

A summary of Copepoda: synthesis, trends, and ecological impacts*

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Abstract Copepoda are one of the most significant animal groups present in aquatic ecosystems. Ecologists, evolutionary biologists, and biotechnologists continue to test new methods to study the application of Copepoda as model organisms in various fields of pure and applied science, from evolution and ecology to aquaculture as live feed, as biological control of mosquito larvae, as biological indicators of water and sediment quality, in environmental monitoring and as a source of protein in the food industry. This paper reviews the current progress and trends within copepod research from a number of different perspectives. We emphasize the importance of Copepoda and the necessity of strengthening research on various topics related to copepod biology, some of which are of great significance to local sustainable development.

Keyword: bioindicators; aquaculture; pollutants; eutrophication; nutrition; halotolerance

1 INTRODUCTION

Copepoda are small aquatic crustaceans, and are one of the most ecologically successful taxon on the earth. They are the largest and most diverse group of crustaceans. Their total biomass in the world's waters makes Copepoda the most abundant metazoan groups on earth (Hardy, 1970; Morales-Ramírez et al., 2014). In their long evolutionary history, Copepoda have been found all over the continents since the lower Cretaceous, and have successfully settled in all available aquatic habitats (Selden et al., 2010 and references therein). At present, they are distributed at different altitudes from the high elevation of the Himalayas to the deepest trench in the world's oceans. They exist as benthic and planktonic organisms living in aquatic habitat of various salinities ranging from freshwater to high

salinity, including estuaries and coastal systems, lakes, ponds, groundwater, artificial containers, and various 'hidden habitats', such as wet organic soils and forest debris, moss and plants (Ho, 2001; Boxshall and Defaye, 2008 and references therein). Copepoda include free-living and parasitic forms, the latter associated with various vertebrate and invertebrate taxa (Huys, 2016; Walter and Boxshall, 2021).

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In general, Copepoda are considered to be an ancient group, which may be separated from other Arthropoda groups in the Devonian period, i.e., 446.2±47.3 million years ago (Eyun, 2017). There are currently ten orders of Copepoda, but their phylogenetic relationships remain unclear (Mikhailov and Ivanenko, 2021). The order Siphonostomatoida is exclusively parasitic (Maran et al., 2016), Monstrilloida are semi-parasitic or protelean parasite (Suárez-Morales, 2011), and some species of the orders Cyclopoida, Calanoida, and Harpacticoida are parasites of or are associated with a wide variety of organisms (Ho, 2001; Boxshall et al., 2016; Huys, 2016). The orders Platycopioidea, Misophrioida, Mormonilloida, and Gelyelloida are exclusively free-living (Varela and Lalana, 2015). Among them, calanoida are the most diverse and widely distributed group, and are the dominant group in marine zooplankton (Huys and Boxshall, 1991). Currently, 10 000 valid species of Copepoda have been recorded and described (Walter and Boxshall, 2021), of which 2 814 are from freshwater (Boxshall and Defaye, 2008).

Free-living Copepoda play an important role in aquatic habitats and benefit aquatic ecosystems in many ways. Copepoda have a high nutritional value and therefore important in aquatic food webs (Fig.1). Many of them feed on primary producers

and are consumed by species belonging to higher nutritional levels (Turner, 2004). Copepoda and their nauplii have high nutritional values (Aragão et al., 2004), are prey for many other zooplankton, and can be used as a food source for fry or larvae (Sampey et al., 2007). Due to their high nutritional value, they are a potential food source for aquaculture and human diet (Eysteinnsson et al., 2018). Several Cyclopoida genera and species feed on mosquito larvae and have been used as biological controls for mosquito-borne diseases (Udayanga et al., 2019). Because copepod populations are very sensitive to the impact of climate change and human activities, Copepoda are a good model group in ecological and ecotoxicology studies (Kulkarni et al., 2013; Montagna et al., 2013). Although free-living Copepoda play an active and positive role in ecosystem function, most parasitic Copepoda have a negative effect on higher trophic levels, thereby causing damage to the host (Pike and Wadsworth, 1999; Johnson et al., 2004). Although Copepoda play a key role in some areas, there is still little research on Copepoda, and little is known about their potential in various fields. This article summarizes the potential utility of Copepoda in ecological research, aquaculture, medicine, etc., and further emphasizes the sustainable development trend of Copepoda.

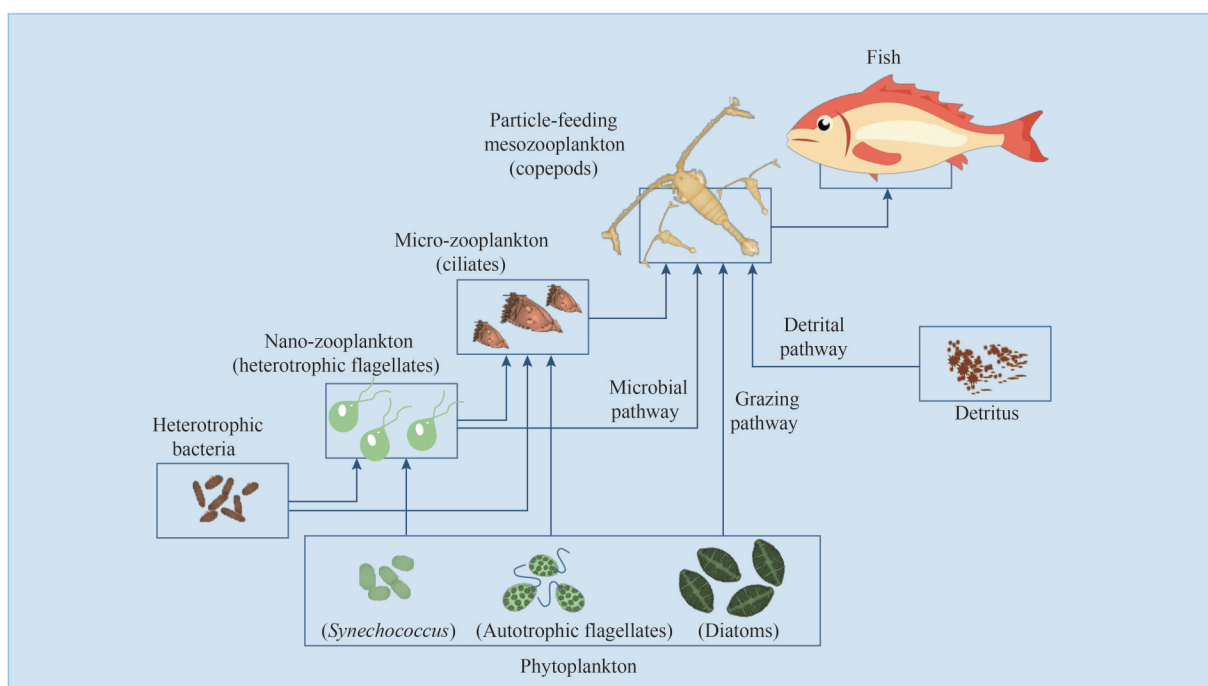


Fig.1 A general flow diagram of a planktonic food web in an aquatic ecosystem

The names in parentheses are examples of each type of organism, adapted from Nakajima et al. (2017).

2 LITERATURE REVIEW

2.1 Copepoda in ecological and evolutionary studies

Climate change and anthropogenic disturbance are the reasons for the continuous change of natural habitats that cause serious global environmental problems (Bellard et al., 2012; Moreno-Mateos et al., 2017). As the earth changes, an interesting challenge is to understand how ecosystems respond to global change. The role of human beings in disturbing the natural habitats around the world is becoming more and more obvious (Moreno-Mateos et al., 2017; Martínez et al., 2020), and the understanding of the impact of these changes on life on earth is paramount. Although 71% of the earth is covered by water, 96.5% of the water exists in the ocean as salt water, and only 3.5% is freshwater lakes, rivers, underground aquifers, and frozen glaciers and polar ice caps (Williams, 2014). In fact, only 0.007% of the world's water is available to the world's population (7.8 billion people), which is not enough for everyone (Mulhern, 2020). At present, due to the existence of point and non-point sources, the availability of water resources is affected by water ecosystem pollution (Wu and Chen, 2013). This kind of environmental change can be monitored by biological indicators in both marine and freshwaters (Parmar et al., 2016).

Among several meiofaunal animals, Copepoda offer have many advantages in the study of aquatic ecosystems because of great variability in greater taxonomic, life history, reproductive strategies, habitat diversity, and ecological functions (Seuront, 2014). Thus, we can understand from an ecological and evolutionary perspective how copepod abundance, diversity patterns, and life histories change in response to broader environmental conditions (Dam, 2013; Zeppilli et al., 2018; Medellín-Mora et al., 2021 and references therein).

2.1.1 Hypoxic environment

Globally, the geographical distribution, duration and frequency of coastal hypoxia is increasing (Doney, 2010). In some areas, hypoxia occurs naturally, while in many other areas, anthropogenic impacts, including fertilizer and sewage runoff, lead to eutrophication, which increases the decline of oxygen through biological processes (Howarth, 2008). Some studies have shown that the low oxygen levels in coastal areas is reflected in the decrease of Copepoda, indicating the decrease of

population growth, the increase in mortality, and the predation and/or migration in the water column with hypoxic bottom water (Roman et al., 2019). Several datasets show that survival, growth, oviposition and feeding rates of Copepoda decrease with reduced oxygen availability (Roman et al., 2019 and references therein). Another study showed that *Calanus pacificus* (Calanoida: Calanidae) from Puget Sound, Washington, failed to survive in laboratory experiments at 0.9-mg/L oxygen concentration (Grodzins et al., 2016). In general, low dissolved oxygen decreased the survival rate of Copepoda. They also exhibit interesting migration patterns under hypoxic and/or anoxic conditions. For example, planktonic Copepoda in the Gulf of Mexico avoided hypoxia of near-bottom waters during their diurnal vertical migration. The median depth of their daytime distribution in the water column is 7 m higher than that of Copepoda in the water column without anoxic bottom waters (Roman et al., 2012); while in the Chesapeake Bay, moderate hypoxia is consistent with stronger migration than lethal or oxygenated conditions (Pierson et al., 2017). Another study in a brackish lake in Japan showed that anoxia at the bottom of the lake inhibited the abundance of *Acartia* (*Acartiura*) *hudsonica* (Calanoida: Acartiidae), resulting in an uneven distribution at a local scale (Chang et al., 2013). They clearly observed that in spring, an increase in oxygen content at the bottom led to a larger number of Copepoda. On the other hand, *Oithona* spp. (Cyclopoida: Oithonidae) is abundant during the summer in the near-surface waters and is unlikely to be affected by hypoxia in the bottom layer (Chang et al., 2013). Different populations and species of Copepoda respond differently due to their life history strategies and hypoxic conditions (Elliott et al., 2012 and references therein) indicating that Copepoda are indicators of anoxic fluctuations.

2.1.2 Eutrophic environment

Eutrophication is characterized by increased availability of one or more restrictive growth factors (Schindler, 2006) required for photosynthesis, such as sunlight, carbon dioxide, and nutrients, leading to overgrowth of plants and algae. As the age of the lake increases, eutrophication naturally occurs for centuries and is deposited in sediments (Carpenter, 1981). However, human activities have accelerated the speed and extent of eutrophication through point source discharges (sewages and effluents) and loading non-point sources with restricted nutrients

such as nitrogen and phosphorus into aquatic ecosystems (i.e., cultural eutrophication), with significant impacts on drinking water sources, fisheries and recreational water bodies (Carpenter et al., 1998). For example, aquaculture scientists and pond managers often intentionally cause water bodies to become eutrophic by adding fertilizers to improve primary productivity, and to increase the density and biomass of recreational and economically important fish through bottom-up impacts on higher trophic levels (Boyd and Tucker, 1998). In the 1960s and 1970s, however, scientists linked algal blooms to nutrient enrichment caused by human activities such as agriculture, industry, and sewage treatment (Schindler, 1974). Nowadays, eutrophication is a global environmental problem and one of the most serious hazards of aquatic ecosystems (Nixon, 1995), which leads to significant changes in community structure and ecosystem function (Zhang et al., 2016). In the United States alone, the loss caused by eutrophication is estimated to be about \$2.2 billion per year (Dodds et al., 2009).

Within the meiofauna, planktonic copepod assemblages are well-known to be affected by eutrophication and pollution (Marcus, 2004; Perbiche-Neves et al., 2016). Eutrophication is one of the reasons for the decrease of diversity of Copepoda (Siokou-Frangou et al., 1998), which often leads to the replacement of large-sized Copepoda by small-sized Copepoda (Zhang and Wong, 2011). As the degree of eutrophication increases, species generally shift to small-sized Copepoda, which is due to the change in food quality; from large diatoms to small flagellates, which are the preferred prey of small-sized species (Marcus, 2004). In laboratory experiments, the hepatotoxic nodular blooms in the Baltic Sea may limit the reproductive output of *Acartia* spp., suggesting that egg production is related to the amount of nodular DNA in the internal organs of Copepoda (Engström-Öst et al., 2015). This result reflects that Baltic cyanobacterial blooms may have a negative impact on copepod population dynamics. In Lake Manzalah in northern Egypt, Cyclopoida dominate rather than Calanoida (Annabi-Trabelsi et al., 2019), which may be explained by the lower metabolic requirements of Cyclopoida compared with Calanoida, and therefore their higher abundance in eutrophic waters (Almeda et al., 2010). In the three eutrophic reservoirs in the semi-arid area of northeastern Brazil, the relationship between Calanoida Copepoda and eutrophication is more intense than that of Cyclopoida, indicating that

the Calanoida Copepoda are associated with increased food supply (Paes et al., 2016). This suggests that the dynamics of Copepoda under eutrophication conditions are unique, depending on the region. There are several types of zooplankton Copepoda that are considered signs of eutrophic water bodies, i.e., bioindicators (Landa et al., 2007; Nogueira et al., 2008).

2.1.3 Oil spill

Petroleum or crude oil is one of the pollutants that are discharged or spilled into the marine environment. The leakage, exploitation, transportation, and consumption of natural oil are the main sources of offshore crude oil (National Research Council, 2003). Although oil spills account for only a small part of the total amount of crude oil discharged into the ocean, they are highly acute and have negative impacts on marine ecosystems, including physical damage (physical pollution and suffocation) and the toxicity of their compounds (Han et al., 2021). Recently, the deep-water horizon (DWH) oil spill in the Gulf of Mexico has raised concerns about the huge environmental and socio-economic impact of oil spills in marine and coastal environments (Allan et al., 2012; White et al., 2012). Copepoda are the dominant taxon of zooplankton in the ocean (Longhurst, 1985). Lethal and sublethal effects, including changes in narcosis, feeding, development and reproduction, were observed in Copepoda exposed to petroleum hydrocarbons (Calbet et al., 2007 and references therein). There is increasing evidence that sunlight, mainly ultraviolet light (UV), can increase the toxicity of polyaromatic compounds (PAC) to Calanoida Copepoda (Duesterloh et al., 2002). Some laboratory experiments clearly showed that Copepoda are particularly vulnerable to acute crude oil exposure (Almeda et al., 2013), showing increased mortality and sub lethal changes in physiological activities (e.g., reduced spawning and delayed hatching).

In the North Atlantic and Arctic marine ecosystems, *Calanus finmarchicus* and *Calanus glacialis* (Calanoida: Calanidae) are key zooplankton species because they transfer phytoplankton with higher nutritional levels to predators on higher trophic levels. Throughout the year, these Calanoida Copepoda spend a few months in deep water in a dormant state called diapause, after which they appear in surface waters, feeding and breeding during the phytoplankton bloom in spring (Lee et al., 2006). The interruption of diapause time may have a huge impact on the

marine ecosystem. In laboratory experiments, the diapause *Calanus* C5 copepodites collected from the Norwegian fjords were exposed to the water-soluble portion of naphthenic North Sea crude oil during the termination of diapause (Skottene et al., 2019). The results show that the exposure of water-soluble naphthenes led to the inhibition of lipid catabolism of C5 copepodites, leading to delay in diapause termination, because lipid composition may be an important factor to stop diapause. Long-term diapause termination may lead to delayed copepod migration to surface water. This delay may adversely affect ecosystem dynamics. Hansen et al. (2017a) demonstrated that crude oil exposure to *C. finmarchicus* showed carcass discoloration and reduced swimming activity and feeding activity. It is worth noting therefore that Copepoda provide some clues to understand the impact of oil spills in the ocean.

2.1.4 Microplastics

Microplastics (1 μm –1 mm) are a ubiquitous and persistent environmental pollutant that affect global terrestrial and aquatic ecosystems (Lusher, 2015; Hartmann et al., 2019). These synthetic particles and fibers are either manufactured directly (e.g., exfoliation in personal care products), or are broken up from larger pieces of plastic (Weinstein et al., 2016). According to conservative estimates, there are more than 4.75×10^{12} plastic particles (0.3–4.5 mm) floating in the global ocean (Eriksen et al., 2014). Due to the fact that complete mineralization of plastic fragments is expected to take between several decades and hundreds of years, and in the foreseeable future, with the increase of plastic input, the marine microplastic concentration is likely to increase (Andrady, 2015; Lusher, 2015). Due to their small size, microplastics can be directly or indirectly (i.e., via trophic interactions) ingested by a series of marine organisms (Duncan et al., 2019 and references therein). Laboratory exposure has demonstrated the capabilities of a range of pelagic and benthic Copepoda, *Acartia* spp., *Centropages* spp., *Calanus* spp., *Limnocalanus* spp., *Tigriopus* spp., and *Temora* spp., can ingest polystyrene microplastic beads and debris (Cole et al., 2013; Lee et al., 2013; Setälä et al., 2014; Vroom et al., 2017). A recent study by Cole et al. (2019) showed that microplastics can reduce feeding, prevent lipid accumulation, and trigger premature moulting in *C. finmarchicus* (Calanoida: Calanidae). Coppock et al. (2019) demonstrated that Copepoda respond very differently to microplastics of different sizes, shapes, and

polymers. Their findings indicate that microplastic fibers have a more pronounced effect on copepod feeding compared to debris, leading to subsequent health problems. Another study showed that polyethylene microplastics are carriers or vectors of chlorpyrifos pollutants, indicating that microplastics and other chemical pollutants can together accelerate negative impacts on Copepoda (Bellas and Gil, 2020).

2.1.5 Chemical pollutant

The highest concentrations of pollutants occur in estuarine and shallow coastal marine systems, as these areas are subject to considerable anthropogenic impacts from point and non-point sources. This potentially dangerous human generated input is often associated with accelerated population growth, coastal development, agricultural, industrial, and municipal emissions, and commercial and recreational activities, with significant impacts on communities and ecosystems (Nipper, 2000). It is well known that sediments can effectively isolate hydrophobic chemical pollutants, such as heavy metals and organic pollutants, which enter the water body (McCready et al., 2006). In order to study the effects of these pollutants in the aquatic system, some Copepoda were used as indicator groups and laboratory tests species (Araújo-Castro et al., 2009).

Heavy metal pollution is an increasingly serious environmental problem in marine, brackish, and freshwater environments, because heavy metals persist in the environment and are toxic to organisms (Pinto et al., 2003). The increase of heavy metals emitted by human activities increases their concentration in the seawater, thus enhancing their bioaccumulation in the marine organisms and influencing them through their toxicity (Neff, 2002). Some metals with low concentrations are necessary for organisms as enzyme components, but high concentrations of metals can cause serious toxicity. In addition, the specific biological functions of some of these metals, such as mercury and lead, are not clear, so they are also toxic at low concentrations. Copepoda accumulate metals by absorbing them from food or water. In addition, the absorption pathway can determine its internal distribution and toxicity (Wang and Fisher, 1998). According to the ecological survey of Salado River Basin in Argentina, there are significant differences in the abundance and diversity of Copepoda between the control points and heavy metal pollution points, indicating that the response of Copepoda to pollution points is

negatively correlated (Gagneten and Paggi, 2009). As Copepoda are sensitive to metal pollutants, they are considered as experimental species for ecotoxicological research (Kadiene et al., 2019). In one study, *Centropages ponticus* (Calanoida: Centropagidae) exposure to cadmium affected malondialdehyde (MDA) levels, suggesting that Copepoda suffered oxidative damage (Ensibi and Yahia, 2017). Another toxicological test on *Amphiascus tenuiremis* (Harpacticoida: Miraciidae) showed that Copepoda were highly sensitive to a mixture of four different metals (copper, lead, nickel, and zinc) compared to exposition to each metal separately (Hagopian-Schlekat et al., 2001). Assessment of the relative sensitivity of *Acartia tonsa* and *Acartia clausi* (Calanoida: Acartiidae) exposed to sediments from the Bagnoli-Coroglio industrial area showed that *A. clausi* is more sensitive than *A. tonsa* and that the two species have convergent responses to the three sediment-derived elutriates. This provides an opportunity for the potential use of *A. clausi* in standardized ecotoxicity testing (Carotenuto et al., 2020). On the other hand, Zhou et al. (2018) elucidated the response of *A. tonsa* when exposed to nickel nanoparticles through a novel approach based on transcriptome assembly and differential gene expression analysis. Thus, highlighting the potential of toxicogenomic approaches in obtaining additional mechanistic and functional information on the mode of action of emerging compounds on marine organisms, as well as for the discovery of crustacean biomarkers.

In addition to heavy metals, some chemical products are also mixed into water bodies through industry. Copepoda are used as indicator species for the negative effects of these chemicals. For example, *Tisbe biminiensis* (Harpacticoida: Tisbidae), showed moderate to relatively constant sensitivity to the reference substance sodium dichromate in bioassays (Araújo-Castro et al., 2009). After 28 days of long-term exposure, zinc oxide nanoparticles (NP) had negative effects on the reproductive characteristics of *Tigriopus fulvus* (Harpacticoida: Harpacticidae), i.e., incubation time, incubation size, and brood number at much lower concentrations (Prato et al., 2020).

2.1.6 Environmental factor

Changes in salinity, temperature, and pH play a key role in the spatiotemporal distribution of aquatic organisms. Several studies have shown that anthropogenic and seasonal/climate changes can

affect these environmental variables, leading to large-scale changes in benthic and planktonic copepod biomass (Barroso et al., 2018; Karlsson et al., 2018). Freshwater runoff dilution of seawater is characteristic of most estuaries. The resulting salinity gradient is the main structural factor of the physical, chemical, and biological processes in these ecosystems (Bianchi, 2007). Low and variable salinity bring stress conditions to aquatic animals (Attrill, 2002), and low taxonomic diversity in estuarine waters usually matches high biological and biomass yield (Day et al., 2013). Laboratory experiments found that populations of *Eurytemora affinis* (Calanoida: Temoridae) from the Black Sea are more sensitive to lower salinity than those exposed to type locations (Karlsson et al., 2018). Their results clearly showed that hatching success rate, development time, and survival rate would be negatively affected under low salinity. In addition, it was found that the response of individuals to salinity was consistent. On the other hand, when salinity increased, all individuals had faster development and higher survival rate. The low salinity treatment method used in the experiment can be found in some areas of the Baltic Sea. It can be speculated that due to climate change and anthropogenic impacts, the same low salinity level can be found anywhere in the world.

Global warming is one of the most urgent threats to our ecosystem (Malhi et al., 2020), over the past few decades, warming effects in water ecosystems have become apparent as surface water temperatures have risen and ice sheets have decreased (Woolway et al., 2017). Temperature is considered one of the basic factors controlling the biodiversity of aquatic ecosystems (Meerhoff et al., 2012). The influence of water temperature on the reproduction and development rate of Copepoda is the key to understanding the population dynamics of Copepoda (Bonnet et al., 2009; Dam, 2013). In this regard, embryonic development is considered a better expression of temperature dependence. Therefore, the development time of eggs can be used to study temperature dependent development, which has also been shown to depend on the size and type of eggs (Bonnet et al., 2009 and references therein). In some laboratory experiments, temperature rise has a negative effect on all fitness related parameters of *Pseudodiaptomus annandalei* (Calanoida: Pseudodiaptomidae), including prolonging development time, reducing the size at maturity, smaller clutch size, lower hatching success rate, and reducing the

production of nauplii (Doan et al., 2019). The quality and quantity of food resources also affects the reproduction and development of Copepoda (Breteler et al., 2005; Saiz and Calbet, 2007). Carotenuto et al. (2011) demonstrated that maternal and neonatal diatom food fed to *Temora stylifera* (Calanoida: Temoridae) impairs development and sexual differentiation.

The perception of pH fluctuations in the marine environment has recently changed. This is mainly due to the enrichment of anthropogenic nutrients in many coastal areas, which leads to the proliferation of phytoplankton, resulting in high pH values in bays, lagoons, salt pools, and tidal pools. For example, the best survey site in Denmark found high pH in Mariager fjord. The average pH value in summer was 8.8, but on a calm sunny day, the pH value was as high as 9.75 (Hansen, 2002). However, considerable values have been recorded in marine ponds, and a small increase in pH has been measured in surface water in the North Sea, where pH increased from 7.9 to 8.7 during the bloom of *Phaeocystis* (Brussaard et al., 1996). Sometimes the duration of the pH rise is very variable; in lagoons off the coast of Portugal, the pH value is more than 8.5 all year round, while in rock pools and sediments, the pH value can increase to 10, but only for a few days or hours (Macedo et al., 2001). The increase of pH value in marine environments, as in freshwater, is expected to cause a change in community structure. Some experimental results showed that the copepod community was not found after incubation for 1–5 days at pH 9 and 9.5, indicating that Copepoda were very sensitive to the increased levels of pH (Pedersen and Hansen, 2003). Another study showed that different species of Copepoda have different responses to pH fluctuations (Hansen et al., 2017b). For example, *Oithona similis* (Cyclopoida: Oithonidae) is a true marine shallow water species with poor tolerance of high pH values, as mortality increased significantly with a slight rise in pH to 8.5; the euryhaline species, such as *Temora longicornis* (Calanoida: Temoridae), *Acartia* spp., *Centropages typicus* (Calanoida: Centropagidae), *Pseudocalanus elongatus* (Calanoida: Clausocalanidae), and in particular *Eurytemora affinis* (Calanoida: Temoridae), adapt to the extremely fluctuating environment in the estuary, while the high pH value is a common source of stimulation (Hansen et al., 2017b). Ocean acidification (OA) has caused major changes in the carbon chemistry of seawater, widely affecting

marine life, and is considered a global threat to the health of marine ecosystems. Due to human activities, the concentration of carbon dioxide (CO₂) in the atmosphere has risen steadily from the pre-industrial 28 Pa to the current 40 Pa (Siegenthaler et al., 2005; Kromdijk et al., 2016). With the increase of CO₂ content in the atmosphere, the chemical composition of carbonates in seawater has undergone significant changes. This is due to the enhanced adsorption of CO₂ by the oceans, which ultimately leads to a continuous decrease in pH and carbonate concentration (Orr et al., 2005). In general, Copepoda are known to have a negative effect on changes in OA (Wang et al., 2018). The effect of OA on Copepoda has species and stage specificity, and different populations of the same species have different sensitivity to OA stress (Wang et al., 2018). The effect of OA on Copepoda can be minimized by physiologic adjustments, and the interaction of OA with common stressors such as heat stress, food deprivation, and metal pollution will further affect the impact of OA on Copepoda (Wang et al., 2018). Several copepod species, such as *Acartia tonsa* (Calanoida: Acartiidae) showed negative effects related to ocean acidification during growth, development and reproduction. Tables 1 and 2 of Wang et al. (2018) provide a list of copepod species for OA analysis in marine and laboratory experiments.

In a survey in Port Phillip Bay, southern Australia, abundance of *Paracalanus indicus* (Calanoida: Paracalanidae), the primary prey of juvenile fish, increased with increasing water temperature, but decreased when the proportion of diatom cells increased and did not correlate with chlorophyll-*a* concentration (Jenkins and Black, 2019). In contrast, the abundance of *Oithona similis* (Cyclopoida: Oithonidae) was independent of the proportion of diatom cells, but positively correlated with water temperature and chlorophyll-*a* concentration. The results verified a negative correlation between diatom proportions and *P. indicus* abundance and thereby significantly impact on important fish recruitment in Port Phillip Bay. Regarding *O. similis*, the results show that this species is not affected by diatom proportions. Instead, food limitation, as measured by chlorophyll-*a* concentration, may be a key factor in determining its abundance in Port Phillip Bay. The negative impact of diatoms on *Paracalanus* directly affects the larval survival of fish, which is not the case for *Oithona*. This difference may reflect the greater reliance of *O. similis* on microzooplankton and

motile phytoplankton in its diet.

Adults of *Calanus helgolandicus* (Copepoda: Calanoida) have an intrinsic mortality and short lifespan at a coastal sampling station in the western English Channel, UK (Maud et al., 2018). They found that 89% of mortality was caused by predators (consumptive mortality). In addition, mortality increased in summer and winter due to high wind speeds, a key factor in generating turbulent kinetic energy, suggesting that extreme weather events may lead to increased mortality (non-consumptive mortality). They found high mortality rates for both males and females in both consumptive and non-consumptive situations, but higher mortality rates for males than females, consistent with other species in previous studies (Maud et al., 2018 and references therein), further supporting the concept of how Copepoda provide complementary insights in food webs, seasonal dynamics, and climate change.

The invasion of *Oithona davisae* (Cyclopoida: Oithonidae) has altered the species composition of the zooplankton community in the Sevastopol Bay of the Black Sea, including changes in dominance among species (Gubanova et al., 2019). *Oithona davisae* has been shown to alter the community structure, but did not cause a decrease in the abundance of native species, only for the early Black Sea invader *Acartia tonsa* (Calanoida: Acartiidae), which accounts for about 80% of the average annual copepod population. As shown in laboratory experiments, the food concentrations that caused *O. davisae* larvae to increase their scavenging rate were lower than those of Calanoida larvae. Thus, *O. davisae* are able to achieve maximum growth and developmental rates at lower food concentrations than Calanoida. In contrast, *A. tonsa* has adapted to high food concentrations and is unable to maintain high reproductive rates at low feed concentrations (Gubanova et al., 2019 and references therein).

Takayama and Toda (2019) investigated the abundance of *Acartia japonica* (Calanoida: Acartiidae), egg morphology, temporal variation in spawning, and hatching patterns of eggs produced by individual females in samples from Sagami Bay, Japan, as well as some laboratory experiments. Their results showed that individual females produced three types of eggs simultaneously, such as subitaneous, delayed hatching and diapause, indicating that the three types of eggs produced by individual females underwent temporal variation throughout the spawning period. The proportion of

different egg types varied over different time scales, ensuring that all three egg types may ensure the viability of the species as a copepod, well adapted to seasonal and abrupt environmental changes. On the other hand, Belmonte and Rubino (2019) also explained that this situation is widespread in various Calanoida species in the wild, suggesting that this is a widely spread phenomenon, and they also suggest that allowing eggs to rest during unfavorable periods is part of a general framework of species and community dynamics, with different strategies for each site or species. Furthermore, Belmonte and Rubino (2019) mentioned that studies conducted over the last 25 years approximately highlighted that the abundance of resting egg assemblages is directly related to environmental instability and that species can induce their investment in long-term future through dormancy and betting strategies (e.g. seed banks) rather than creating the next generation. From laboratory experiments and ecological data, this phenomenon provides some clues to understand stress and fluctuations under environmental conditions.

Maladaptation (negative population growth) is widespread in natural populations. Dastis et al. (2019) demonstrated in a field experiment with freshwater Copepoda how asymmetric selection for dispersal and pH acts on fitness surfaces to maintain phenotype-environment mismatches of maladaptation at local and regional scales in metapopulations. They find that environmental stochasticity leads to the maintenance of maladaptation, which is robust to dispersal, but also reveal an interplay between selection asymmetry and environmental correlation. Their findings highlight the importance of maladaptation in copepod species for planning conservation strategies that can support adaptive potential in dispersed and changing landscapes.

Abundance and population dynamics of planktonic Copepoda are governed by life history trade-offs related to resource (food) availability, reproduction and predation pressure (Saiz et al., 2015). Trade-offs related to the aging process and its underlying biological mechanisms. Aging in Copepoda involves deterioration of their vital rates and increased mortality associated with increased oxidative damage (lipid peroxidation); the activity of cell repair enzymatic mechanisms also increases with age. Caloric (food) limitation in marine Copepoda reduces mortality at their age and extends female longevity and reproductive lifespan. Given the overall low productivity of the ocean, this may be a strategy, at least in some copepod species, to

improve their reproductive chances in a nutritionally sparse, time-staggered environment. This marks how Copepoda can help understand adaptation from an ecological and evolutionary perspective.

2.1.7 Chemical ecology of copepod

Heuschele and Selander (2014) emphasized the importance of the chemical ecology of Copepoda in the water column for reproduction, foraging, and predator avoidance. The role of planktonic Copepoda in finding mates varies between the sexes. Copepod males, as active partners, usually play the role of searching for females, while females play the role of passive partners. This asymmetry in mating behavior between the sexes results in sexual dimorphism. To increase detection of female cues, male copepods are equipped with appendages carrying setae and sensilla, an enhanced chemosensory system that includes infochemical cues and sensors, and in many species, first antennular genitalia that can grasp females during mating. Finally, to optimize the mating process, males tend to swim more, faster, and with more direction than females. Thus, researchers have recognized the importance of infochemical cues for copepod reproduction (Heuschele and Selander, 2014). These sex differences in mating behavior may lead to differences in foraging efficiency. Males have lower ingestion and scavenging rates than females, and these differences arise primarily from differences in body size between the sexes. In addition, conflicts between mate searching and feeding can lead to significant sex differences in feeding efficiency in ambush feeders. Subsequently, several studies have shown that chemicals are involved in the discovery and evaluation of food (Heuschele and Selander, 2014). Several studies have shown that predators elicit responses from Copepoda and that chemical predator cues have the potential to serve as early warning in environments with changing predator densities. Copepod responses to predator cues include changes in behavior, morphology, or life history. For example, fish predation causes a decrease in gut fullness of the estuarine copepod *Acartia tonsa* (Calanoida: Acartiidae) during the day time in conditioned waters; *Tigriopus californicus* (Harpacticoida: Harpacticidae) to reduce swimming activity if the anemone *Anthopleura elegantissima* (Actiniaria: Actiniidae) present, stayed near the surface; other Copepoda reduced swimming speed and visible pigmentation. This further illustrates how pheromones in zooplankton hold information to

understand population dynamics, reproductive isolation, species formation, and food web dynamics.

2.1.8 Potential biological control effect of Copepoda on algal blooms

Hypersaline environments have higher salinity than seawater and may even be salt saturated. High salt environments are toxic to most organisms, resulting in the loss of cellular water, and life in high salt environments requires more energy (Oren, 2011). Interestingly, some Copepoda can survive in high salt ecosystems all over the world, and can survive at a salinity of more than 300–360 g/L. Copepoda are usually osmoregulators that exhibit osmotic adaptation at the cellular level, increasing the concentration of cytocompatible organic osmoregulation cells/solutes (Bayly and Boxshall, 2009; Svetlichny et al., 2012). This increased concentration of organic solute is synthesized in cells or obtained from the environment (Yancey, 2001). There are four chemical categories of these osmolytes and/or other solutes, namely, small amino acids and their derivatives, carbohydrates, polyols and their derivatives, and methyl sulfones and methylamines (Yancey, 2001). Some authors point out that in high salinity waters, permeable Copepoda cannot meet their energy consumption through their own synthesis of osmoregulation substances, but they gain salt tolerance through the consumption of external osmotic regulators in algal blooms (Shadrin and Anufrieva, 2013; Anufrieva and Shadrin, 2014). Previous studies have shown that when the concentration of *Dunaliella* reaches 6×10^7 cells/L and 60 g/m³, the biomass of *Arctodiaptomus salinus* (Calanoida: Diaptomidae) and *Cletocamptus retrogressus* (Harpacticoida: Canthocamptidae *incertae sedis*) in Crimea high salinity Lake were very high (Senicheva et al., 2008; Anufrieva and Shadrin, 2014). Similarly, during the bloom of cyanobacteria, *Apocyclops* cf. *dengizicus* showed tolerance to high salt conditions (Carrasco and Perissinotto, 2012), which indicated that Cyanobacteria may produce compatible osmotic pressure cells under high salt conditions (Oren, 2011). Therefore, the salt tolerance of Copepoda may be due to the consumption of exoosmolytes in microalgae, cyanobacteria, and other resources. Several Copepoda with salt tolerance have been recorded worldwide (Anufrieva, 2015). The mechanism of copepod salt tolerance is not clear at present. The study of functional genomics at the cellular and physiological level may be helpful to understand this biological phenomenon fully. The

feasibility of using Copepoda to control algal blooms is a potential field that has not yet been studied in depth (Turner 2014).

2.2 Impact of Copepoda in aquaculture

Aquaculture has become an increasingly important part of the world economy. In 2016, fishery and aquaculture annual production was at 1.71 billion tons of fish, “first sale” value is estimated to be \$362 billion, with exports exceeding \$232 billion (FAO, 2018). With market issues in the aquaculture industry, the biggest challenge is to control many complex abiotic and biological factors that affect the success of fish farming (Sipaúba-Tavares et al., 2017). An example of the complexity of managing aquatic systems is the need to control the number of Copepoda by manipulating the pond environment. Copepoda play an important role in the pond ecosystems, such as:

2.2.1 Food for small fish

Marine Copepoda are the main food for most marine fish larvae in nature (Turner, 2004). They contain high levels of DHA and other polyunsaturated fatty acids. These polyunsaturated fatty acids are either obtained from the diet of phytoplankton or accumulated even though the content of polyunsaturated fatty acids in the diet is low (Støttrup et al., 1999; Hiltunen et al., 2014). Copepoda are also an important source of exogenous digestive enzymes and play an important role in the digestive process of fish larvae (Munilla-Moran et al., 1990). Therefore, Copepoda are the first important link in the marine food chain from primary producers to fish (Turner, 2004). With the rapid expansion of breeding nurseries, aquaculture industries have a strong interest in a variety of aquatic animals, including edible, new, and ornamental fishes (FAO, 2020). Therefore, it is necessary to develop suitable larval feed for the shortage of traditional live food such as Rotifera and *Artemia* (Conceição et al., 2010). In this regard, the aquaculture industry is increasingly interested in Copepoda, which have developed into live feed for aquaculture (Conceição et al., 2010). Copepoda are ideal live feed for a variety of fish in aquaculture and using them can improve the survival rate of all kinds of fish larvae (Anton-Pardo and Adámek, 2015 and references therein).

As Copepoda are rich in fatty acids, they are essential for fish development (Molejón and Alvarez-Lajonchère, 2003). In order to improve the

yield and nutritional value of Copepoda, different concentrations of nitrogen and phosphorus nutrient solution were added to the eutrophic medium according to the requirements of the incubator to increase the yield of Copepoda (Caramujo et al., 2008). The different concentrations of nitrogen and phosphorus in the nutrient medium can affect the quality of algae for Copepoda (Breteler et al., 2005). In addition, the nutrient medium of microalgae includes micronutrients, including copper, selenium, vitamin C, and vitamin E (Olsen et al., 2000; Vismara et al., 2003; Hamre et al., 2008). Copepoda have a picky palate, so the traditional method of enriching Copepoda is not suitable for fish. The nutritional change of Copepoda is achieved by changing the nutritional diet of algae. This can be further improved through extensive nutrition research and copepod breeding.

Mostly Copepoda lack parthenogenesis or asexual reproduction (Bron et al., 2011). However, some researchers have suggested parthenogenetic Copepoda as a live feed for fishes in aquaculture because sexual reproductive Copepoda have several developmental stages and have lower growth rates (Nandini et al., 2011). Thus, the sexually reproductive Copepoda usually reach lower population densities than rotifers or cladocerans, which are mostly parthenogenetic forms. *Elaphoidella grandidieri* (Harpacticoida: Copepoda) is a tropical cosmopolitan species originally found in Africa, but also in North America, South America, and Asia (Nandini et al., 2011 and references therein). *Elaphoidella grandidieri* was found to have high fecundity, with more than 300 newborns per female, which is considerably higher than that reported for the *Eucyclops serrulatus* (Cyclopoida: Cyclopida), but close to that reported for *Calanus helgolandicus* (Calanoida: Calanidae) or the predatory Cyclopoida *Acanthocyclops americanus* (Cyclopoida: Cyclopida) in the range of 400–700. This suggests that parthenogenetic reproductive forms of Copepoda open up new avenues for use as live feed in aquaculture. Generally, Calanoida, Cyclopoida, and Harpacticoida are commonly used as live feed for fish larvae and juveniles in aquaculture (Table 1).

2.2.2 Carnivores of fish and other organisms

Some Cyclopoida are small carnivores of fish larvae, especially the early stages of some fishes, which are particularly vulnerable due to their small size (Hartig et al., 1982). For example, Copepoda (e.g., *Diacyclops thomasi* and *Acanthocyclops vernalis*)

Table 1 Major Copepoda used in aquaculture

Order	Genus	Species	Reference	
Calanoida	<i>Acartia</i>	<i>A. tonsa</i>	Marcus (2005); Santhosh et al. (2015)	
		<i>A. tsuensis</i>	Ohno et al. (1990)	
		<i>A. centrura</i>	Santhosh et al. (2015)	
		<i>A. erythraea</i>	Santhosh et al. (2015)	
		<i>A. clausi</i>	Marcus (2005)	
		<i>A. sinjiensis</i>	McKinnon et al. (2003)	
		<i>Bestiolina</i>	<i>B. similis</i>	McKinnon et al. (2003)
		<i>Eurytemora</i>	<i>E. affinis</i>	Santhosh et al. (2015)
		<i>Parvocalanus</i>	<i>P. crassirostris</i>	Schipp (2006)
		<i>Paracalanus</i>	<i>P. parvus parvus</i>	Marcus (2005)
	<i>Centropages</i>	<i>C. hamatus</i>	Marcus (2005); Santhosh et al. (2015)	
		<i>C. typicus</i>	Marcus (2005)	
	<i>Gladioferens</i>	<i>G. imparipes</i>	Santhosh et al. (2015)	
		<i>P. euryhalinus</i>	Puello-Cruz et al. (2013)	
	<i>Pseudodiaptomus</i>	<i>P. annandalei</i>	Santhosh et al. (2015)	
		<i>P. serricaudatus</i>	Santhosh et al. (2015)	
	<i>Calanus</i>	<i>C. finmarchicus</i>	Marcus (2005)	
		<i>C. helgolandicus</i>	Marcus (2005)	
	<i>Temora</i>	<i>T. longicornis</i>	Marcus (2005); Santhosh et al. (2015)	
		<i>T. stylifera</i>	Marcus (2005); Santhosh et al. (2015)	
		<i>T. turbinata</i>	Santhosh et al. (2015)	
		<i>Pseudocalanus</i>	<i>P. elongatus</i>	Marcus (2005)
Cyclopoida	<i>Pseudomyicola</i>	<i>P. spinosus</i>	Santhosh et al. (2015)	
	<i>Dioithona</i>	<i>D. oculata</i>	Molejón and Alvarez-Lajonchère (2003)	
	<i>Apocyclops</i>	<i>A. royi</i>	Piasecki et al. (2004)	
		<i>A. panamensis</i>	Piasecki et al. (2004)	
	<i>Dioithona</i>	<i>D. rigida</i>	Vasudevan et al. (2013)	
	<i>Acanthocyclops</i>	<i>A. robustus robustus</i>	Piasecki et al. (2004)	
	Harpacticoida	<i>Schizopera</i>	<i>S. elatensis</i>	Kahan et al. (1982)
<i>Amphiascus</i>		<i>A. parvula</i>	Santhosh et al. (2015)	
<i>Amonordia</i>		<i>A. normani</i>	Santhosh et al. (2015)	
<i>Tisbe</i>		<i>T. monozota</i>	Puello-Cruz et al. (2013)	
		<i>T. biminiensis</i>	Ribeiro and Souza-Santos (2011)	
<i>Tigriopus</i>		<i>T. japonicus</i>	Fukusho (1980)	
<i>Amphiascoides</i>		<i>A. atopus</i>	Santhosh et al. (2015)	
<i>Tachidius (Tachidius)</i>		<i>T. discipes</i>	Santhosh et al. (2015)	
<i>Macrosetella</i>		<i>M. gracilis</i>	Santhosh et al. (2015)	
<i>Elaphoidella</i>		<i>E. grandidieri</i>	Nandini et al. (2011)	

in Lake Michigan, which includes Pigeon Lake (Hartig et al., 1982; Hartig and Jude, 1984), prey on

fish larvae such as alewife (*Alosa pseudoharengus*), spottail shiner (*Notropis hudsonius*), yellow perch

(*Perca flavescens*), rainbow smelt (*Osmerus mordax*), *Pomoxis* spp., Gizzard shad (*Dorosoma cepedianum*), and Johnny darter (*Etheostoma nigrum*). The larvae of fish are attacked by *Acanthocyclops robustus* including both adult Copepoda and advanced stages of copepodites. The result is severe injury of fins, blood vessels, yolk sac, head, nostril, especially gills (Piasecki, 2000 and reference therein). The most common fish attackers were adult males (33%), copepodids IV (29%), and copepodids V (22%), while females usually feed on killed larvae (Piasecki, 2000). In Arkansas, carp and hybrid striped bass are stored in ponds as small fry, which are vulnerable to Cyclopoida. However, some copepod micropredators may be beneficial to aquaculture because they eat some Copepoda that are parasitic on fishes. The results showed that some species of *Mesocyclops* preyed on the free-swimming larva of *Lernaea* spp. (Kasahara, 1962).

2.2.3 Parasites to a variety of aquaculture species

In general, parasitic Copepoda are common in farmed fishes, wild fishes, and other seafood. There is a large amount of literature describing their classification and host ranges (Palm and Bray, 2014; Soler-Jiménez et al., 2019 and references therein). Many parasitic Copepoda have long been thought to affect the growth, reproduction and survival of wild hosts (Palacios-Fuentes et al., 2012 and references therein). They usually feed on host mucus, tissues and blood, and their attachment and feeding activities are the cause of primary disease (Johnson et al., 2004). The relationship between the number of parasitic Copepoda and the severity of the disease depends on 1) the size and age of the fish, 2) the species of copepod and the current developmental stage, and 3) the general health of the fish (Pike and Wadsworth, 1999 and references therein). With the development of mariculture, the importance of parasitic Copepoda as pathogenic factors is becoming more and more apparent (Johnson et al., 2004; Todd, 2007; Nagasawa, 2015). Among all orders and suborders of Copepoda, Siphonostomatoida, Monstrilloida, and Poecilostomatoida are exclusively parasites (Fogel et al., 2017; Suárez-Morales, 2018), and only some species of the orders Calanoida, Cyclopoida, and Harpacticoida are parasites (Ho, 2001; Boxshall et al., 2016; Huys, 2016). According to the study of Kabata (1988), parasitic Copepoda belong to the class of Siphonostomatoida (75%), about 20% belong to the Poecilostomatoida, and only about 5% belong to the Cyclopoida. Family

Caligidae, also known as sea lice, are the most common parasitic taxon of marine and saltwater cultured fish in the world, accounting for about 61% of all reported species (Johnson et al., 2004). Thus, the members of Caligidae are the culprits of most outbreaks recorded (Johnson et al., 2004), followed by Ergasilidae Copepoda. Parasitic Copepoda from other families have also been reported from farmed fish, and in some cases are the causes of disease (Johnson et al., 2004). Some examples of copepod infections; in *Acanthopagrus schlegelii schlegelii* (blackhead seabream; Pisces: Sparidae) gills and gill cavity are infected by *Caligus stromatei* (Siphonostomatoida: Caligidae), causing mucus hyperplasia and gill hyperemia (Lin et al., 1994); infection by *Alella macrotrachelus* (Siphonostomatoida: Lernaeopodidae) on black sea bream caused hyperplasia of the gill lamellae (Muroga et al., 1981); *Lepeophtheirus salmonis salmonis* infects Atlantic *Salmo salar* (Pisces: Salmonidae), resulting in severe skin erosion and bleeding on the head and back, and a distinct area of erosion and subcutaneous bleeding are observed in the perianal region (Brandal and Egildus, 1979); *Ergasilus labracis* (Poecilostomatoida: Ergasilidae) infects Atlantic salmon, which is characterized as severe gill hyperplasia and high levels of mortality (Hogans, 1989). In addition to fish, parasitic Copepoda also exist on some hosts, such as sponges, cnidarians, echinoderms, chordates, ascidians, molluscs, and mammals (Boxshall, 2005; Roubledakis et al., 2018).

Due to the presence of parasitic Copepoda and/or chemical treatments to reduce parasites and the cost of the treatment itself, the growth performance of the fish decreases, so the presence of these parasites has a significant economic impact (Rae, 2002). It is estimated that the annual cost of sea lice in the Scottish salmon farming industry is between US \$31 million and US \$46 million, calculated based on the 130 000 tons of annual harvest (Rae, 2002). This cost includes pressure and growth losses of approximately US \$20 million, as well as loss of treatment costs of US \$6.2 to US \$7.2 million. The estimated annual loss due to sea lice infection in Norway is approximately US \$67 million (Johnson et al., 2004). Although there are still a lot of economic losses due to indirect mortality, feed conversion rate and growth rate reduction, product value loss and treatment costs, there are few studies on their diseases and treatment methods. In order to reduce the impact of parasitic Copepoda in

aquaculture, further extensive research is urgently needed.

2.2.4 Intermediate hosts of fish parasites and vectors of viral and bacterial diseases

Some Copepoda are necessary intermediate hosts in the life cycle of parasitic species (Cleveland et al., 2018, 2020). Some parasitic nematodes infect Cyclopoida, infected Copepoda are eaten by fish and other aquatic animals, and then parasitic nematodes spread in fish and other aquatic animals, so Copepoda are considered intermediate hosts (Cleveland et al., 2018). For example, in the United States and Canada, parasitic nematodes (*Dracunculus insignis*) of terrestrial mammals enter the water and infect Cyclopoida Copepoda (*Acanthocyclops vernalis*). These infected Copepoda are accidentally eaten by various amphibians, and then the parasitic nematodes infect amphibians (Cleveland et al., 2018). In the study of Glazunova and Polunina (2009), seven Cyclopoida species in the Baltic Vistula Lagoon were intermediate hosts, because *Abramis brama* (bream fish) was found to carry *Ligula intestinalis* parasites transformed by Copepoda.

Because of the feeding effect of parasitic Copepoda on the host mucosa, tissues, and blood, it is believed that parasitic Copepoda may be the vector of viral and bacterial diseases in fish (Nylund et al., 1991; Overstreet et al., 2009). For example, Lymphocystis virus may be transmitted to the dermis of host fish through Copepoda (Overstreet et al., 2009). Copepoda are associated with the spread of infectious hematopoietic necrosis, infectious anemia, and infectious pancreatic necrosis to salmon (Overstreet et al., 2009). In natural water samples collected from Chesapeake Bay and Bangladesh, it was found that *Vibrio cholerae* O1 and non-O1 serotype strains were attached to the surface of live Copepoda (Huq et al., 1983).

2.2.5 Copepoda as food for human consumption

Fisheries are an important source of food and other products around the world. Increased demand for seafood and fish products has had a negative impact on global fish stocks (FAO, 2020). As mentioned above, Copepoda have good nutritional value and are used as live feed for fish in aquaculture (Molejón and Álvarez-Lajonchère, 2003; Anton-Pardo and Adámek, 2015). In the same way, researchers have come up with the idea of using Copepoda for human consumption (Kottelat, 2007), which would reduce the pressure of over

exploitation of fisheries (Olsen, 2011). Some studies have shown that *Calanus finmarchicus* (Calanoida: Calanidae) and *Allodiaptomus* (Calanoida: Diaptomidae) have unique fat composition, oil, proteolytic enzymes and lipases, wax esters, astaxanthin (carotene), chitin, and other nutrients, which are very valuable and a potential supplement to human consumption (Kottelat, 2007; Eysteinnsson et al., 2018). When it comes to omega-3 fatty acid concentrations, *Apocyclops royi* (Cyclopoida: Cyclopidae) can have a huge nutritional impact (Nielsen et al., 2019). In the study of Nielsen et al. (2019), it is found that *Apocyclops royi* can regulate the metabolic activity of n-3 polyunsaturated fatty acid biosynthesis during polyunsaturated fatty acid starvation. Similarly, Rayner et al. (2017) study also shows *Pseudodiaptomus annandalei* (Calanoida: Pseudodiaptomidae) has strong indications of this capability. According to a report in the Coast Science and Societies magazine (Cirino, 2019), when *A. royi* eats yeast, it produces fatty acids by converting simple fats found in yeast into coveted omega-3 fatty acids. In general, Copepoda eat algae to improve their nutritional levels, because yeast is cheaper than algae; it turns out that this is a low-cost method that can produce the world's most coveted food for human consumption. Therefore, Copepoda can indeed be a source of fatty acids in the future. However, the potential of Copepoda to replace wild caught fish in human dietary supplements is just beginning to be explored, which needs further extensive research.

2.3 Copepoda in medical fields

One of the sustainable development goals is to ensure the health and well-being of people of all ages (Chavarro et al., 2017). Many diseases are transmitted by mosquitoes, which account for more than 17% of all infections, including dengue fever, yellow fever, malaria, Zika disease, chikungunya disease, West Nile virus, Japanese encephalitis, Rift Valley fever, and lymphatic filariasis, killing millions of people every year (Murugan et al., 2015; WHO, 2020). The best way to prevent and eradicate these diseases is to interrupt the life cycle of the vector through biological control (Buxton et al., 2020). Freshwater free-living Copepoda are commonly used for biological control because they feed on mosquito larvae, which are the main vectors of several infectious diseases (Früh et al., 2019 and references therein). In the study of Früh et al. (2019), seven species of Cyclopoida of Cyclopidae

family were collected in the field in Germany, and bioassays were carried out for the first time in the laboratory to determine their potential as biological control agents for invasive Asian Bush mosquitoes, *Aedes japonicus*, which are vectors for the transmission of various pathogens. Among them, two species of *Megacyclops* seem to be promising candidates for biological control of *A. japonicus*. Dengue fever and hemorrhagic fever have become one of the most important public health issues in Southeast Asia and are widespread mosquito-borne viral diseases (Julo-Réminiac et al., 2014; WHO, 2020). It is estimated that there are 390 million cases of dengue fever worldwide each year, the incidence is increasing, and epidemics are becoming more frequent (Tran et al., 2015; WHO, 2021). As of now, there is only one dengue vaccine on the market. Despite vaccines, prevention is one of the key steps to control this infection. In Vietnam, the Philippines, and Sri Lanka, Copepoda are used as biological controls for mosquito larvae in artificial containers (Panogadia-Reyes et al., 2004; Nam et al., 2000, 2005; Udayanga et al., 2019). The results of a large mosquito vector project in Vietnam indicate that the use of *Mesocyclops* (Cyclopoida: Cyclopidae) is a potential method of controlling mosquito-borne diseases (Chang et al., 2011).

Generally, omnivorous Cyclopoida are used for the biological control of vector mosquitoes, of which the most commonly used are *Acanthocyclops*, *Macrocyclops*, *Megacyclops*, *Mesocyclops*, and *Thermocyclops* (Table 2). (Among the more frequently used species, for example, *Mesocyclops aspericornis*, *M. pehpeiensis*, *M. longisetus longisetus*, *Macrocyclops distinctus*, *M. albidus albidus*, and *Megacyclops viridis viridis*, *M. aspericornis*), *M. longisetus longisetus* are the most popular because of their wide distribution and strong mandibles for easy predation (Suárez-Morales et al., 2003). Some Italian researchers tested the predation effect of two European Cyclopoida species, such as *Macrocyclops albidus* and *Mesocyclops leuckarti* on the invasive mosquito *Aedes koreicus* (Baldacchino et al., 2017). The results show that both species are effective predators of the larvae of *Ae. koreicus*. In recent years, researchers have also used Calanoida Copepoda to study the control effects of vector mosquitoes (Cuthbert et al., 2018). The predation efficiency of *Lovenula raynerae* (Calanoida: Diaptomidae) on *Culex pipiens* larvae was studied (Cuthbert et al., 2018) and it was found that *L. raynerae* is an effective species for controlling vector mosquitoes (Cuthbert et al., 2018). As Copepoda feed on mosquito larvae, they can control several mosquito-

Table 2 Major Cyclopoida genera and species used as biological controls

Genera	Species	Geographic distribution	Reference
<i>Acontocyclops</i>	<i>A. vernalis</i>	Cosmopolitan	Silva (2008)
<i>Diacyclops</i>	<i>D. navus</i>	Nearctic region	Reid et al. (1989)
	<i>M. viridis</i>	Cosmopolitan	Dieng et al. (2002); Alekseev et al. (2016)
<i>Megacyclops</i>	<i>M. latipes</i>	Cosmopolitan	Alekseev et al. (2016)
	<i>M. formosanus</i>	Oriental region	Alekseev et al. (2016)
	<i>M. aspericornis</i>	Tropical and subtropical	Silva (2008)
	<i>M. pehpeiensis</i>	Oriental, Palearctic, and Nearctic region	Dieng et al. (2002); Holyńska et al. (2003)
	<i>M. woutersi</i>	Australasian, Palearctic, and Oriental region	Holyńska et al. (2003)
	<i>M. thermocyclopoides</i>	Australasian, Neotropical, and Oriental region	Holyńska et al. (2003); Gutiérrez-Aguirre et al. (2006)
<i>Mesocyclops</i>	<i>M. brasiliensis</i>	Neotropical region	Gutiérrez-Aguirre et al. (2006)
	<i>M. edax</i>	Neotropical region	Gutiérrez-Aguirre et al. (2006); Silva (2008)
	<i>M. rutneri</i>	Oriental region	Marten (1990); Marten et al. (1994)
	<i>M. guangxiensis</i>	Oriental region	Reid and Kay (1992)
	<i>M. annulatus</i>	Neotropical region	Silva (2008)
	<i>M. albidus</i>	Neotropical region	Silva (2008)
<i>Macrocyclops</i>	<i>M. longisetus</i>	Neotropical region	Silva (2008)
	<i>M. distinctus</i>	Oriental, Palearctic, and Australasian region	Dieng et al. (2002)

borne diseases. Using Copepoda for biological control is a strategy to reduce pesticide use, but it is important to conduct accurate taxonomic studies to determine the most suitable copepod species. In summary, the use of Copepoda to control vector mosquitoes may be an effective method, and future research will help implement sustainable biological methods for mosquito-related diseases.

3 CONCLUSION

In this article, we summarize the potential importance of Copepoda. A review of the literature on various aspects of Copepoda highlights the relevance and importance of Copepoda in ecology, aquaculture, and human health. A large body of literature suggests that they can be used to understand hypoxia-induced climate change under natural and laboratory conditions. Further literature shows that Copepoda are highly responsive to global eutrophication; oil spills have been an issue for vulnerable aquatic animals and the literature shows that Copepoda enable scientists to effectively predict water quality and ecological dynamics; and Copepoda have proven to be an effective animal for testing the toxicity of microplastic pollution in aquatic environments around the world. Copepoda have been further used to test the effects of industrial chemicals and metals on planktonic organisms in estuaries and beaches around the world. Many reports further support the importance of Copepoda when studying various environmental factors, including salinity, pH, temperature, and ocean acidification (global warming). They have been used to study aquatic food webs because their composition and fish recruitment depend on the abundance of phytoplankton, but are also associated with the dominance of diatoms. Life history strategies were further demonstrated under consumptive and non-consumptive parameters to understand predation, food availability and seasonal dynamics. The competitive structure among copepod communities was also demonstrated in terms of food availability and reproductive rates. Copepods were further used to test maladaptation in terms of spatial environmental heterogeneity, dispersal, and (a) symmetric selection and ecological (abundance distribution) changes at the landscape level. The aging process and increased mortality in copepods are associated with oxidative damage, while the longevity of females under limited food suggests adaptation and reproductive strategies under vulnerable

conditions. Copepods have also been studied for chemical cues and signals that mediate foraging, reproduction, and predator avoidance, which are useful in understanding population dynamics, reproductive isolation, species formation, and food web dynamics.

Copepoda have also been shown to be an effective medium for controlling algal blooms. Copepoda have played a landmark role in aquaculture, serving as nutrition for a variety of fish species and in most cases generating significant profits for aquaculture. In some cases, aquaculture and natural populations face significant losses due to the presence of parasitic Copepoda, and further research is recommended to control the spread of these parasites. Recent studies have proven that Copepoda are an alternative source of fish nutrition, especially omega-3 fatty acids as well as protein for human diet. Freshwater Copepoda are further effectively used in many cases to prevent mosquito-borne diseases, a public health issue of major global concern. This clearly proves that any attempt to learn more about Copepoda is worthwhile and will lead to the implementation and development of sustainable and effective methods in all areas of Copepoda research.

4 DATA AVAILABILITY STATEMENT

All data generated or analyzed during this study are included in this article.

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