunostimulants, and integrated disease management approaches. Due to the adaptive nature of parasites, implementation of combination therapies under integrated control frameworks is recommended (Jerônimo et al., 2022). However, the global disparity in legislation governing the use of biocides and therapeutants presents a challenge, as authorisation varies significantly across countries.

2. Ecology and epidemiology of parasites in aquaculture

Complex host-parasite-environment interactions that control disease outcomes and transmission patterns effect the ecology and epidemiology of parasites in aquaculture (Khan, 2012). The prevalence and severity of parasites are influenced by both biotic and abiotic factors, including host density, species diversity, and the presence of intermediate or reservoir hosts, as well as temperature, salinity, pH, and dissolved oxygen. Intensive practices like high stocking densities and reduced genetic variability sometimes create conditions that encourage the establishment and spread of parasites (Khan, 2012). While hydrodynamics and water exchange patterns affect the geographical distribution of infectious parasitic stages, seasonal variations can accelerate the developmental stages of parasites. Additionally, anthropogenic causes might introduce new parasite species or strains, changing local epidemiological trends. These variables include habitat change and transboundary

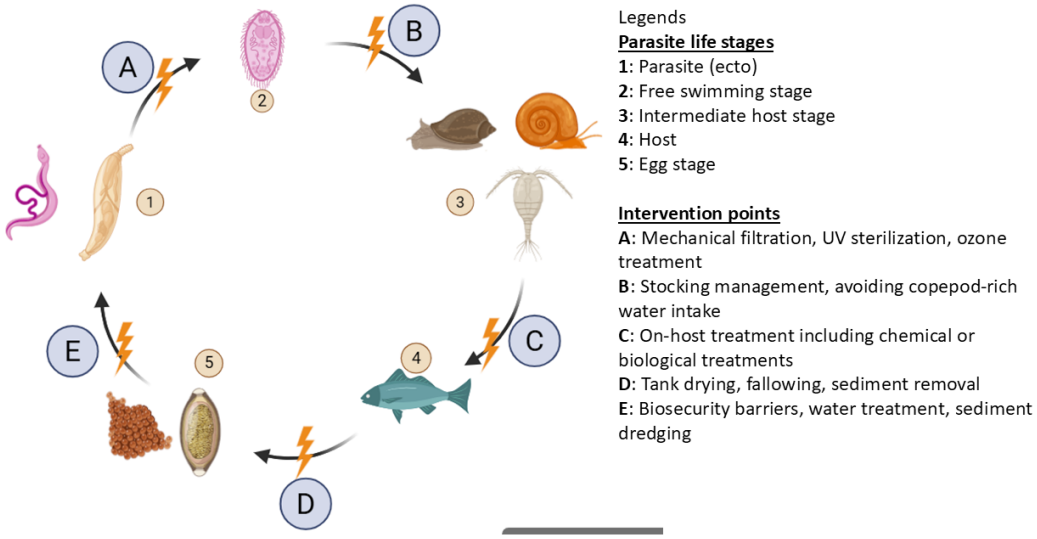


Fig. 1. Intervention spots for parasite management in aquaculture

movement of seed stock (Blondel et al., 2024; Hockley et al., 2014). A thorough understanding of these ecological factors is indispensable for developing predictive models of parasite outbreaks, identifying high-risk geographic locations and time periods, and developing integrated, ecosystem-based management techniques that enhance the sustainability and resilience of aquaculture systems.

3. Chemical and biochemical control measures

As part of indigenous technical expertise, aquaculture has traditionally used a variety of drugs with recognized toxicity risks to address ectoparasitic infestations. Intervention points within the parasitic life cycle stages are critical, as these are the stages at which these chemical agents should be applied (Fig 1). One of the most widely used drugs in the past was the malachite green, which demonstrated high efficacy at low concentrations in controlling oomycetes such as *Saprolegnia* in fish eggs and larvae (Lindholm-Lehto & Pylkkö, 2024). Additionally, it was effective against protozoan ciliates such as *Ichthyophthirius multifiliis* and flagellates such as *Ichthyobodo, Piscinoodinium,* and *Amyloodinium* (Buchmann, 2015, 2022). However, early concerns about the compound's safety profile prompted further toxicological evaluations. Subsequent research established that both malachite green and its primary metabolite, leucomalachite green, possess carcinogenic and genotoxic properties (Gharavi-Nakhjavani et al., 2023). Owing to these findings, the use of malachite green was ultimately prohibited in many regions, prompting the search for alternative therapeutics. , Various organophosphate insecticides, such as malathion and parathion, were formerly applied for the control of parasitic crustaceans (Rigos et al., 2024) and are still used occasionally. A list of all natural and synthetic antiparasiticides is detailed in Table 1. Nonetheless, the associated environmental risks, including toxicity to non-target aquatic fauna and health hazards to aquaculture workers, have significantly restricted their use in modern aquaculture (Rumschlag et al., 2019). This shift in treatment paradigms underscores the ongoing need for safer and more sustainable parasitic control strategies in aquaculture settings.

3.1 Oxidizing agents

Potassium permanganate has been extensively utilized for the control of external protozoan and metazoan parasites. Its oxidizing capacity disrupts cellular function in targeted pathogens, making it an effective treatment for a broad spectrum of ectoparasites (Farmer et al., 2013; Mitchell et al., 2008). However, it raises ecological concern due to its non-selective toxicity, which can adversely affect non-target flora and fauna, including beneficial algal communities and microbial flora (Fan et al., 2013). These environmental implications have led to increased scrutiny and regulatory constraints on their use in intensive aquaculture settings, potentially limiting future applications.

Hydrogen peroxide (H_2O_2) and its derivatives, such as sodium percarbonate and peracetic acid, have emerged as widely accepted oxidative agents in aquaculture, offering an alternative to more hazardous substances such as malachite green and formalin (Bögner et al., 2021; Jaafar et al., 2013). These compounds are chiefly used in immersion treatments for ectoparasitic infestations. They confer oxidative damage to external parasites and their developmental stages, leading to effective control of *I. multifiliis* and *Ichthyobodo necator* (Russo et al., 2007). In Mediterranean mariculture systems, including seabream (*Sparus aurata*) farms, H_2O_2has shown efficacy against gill-infesting monogeneans such as *Sparicotyle chrysophrii* (Mladineo et al., 2024). H_2O_2has also played a significant role in controlling salmon lice, *Lepeophtheirus salmonis,* on Atlantic salmon, *Salmo salar*, where it was initially effective as a surface treatment (Helgesen et al., 2015; Overton et al., 2018). However, with continual usage, partial resistance has been observed in some parasite populations, emphasizing the crucial role of IPM strategies and rotation of therapeutic agents to prevent resistance development. Collectively, H_2O_2-based treatments offer broad-spectrum efficacy with a more favourable environmental and safety

Table 1. Comprehensive detailing of synthetic and natural antiparasiticides used in aquaculture

Chemical Group	Application Methods			Mode of Action	Safety Considerations
	Bath/dip	Feed	Pond		
Ectoparasites					
Organophosphates	√	√		Inhibit acetylcholinesterase, causing neuromuscular paralysis	Narrow safety margin toxic to fish at high doses environmental toxicity
Pyrethroids	√			Disrupt sodium channel function in nerve membranes	Highly toxic to fish and non-target aquatic organisms; bioaccumulative
Formalin and aldehydes	√			Protein denaturation and cell lysis	Carcinogenic risk to handlers; not for food fish close to harvest
Peroxides	√			Oxidative damage to parasite membranes and tissues	Caustic at high concentration; oxygen supersaturation risk
Salts and inorganics	√		√	Oxidative stress and ion imbalance in parasites	Toxic to invertebrates; accumulation in sediments
Biguanides	√			Disrupt cell membranes and precipitate cell contents	Limited use in food fish; potential gill irritation
Halogenated compounds	√			Oxidative damage to cellular components	Strong oxidizers; handle with care; inactivate in organic matter
Endoparasites					
Benzimidazoles		√		Inhibit microtubule polymerization by binding β-tubulin	Teratogenic risk; resistance possible; environmental persistence
Quinolines and isoquinolines	√	√		Disrupt calcium homeostasis in parasite tegument	Generally safe; high cost; may require repeated treatment
Both ecto and endoparasites					
Avermectins and milbemycins		√		Bind to glutamate-gated chloride channels, causing paralysis	Safe at recommended dose; potential toxicity in overdose; residue concerns

profile compared to previously employed drugs (Helgesen et al., 2015).

3.2 Halogenated and chlorinated compounds

Formalin remains a commonly used chemotherapeutic agent in traditional aquaculture and, to a lesser extent, in recirculating aquaculture systems for the management of ectoparasites(Fajer-Ávila et al., 2003; Tavares-Dias, 2021). It is typically administered via bath treatments at 20 to 50 mg/L. This treatment effectively removes a variety of surface-associated protozoans and metazoans, including sessile ciliates, flagellates, and amoebae (Fajer-Ávila et al., 2003; Tavares-Dias, 2021). Notably, parasites such as *Amyloodinium* and *Ichthyobodo* are susceptible to formalin treatment, leading to their detachment or death (Kayış et al., 2015; Seoud et al., 2017). Additionally, formalin has demonstrated efficacy in eradicating monogeneans from both the skin (Tavares-Dias, 2021) and gills (Seoud et al., 2017; Tancredo et al., 2019) of fish. Formalin also targets free-living infectious stages of ,*I. multifiliis,* and trematodes, such as *Diplostomum,* within the water column, thereby reducing transmission risk in the culture environment (Buchmann, 2015; Tavares-Dias, 2021). Moreover, the treatment lowers overall bacterial loads and may decrease the infective pressure from other opportunistic pathogens. Despite its efficacy, formalin use can elicit a physiological stress response in treated fish, evidenced by elevated plasma cortisol levels (Tavares-Dias, 2021) and the upregulation of pro-inflammatory cytokines in epithelial tissues (Mathiessen et al., 2021). However, due to its allergenic and carcinogenic properties, formalin poses significant health risks to humans, necessitating cautious handling and appropriate safety protocols (Kim et al., 2011; Mathiessen et al., 2021).

Chloramine-T, another compound previously used for bath treatments against ectoparasites, has seen limited application in recent years due to regulatory constraints and a lack of formal approval from relevant authorities (Bentes et al., 2022; Powell & Clark, 2004). This oxidizing agent breaks down vital proteins and enzymes, cell membranes, and interfering with important metabolic processes including kinase and ATPase function (Bentes et al., 2022; Pant et al., 2024). It has efficacy against *Saprolegnia* at 400–600 mg/L (Pant et al., 2024) and is effective against *Trichodina* and *I. multifiliis*, lowering burdens by up to 50% at 20 mg/L (Bentes et al., 2022; Rintamäki-Kinnunen et al., 2005). However, higher doses can result in more severe gill damage, highlighting the necessity for accurate dosage. At optimal therapeutic doses of 10-20 mg/L, it induces minor and reversible histological and physiological alterations (Dar et al., 2024).

3.3 Ionic and metal-based treatments

Salinity manipulation remains an effective non-chemical strategy for controlling ectoparasitic infections in aquaculture (Tavares-Dias, 2022). In freshwater culture, immersion of parasitised fish in solutions with elevated sodium chloride levels can effectively eliminate several ectoparasites (Lanikova et al., 2021; Naas et al., 2024; Tavares-Dias, 2022). Conversely, many marine ectoparasites have a low tolerance for reduced salinity. When marine fish are briefly exposed to freshwater, these parasites may experience severe osmotic imbalance, which can lead to their detachment or death. The success of this approach depends on the parasite's ability to regulate internal salt balance. Stenohaline species are therefore more vulnerable to freshwater exposure (Pironet & Jones, 2000). Subsequently, shifts in salinity can disrupt the survival of ,amoebae, flagellates, ciliates, as well as metazoans, such as monogeneans. A practical application of this approach is seen in the management of amoebic gill disease (AGD) in *Salmo salar*, caused by *Neoparamoeba perurans*wherein

freshwater immersion has proven effective (Buchmann, 2015, 2022; Pironet & Jones, 2000).

Copper sulphate is a long-standing chemotherapeutant employed in aquaculture for the treatment of ectoparasitic infections and the elimination of external infective stages (Farmer et al., 2013; Man et al., 2020). Its parasiticidal efficacy is well established against a variety of pathogens, including *I. multifiliis, Ichthyobodo necator, Amyloodinium* spp., and crustaceans such as *Argulus* spp. (Farmer et al., 2013, 2014; Man et al., 2020). This compound is widely recognised for its potent biocidal properties and remains a valuable tool for managing parasitic outbreaks in fish culture systems.

Metal nanoparticles such as silver, copper, and selenium, along with nanoemulsions, are increasingly being explored as potential tools for controlling fish parasites. These materials can act directly against parasites, help deliver antiparasitic drugs more effectively, and improve water quality through disinfection, making them useful additions to parasite management strategies in aquaculture.Silver nanoparticles exhibit broad-spectrum activity against monogeneans, *Argulus*, and protozoa, achieving complete efficacy at low concentrations by damaging the tegument, altering metabolic pathways, and affecting gene expression (Bajwa et al., 2022; Kumari et al., 2025; Pimentel-Acosta et al., 2019; Zhang et al., 2023). Copper nanoparticles, while effective against monogeneans, cestodes, and *Saprolegnia* spp., require higher concentrations that may induce toxicity (Dos Santos et al., 2024; Ramyadevi et al., 2011; Zhou et al., 2023). Selenium nanoparticles show moderate antiparasitic efficacy, primarily through tegument damage and oxidative stress induction (Mahdy et al., 2024). Nanoemulsions can improve how plant-derived compounds are delivered and absorbed by the target organism. For example, nanoemulsions prepared with *Copaifera reticulata* oleoresin have been shown to increase the stability and availability of these bioactive compounds, which enhances their safety and effectiveness against monogenean parasites compared with conventional, non-nano formulations (Malheiros et al., 2020).

3.4 Synthetic antiparasitic drugs

The traditional strategy for managing parasitic infections in aquaculture involves the application of drugs with antiparasitic properties (Buchmann, 2022). However, the use of such medications is governed by strict regulatory frameworks and legislation that must be adhered to during both the investigational and validation phases preceding product approval, as well as during the administration of licensed therapeutics (Buchmann, 2022).

Benzimidazoles are broad-spectrum anthelmintics commonly used in aquaculture to control helminth parasites in freshwater and marine fish, especially nematodes (Yang et al., 2025). Albendazole, mebendazole, fenbendazole, flubendazole, oxibendazole, oxfendazole, parbendazole, and ricobendazole are among the frequently utilized substances. They work by preventing parasites' microtubules from forming, thereby disrupting cellular function and causing death (Doan et al., 2020; Zamanian et al., 2018). Mebendazole is widely used in both human and veterinary medicine and, as demonstrated by Chagas et al. (2016), is highly effective against monogeneans. Nevertheless, prior studies hinted at gill injury in Mugil liza following its use (Führ et al., 2012). Although flubendazole is effective against nematodes, its environmental and developmental toxicity in non-target species, such as zebrafish, has raised concerns (Kim et al., 2023; Muniz et al., 2023).. When used at the recommended doses, these drugs are generally effective and relatively safe for fish. However, their use should still be carefully managed because drug residues can pose ecological risks if withdrawal periods are not properly followed. In addition, these compounds share a similar mode of action by binding to tubulin, which means that repeated use may lead to cross-resistance among them (Bhinsara et al., 2018).

Praziquantel, an anthelmintic introduced approximately four decades ago, initially demonstrated strong efficacy against *Schistosoma* trematodes and has since been widely applied in aquaculture for control of monogeneans (Sitjà-Bobadilla et al., 2006),*Diplostomum* eye flukes (Bader et al., 2019; Zuskova et al., 2018) and *Bothriocephalus* (Bader et al., 2019; Vasilyeva & Skachkov, 2022). Despite its continued use, reports have emerged of decreased sensitivity in some parasite species.

From the beginning, the aquaculture industry depended on a variety of organophosphate chemicals, including metrifonate, dichlorvos, and azamethiphos. These substances primarily work against parasites by inhibiting their acetylcholinesterase activity, thereby paralysing them and leading to their death. Sublethal concentrations have demonstrated efficacy in controlling infections caused by *Dactylogyrus* (Reimschuessel et al., 2011), as well as *Lernaea* and *Argulus* in cyprinids (Iqbal et al., 2012), and *Lepeophtheirus* species in salmon aquaculture (Kaur et al., 2015; Myhre Jensen et al., 2017). Early cautionary reports highlighted the risk of anthelmintic resistance development in monogenean populations. This concern was substantiated in salmonid mariculture, where the extensive application of organophosphates, particularly azamethiphos, has led to the rapid and well-documented emergence of resistant strains of salmon lice (Kaur et al., 2015).

Synthetic pyrethroids such as cypermethrin, deltamethrin, and lambda-cyhalothrin are widely used insecticides that affect the nervous system of ectoparasites. They interfere with voltage-gated sodium channels in nerve cells, which disrupts normal nerve signaling and quickly leads to paralysis and death of the parasites (Farag et al., 2021; Myhre Jensen et al., 2017; Richterová & Svobodova, 2012).In aquaculture, they are primarily applied via bath therapy to control lice and other external parasites due to their fast knockdown effect (Farag et al., 2021; Richterová & Svobodova, 2012). While highly effective against a range of ectoparasites, pyrethroids have a narrow safety margin for fish, as they are rapidly absorbed through the gills, leading to acute toxicity at concentrations only slightly above therapeutic levels (Farag et al., 2021; Richterová & Svobodova, 2012). Reported 96-h LC_{50} values for cypermethrin and deltamethrin are often below

10 µg/L for many species (Soltanian & Fereidouni, 2017). Sublethal exposures can cause behavioural abnormalities, gill and liver problems, and disruption of metabolic and reproductive processes (Amin et al., 2022; Ullah et al., 2022). Environmental concerns are significant. Pyrethroids are lipophilic, persistent in sediments, and can bioaccumulate in aquatic organisms, posing risks to non-target species including invertebrates and fish (Ranatunga et al., 2023). These properties have led to strict regulations or outright bans in several countries (Prusty et al., 2015; Ranatunga et al., 2023).

The introduction of emamectin benzoate (EB), an avermectin derivative, in the late 1990s provided an effective and convenient in-feed treatment option (Stone et al., 2002). EB is widely used in aquaculture to control internal and external parasites by binding to gamma-aminobutyric acid (GABA) receptors and glutamate-gated chloride channels, thereby causing neuromuscular paralysis and parasite death (Mallik et al., 2023). Administered primarily as an in-feed treatment at ~50 µg/kg fish body weight for 7–10 days, EB offers high efficacy, often up to 100%, against sea lice (*Caligus minimus*), anchor worm (*Lernaea sp.*), gill parasites (*Salmincola edwardsii*), and nematodes (*Philometra rubra*, *Pseudocapillaria tomentosa*) (Baia et al., 2024; Duston & Cusack, 2002; Hakalahti et al., 2004; Kent et al., 2019; Raja et al., 2023). Also, reduced parasite load, improved survival, and restored hematological parameters within days of treatment (Kent et al., 2019; Raja et al., 2023) were observed upon EB treatment.

3.5 Antimicrobial adjuncts

Myxozoan infections constitute a significant concern in both freshwater and marine aquaculture systems. Although these infections are difficult to treat, the antibiotic fumagillin, derived from *Aspergillus fumigatus*, has been shown to inhibit parasite development and cyst formation. Effective control has been documented for *Tetracapsuloides bryosalmonae* in salmonids (Ahmad et al., 2021), *Myxidium giardi* in eel (Athanassopoulou et al., 2004), *Myxobolus* species in common carp (Banu & Rathinam, 2023), and *Enteromyxum leei* in bream (Golomazou et al., 2006).Among the antiparasitic agents that have been prohibited are nitroimidazole compounds such as metronidazole, secnidazole, and dimetridazole. These drugs have demonstrated high efficacy against flagellates, including *Spironucleus vortens* (Williams et al., 2012), as well as against ciliates such as *Ichthyophthirius* (Buchmann, 2022; Tokşen & Nemli, 2010). However, their use in food-producing animals has been banned within the European Community for several decades, primarily due to insufficient safety data and concerns regarding drug residues.

In certain regulatory frameworks, medications approved for one host species may be prescribed for the treatment of similar infections in other species, contingent on adequate evidence demonstrating therapeutic efficacy and host safety. Cascade regulations typically govern such prescriptions. Toltrazuril (commercially known as Baycox®) is an anticoccidial agent identified as a potential parasiticide following in vitro studies with various ciliate parasites, including *Ichthyophthirius, Apiosoma,* and *Trichodina* (Athanassopoulou et al., 2009; Bermúdez et al., 2006; Jaafar & Buchmann, 2011). Subsequent in vivo investigations demonstrated a prophylactic effect of toltrazuril when administered in-feed against *Ichthyophthirius* (Abdel-Hafez et al., 2014); however, the treatment did not affect trophonts embedded in the fish skin. Environmental concerns arise from the compound's prolonged half-life, raising questions about its sustainability and ecological impact (Lee et al., 2025). Additionally, other anticoccidial compounds, such as amprolium and salinomycin, have shown efficacy against the myxozoan *Enteromyxum leei* in mariculture of gilthead seabream, although their precise mechanisms of action remain to be elucidated (Ahn et al., 2017; Dohle et al., 2002; Farmer et al., 2025).

3.6 Biologically derived agents

Protozoan parasites, including ciliates, are highly susceptible to surfactants produced by certain bacterial strains. Specifically, a surfactant secreted by *Pseudomonas* strain H6 exhibits potent antiparasitic activity against multiple life stages of *Ichthyophthirius multifiliis*, as demonstrated by in vitro assays showing complete lethality at low concentrations (Al-Jubury et al., 2018; Li et al., 2022). Subsequent in vivo investigations revealed that maintaining a concentration of 10 mg/L of this bacterial surfactant in tanks significantly inhibited *I. multifiliis* infection in rainbow trout (*Oncorhynchus mykiss*), effectively interrupting parasite transmission (Marana et al., 2023; Sueiro et al., 2022). Importantly, toxicity assessments indicated minimal adverse effects on the host species (Mathiessen et al., 2021) and on non-target aquatic flora and fauna, including cyanobacteria, green algae, crustaceans, and zebrafish (Korbut et al., 2022). These results indicate that the bacterial surfactant appears to have a good safety profile and may serve as a promising option for parasite control in aquaculture. Its potential effectiveness, along with its environmentally friendly nature, supports further investigation into its use as a sustainable parasiticide.A variety of organic compounds, including essential oils from plants such as *Origanum*, *Lippia*, *Allium sativum*, and *Mentha* spp., containing terpenes, terpenoids, phenylpropenes, and isothiocyanates, have shown antiparasitic activity against *Ichthyophthirius multifiliis* and *Gyrodactylus spp.* through membrane disruption and cytotoxicity (Dawood et al., 2021; Gadallah et al., 2024; Li et al., 2022). A detailed phytotherapeutic measures are provided in Fig 2. Fatty acid ethyl esters from microalgae, such as ethyl laurate and ethyl eicosapentaenoate, exhibit activity against *Gyrodactylus turnbulli* and *Trichodina sp.* (Jawaji et al., 2024). ,such asOnonin and steroidal saponins, have proven effective against monogeneans (Ukwa et al., 2023; Yang et al., 2022). Silver nanoparticles, both chemically and green-synthesized, target *Argulus siamensis, Lernaea cyprinacea, and monogeneans* (Kumari et al., 2025).

Extracts from various medicinal plants have shown promise in controlling fish pathogens due to their bioactive constituents (Gadallah et al., 2024; Li et al., 2022). Extracts from *Origanum* were found to be effective against

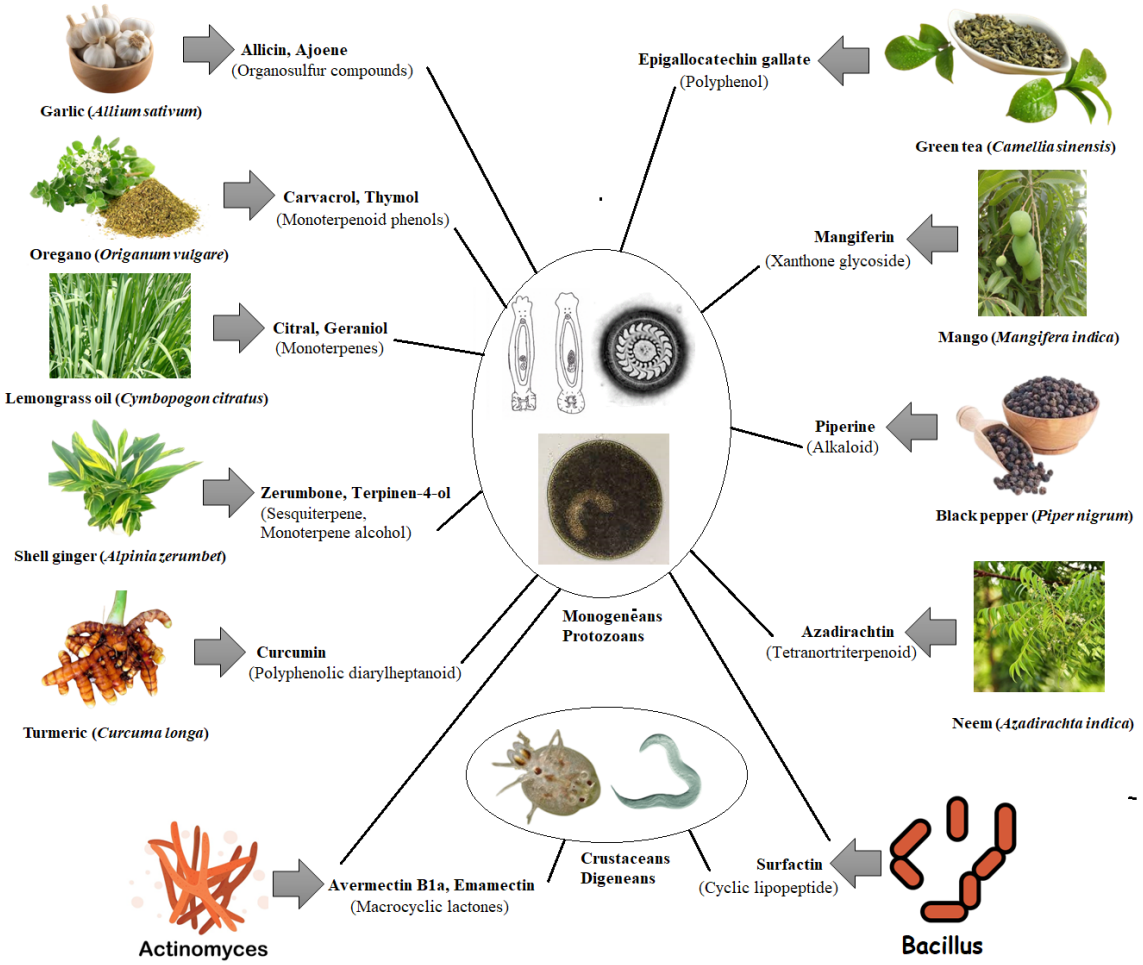


Fig. 2. Parasitic phytotherapeutic applications in aquaculture

Trichodina and *Ichthyobodo* (Mizuno et al., 2018; Zica & dos Santos Ayres, 2017). In addition to topical applications, dietary administration of phytochemicals has also yielded positive outcomes. The incorporation of ginger (*Zingiber officinale*) into the diet significantly reduced the intensity of *I. multifiliis* infection in grass carp (*Ctenopharyngodon idella*) (Ahmad et al., 2024; Fu et al., 2019). Further screening identified 18 phytochemicals with activity against the parasitic dinoflagellate *Amyloodinium ocellatum* (Tedesco et al., 2020). However, some compounds demonstrated cytotoxic effects in in vitro systems, highlighting the importance of careful toxicity evaluation before field application. Moreover, functional feeds augmented with botanical extracts, organic acids, and yeast components have been shown to alleviate the pathological impact of *Enteromyxum leei* in gilthead seabream (*Sparus aurata*) (Palenzuela et al., 2020). The protective mechanisms of these phyto-treatments are likely multifaceted, involving direct antiparasitic action, host immune modulation (Mathiessen et al., 2021), and interference with parasite-host interactions. Notably, certain herbal extracts can interfere with the parasite's ability to located and recognize hosts, thereby preventing infections before they establish (O'Shea et al., 2017).

4. Engineering and farm management innovations

4.1 Mechanical filtration and water treatment units

Physically preventing the spread of infectious stages is a useful strategy for interposing the parasite life cycle in culture systems. Continuous filtration of fish tank water can reduce infection rates for parasites that display free-living infectious phases. Targeted elimination of specific parasite stages is enabled by selecting appropriate mesh sizes. For instance, tomonts of *Ichthyophthirius* released from infected fish skin are efficiently retained by filters with mesh sizes as fine as 80 µm (Heinecke & Buchmann, 2009; Shinn et al., 2009). By capturing and removing these tomonts, cyst formation is prevented, thereby inhibiting the production of up to 1,000 infective theronts within a 36-hour period, depending on ambient temperature. Similarly, infective cercariae of eye flukes can be removed through mechanical filtration (Abbas et al., 2023). In eel aquaculture, filtration through 40 µm screens has proven effective in eliminating eggs and oncomiracidia of gill monogeneans *Pseudodactylogyrus anguillae* and *P. bini* (Buchmann, 2012; Huston et al., 2020).

4.2 Egg and cyst trapping devices

The branchiuran *Argulus* employs oviposition on submerged substrates such as aquatic vegetation, branches, and roots.

Upon hatching, larvae develop into infective stages that attach to fish hosts. This reproductive behaviour facilitates control by using "egg traps" which are submerged wooden slats, lattices, or bundles of branches into infested ponds at regular intervals to encourage parasite oviposition. Subsequent removal of these traps at intervals of a few days destroys eggs, thereby reducing parasite reproductive output and lowering infection pressure within the pond (Hakalahti-Sirén et al., 2008; Huston et al., 2020). Mechanical control of parasite larval stages can involve deploying species-specific traps infused with attractants (urea) timed to coincide with peak parasite emergence e.g. before sunset for *C. irritans* theronts and before sunrise for *N. girellae* oncomiracidia. Strategic use of chemical and light cues can enhance capture efficiency, reducing parasite loads and refining fish welfare (Skilton et al., 2020).

4.3 Net-pen design innovations to reduce parasite settlement

Modifications to netpen architecture reduce host-parasite interactions by limiting access of infective parasite stages. Since salmon louse copepodids preferentially occupy surface waters, physical barriers such as skirts or tarpaulins are installed around the upper sections of netpens to reduce exposure. The "snorkel netpen" design submerges salmon deeper in the water column where infective stages are less abundant, resulting in lower lice infection intensities (Geitung et al., 2019).

4.4 De-lousing management

Due to increasing resistance of *Lepeophtheirus salmonis* to chemical treatments in salmon mariculture, alternative mechanical control methods like heat treatment, brushing and freshwater flushing have gained prominence. Nevertheless, these approaches require fish capture and handling, which may impose stress and welfare challenges (Coates et al., 2021; Hülsmann & Galil, 2001). Technological innovations involving laser-based removal have also been explored. Automated underwater camera systems detect lice on salmon in netpens and trigger laser pulses to kill the parasites in situ. Despite the conceptual promise, controlled full-scale trials have not demonstrated a significant reduction in mean lice load following laser treatment (Bui et al., 2020).

4.5 Stocking density and hydrodynamic flow management

In aquaculture, stocking density and hydrodynamic flow are important factors that influence parasite prevalence and transmission; the effects differ based on the species, system architecture, and management techniques. As evidenced by *Capillaria pterophylli* in angelfish raised in ceramic tanks, high stocking densities often increase parasite burden and transmission risk, underscoring the need for routine cleaning (Santos et al., 2024). The immune responses of Nile tilapia to parasitic infection are influenced by rearing density; low densities can cause stress and immune suppression, increasing mortality, while higher densities may improve immunity but also facilitate the spread of infection through closer contact (Indahsari & Ulkhaq, 2019). Parasite dynamics are also influenced by hydrodynamic flow: uninterrupted flow lessens per-fish intensity but more evenly distributes infection; no-flow conditions may change shoaling, possibly decreasing close contact; and continuous flow can increase parasite intensity and abundance, as demonstrated for *Gyrodactylus turnbulli* in guppies (Reynolds et al., 2019).

4.6 Farm location and site rotation strategies

Two important tactics for managing parasites in aquaculture are farm location and site rotation. While choosing locations with sufficient water flow and appropriate environmental conditions restricts parasite survival and reproduction, locating farms away from wild fish populations and other aquaculture sites reduces the risk of parasite transmission (Athanassopoulou et al., 2009). Fish-grass rotation further minimizes invasion, lowers input costs, and can quadruple productivity. Site rotation and pond drying between cycles interrupt parasite life cycles, boosting fish health and production (Naumova & Naumova, n.d.). To create a comprehensive parasite control strategy, these actions work best when combined with improved sanitation, reduced chemical use, and farmer education on parasite biology (Athanassopoulou et al., 2009; Naumova & Naumova, n.d.; Rigos et al., 2024).

5. Biological and ecological control approaches

5.1 Cleaner fish species selection and management

Symbiotic interactions between fish and ectoparasite-removing species are common in natural marine and freshwater ecosystems. In tropical aquaculture, the mosquito fish *Gambusia* actively feeds on the branchiuran parasite Argulus during its free-swimming phase (Datta et al., 2024). This ecological phenomenon has been harnessed in aquaculture by introducing cleaner fish into salmon netpens to control salmon lice infestations. Over the past three decades, various wrasse species have been employed to reduce lice burdens on salmonids (Binning et al., 2018; Overton et al., 2020). Although the efficacy of wrasse declines during colder months, the lumpsucker (*Cyclopterus lumpus*) demonstrates superior parasite removal capabilities at low temperatures (Powell et al., 2018). Consequently, a substantial aquaculture sector has developed around the production of lumpsuckers, capitalizing on their appetite for salmon lice attached to salmon skin (Overton et al., 2020). Nonetheless, the long-term sustainability of this biological control is challenged by *Lepeophtheirus salmonis's* adaptive capacity. Additionally, certain fish species that prey on gastropods may serve as biological control agents against digenean parasites by reducing snail intermediate host populations, thereby lowering infection rates (Narvaez et al., 2015).

5.2 Cleaner invertebrates and co-culture approaches

Beyond the role of cleaner fish, several invertebrate species contribute to parasite control through predation. The blue mussel (*Mytilus edulis*) filters large volumes of water and can effectively capture free-swimming larval stages (copepodids) of salmon lice (*Lepeophtheirus salmonis*), thereby reducing the potential for parasite transmission (Montory et al., 2020). Free-living copepods, such as *Cyclops* sp., prey on cercariae of fish parasites like

Diplostomum and oncomiracidia of *Pseudodactylogyrus* monogeneans (Mironova et al., 2019, 2020). Similarly, free-living turbellarians, for example *Stephanostomum* spp., consume freshly released eggs of *Pseudodactylogyrus*, thereby contributing to a waning in infection pressure on fish hosts (Athanassopoulou et al., 2009).

5.3 Ecological barriers and habitat modification

Although its effectiveness depends on environmental factors and possible parasite adaptation, ecological barriers and habitat alteration can effectively reduce parasite burdens in aquaculture. Although performance decreases with changing salinity and temperature, depth-based measures such as "snorkel" sea lice barriers reduce parasite burdens by 24–65% without a significant negative welfare impact (Oldham et al., 2023). Invasive parasites like sea lamprey can be prevented by habitat barriers such as dams, although native fish connectivity may be hampered (Miehls et al., 2020). Salmon lice and other parasites, however, could evolve ways to overcome depth-based obstacles (Coates et al., 2020). In addition, parasite diversity and infection levels can serve as ecological indicators. In general, ecosystems that are simplified or altered by barriers tend to support fewer parasite species (Almeida et al., 2024). Therefore, any management strategies should be applied carefully to avoid unintended ecological trade-offs. Host directed approaches

5.4 Immunostimulants and dietary functional additives

The inclusion of immunostimulants in aquafeeds to strengthen the innate immune responses of teleost hosts has become a common strategy in aquaculture. Dietary supplementation with various immunostimulatory compounds has been reported to moderately reduce infection intensity caused by protozoan parasites such as *Ichthyophthirius* and metazoan parasites such as *Lepeophtheirus salmonis* (Farooqi & Qureshi, 2018). Rigos et al. (2016) documented that seabream fed with diets containing caprylic acid combined with iron and mannan exhibited reduced monogenean (*Sparicotyle chrysophrii*) infection levels in Mediterranean mariculture settings. Despite these encouraging observations, the exact immunological mechanisms through which these compounds act remain to be fully explained. Nevertheless, when compared to vaccination, the effectiveness of in-feed immunostimulants against pathogenic infections generally remains partial.

5.5 Vaccination strategies against parasites

Vaccination currently epitomizes the most effective and sustainable method for controlling bacterial and viral ailments within aquaculture. Exposure to various protozoan and metazoan parasites often elicits strong immune responses in fish survivors, which can confer a degree of protective immunity. Such acquired immunity has been well documented in parasitic ciliates, monogeneans, and crustacean parasites such as *Lernaea* (Shivam et al., 2021; von Gersdorff Jørgensen et al., 2017). However, to date, no commercially licensed antiparasitic vaccines exist for aquaculture. Protection against parasitic infections appears to involve complex interactions among the cellular and humoral components of both innate and adaptive immunity. Because of this complexity, it is often difficult to reproduce the same level of immune response through vaccination alone. As a result, controlled exposure to low or moderate parasite burdens has been suggested as a way to stimulate protective immunity and complement other control strategies. Such natural infection-induced responses are thought to activate key immune pathways that help the host develop partial protection during later exposures (Shivam et al., 2021).

5.6 Host genetic improvement and selective breeding for resistance

Resistance to parasitic infections in fish is largely influenced by genetic factors, as demonstrated for *Ichthyophthirius* and *Myxobolus* infections in rainbow trout (Avila et al., 2022). Selective breeding for enhanced disease resistance characterizes a promising approach in aquaculture, with marker-assisted selection becoming an gradually valuable tool in breeding programs. Although traditional selective breeding has been exploited for several decades to improve desirable traits in cultured fish species, the extended generation times often adjourn observable benefits. Advances in quantitative genetics have enabled the identification of quantitative trait loci (QTL) associated with resistance to viral, bacterial, and parasitic diseases. Atlantic salmon display QTL related with resistance to amoebic gill disease (Robledo et al., 2020), while resistance to the scuticociliate *Philasterides dicentrarchi* has been reported in turbot (Saura et al., 2019). In rainbow trout, QTL conferring resistance to *Myxobolus cerebralis* have been characterized (Avila et al., 2025). Additionally, investigations using single-nucleotide polymorphism (SNP) markers suggest that genes linked to resistance to *Ichthyophthirius multifiliis* localise to chromosomes 16 and 17 in rainbow trout (Buchmann et al., 2022). Technological developments in genotyping, such as high-density SNP microarrays, have permitted efficient identification of resistance-associated loci. A microarray containing 57,501 SNP markers was used to pinpoint genes conferring resistance to *Vibrio anguillarum* on chromosome 21 (*Omy21*) (Karami et al., 2023) and to locate genes related to *Ichthyophthirius* resistance on chromosomes 16 and 17 (Buchmann et al., 2022). Selecting broodstock carrying required alleles associated with disease resistance, facilitates the production of offspring with improved innate defenses (Buchmann et al., 2022). While the genetic basis of this heritable protection likely involves immune-related factors, non-immunological elements, such as parasite chemoattraction mechanisms, may also contribute to improved resistance observed in QTL-selected fish.

5.7 Gut microbiota modulation for enhanced resilience

Recent research has begun to shed light on the interplay between mucosal immunity, gut microbiota composition, and resistance to parasitic infections. Functional feed additives such as sodium butyrate have demonstrated the capacity to modulate gut microbiota and enhance resistance against the myxozoan *Enteromyxum leei* in maricultured seabream (Piazzon et al., 2020). Additionally, it has been hypothesised that feed additives such as caprylic acid

and mannan may exert their effects on monogeneans (*Sparicotyle chrysophrii*) by stimulating generalised systemic immunity in seabream (Rigos et al., 2016), though further studies are required to confirm these mechanisms.

6. Integrated multi-modal control strategies

Parasites exhibit a high degree of adaptability to environmental pressures, often ensuing rapid development of resistance to control measures (Bhinsara et al., 2018; Kaur et al., 2015). This adaptive potential emphasize the necessity of using integrated parasite management strategies that combine multiple control approaches to sustainably protect fish stocks from heavy parasite burdens. Current management of *Ichthyophthirius* infections in freshwater trout farms typifies such integrated control efforts. These include mechanical filtration systems employing micro-sieves to remove tomonts from the water, periodic application of biocidal agents to eliminate infective theronts, tolerance of low-level parasite exposure to stimulate partial protective immunity, and the use of genetically resistant fish strains (Buchmann et al., 2022). Combining genetic resistance with effective environmental management and appropriate chemical treatments represents a holistic approach necessary to mitigate the evolving challenges posed by parasitic diseases in aquaculture. In mariculture, anisakid nematode infections can be prevented by using netpens combined with heat-treated feed, effectively blocking live parasite larvae from infecting fish (Fioravanti et al., 2021). Allowing controlled, low-level infections in farms may help fish develop partial immunity, which can keep parasite populations within manageable limits. At the same time, parasites can gradually develop resistance to treatments, making control more difficult over time. For this reason, alternating or combining different control methods is important to slow the development of resistance. Using a mix of strategies can reduce the risk of multi-resistant parasite strains, highlighting the value of integrated parasite management for maintaining sustainable aquaculture practices. A list of innovative parasite management strategies have been mentioned in Table 2.

7. Hyperparasitism in aquaculture

In aquaculture, hyperparasitism is the phenomena when a parasite becomes infected by another parasite. Trichodinid ciliates colonizing monogenean gill flukes or microsporidians infecting the salmon louse (*Lepeophtheirus salmonis*) are examples of hyperparasitism (Freeman et al., 2003). By naturally controlling primary parasite populations, these interactions may lessen the burden of illness on farmed fish and promote ecological stability (Bojko & Stentiford, 2022). Understanding hyperparasitism offers opportunities to develop environmentally friendly, sustainable biocontrol techniques as part of integrated health management in aquaculture, although its direct use in parasite management is still in its infancy (Soares et al., 2025).

8. Conclusion and future perspectives

Achieving efficient, long-lasting management of parasitic infections in aquaculture systems is extremely difficult due to parasites' remarkable resilience to environmental stresses. At the farm level, even highly successful new chemicals risk losing potency after repeated use over a short period of time. Aquaculture professionals must so embrace an integrated management strategy that incorporates a variety of chemical, biological, medicinal, and mechanical control techniques. Such technique substitutions and combinations may lessen the selection pressure that leads to the establishment of resistant parasite strains. To find novel control strategies that can replace antiquated or ineffective methods, basic research into parasite biology and biochemistry must continue. Innovative parasite management strategies, including some

Table 2. Novel and/or improved strategies for parasite management in aquaculture

Technology	Category	Main target parasites	Remarks	References
Permeable barrier skirts lice-shield fabrics	Mechanical	*Lepeophtheirus salmonis*	High-efficiency physical barrier blocking >99% nauplii/copepodids	Guttu, 2024
Implementation of diel light cycle vertical migration	Mechanical	*L. salmonis*	High-efficiency barrier and dependence on diurnal stratification	Hagemann et al., 2024
Nanoemulsions, nanocomplexes	Chemical	Ich, *Gyrodactylus*, external protozoans	Improved solubility, stability, potency of plant actives (e.g., thymol)	Bezerra et al., 2024
Peracetic acid optimized protocols	Chemical	Ich, *Trichodina*, copepods	Renewed safe/effective use as broad-spectrum oxidant. Showed effectivity against copepod infected squid egg	Farmer et al., 2024; Zoral et al., 2024
Genetic selection (WGS/QTL mapping)	Host genetics	Sea lice (salmon), White spot (carps)	Identifies resistance loci; integrates genomic selection & hybrids	Onabanjo et al., 2024; Li et al., 2025
Native micro-predator enhancement (copepods vs. Ich)	Biological	*Ichthyophthirius* theronts	Uses natural pond copepod predators to suppress infective stages	Cao et al., 2023; Wang et al., 2024
Peppermint cleaner shrimp (Lysmata vittata)	Biological	Monogeneans, protozoans and leeches	Reduced infection by about 87% in RAS trials; sustainable shrimp alternative to cleaner fish	Vaughan et al., 2018
Cunner fish in Newfoundland	Biological	Sea lice on salmon	Explored as a regional, native alternative for biological control in Newfoundland	Chen, 2019

recent advancements in indigenous technical knowledge have been devised. Interestingly, there is presently no recorded use of hyperparasites for parasite control in aquaculture, even though hyperparasitism occurs in natural aquatic environments. Future research should examine how hyperparasitism can be used as an additional strategy for long-term control of fish parasites.

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