



Review

A review of the neurobehavioural, physiological, and reproductive toxicity of microplastics in fishes

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ABSTRACT

Microplastics (MPs) have emerged as widespread environmental pollutants, causing significant threats to aquatic ecosystems and organisms. This review examines the toxic effects of MPs on fishes, with a focus on neurobehavioural, physiological, and reproductive impacts, as well as the underlying mechanisms of toxicity. Evidence indicates that MPs induce a range of neurobehavioural abnormalities in fishes, affecting social interactions and cognitive functions. Altered neurotransmitter levels are identified as a key mechanism driving behavioural alterations following MP exposure. Physiological abnormalities in fishes exposed to MPs are also reported, including neurotoxicity, immunotoxicity, and oxidative stress. These physiological disruptions can compromise the individual health of aquatic organisms. Furthermore, reproductive abnormalities linked to MP exposure are discussed, with a particular emphasis on disruptions in endocrine signaling pathways. These disruptions can impair reproductive success in fish species, impacting population numbers. Here we explore the critical role of endocrine disruptions in mediating reproductive effects after exposure to MPs, focusing primarily on the hypothalamic-pituitary-gonadal axis. Our review highlights the urgent need for interdisciplinary research efforts aimed at elucidating the full extent of MP toxicity and its implications for aquatic ecosystems. Lastly, we identify knowledge gaps for future research, including investigations into the transgenerational impacts, if any, of MP exposure and quantifying synergetic/antagonistic effects of MPs with other environmental pollutants. This expanded knowledge regarding the potential risks of MPs to aquatic wildlife is expected to aid policymakers in developing mitigation strategies to protect aquatic species.

1. Introduction

Aquatic ecosystems are negatively impacted by anthropogenic pollutants, many of which pose significant threats to the health and structure of global ecological systems. Not surprisingly, these pollutants raise environmental concerns but also public health concerns when fishes and seafood are consumed by humans (Choi et al., 2023; Häder et al., 2020; Lu et al., 2018). Microplastics (MPs) represent one group of pollutants that are emerging as contaminants of critical concern. MPs enter freshwater and marine environment through diverse routes, including point sources of industrial effluents and domestic sewage. MPs are often

wind-driven into aquatic systems particularly near urban areas and landfill sites. Poor waste management of plastic materials are frequently associated with commercial fishing, and marine shipping (Alfonso et al., 2021; Su et al., 2022; Zhang, 2017). MPs can travel long distances and can become widespread along coastlines due to their small size, low density, and durability (Shim et al., 2018). MPs within the size range of food typically are consumed by aquatic animals such as fish and fish-eating birds, crustaceans, mollusks, and zooplankton (Kibria, 2023; McCormick et al., 2020). This means that MPs can be incorporated into food webs including human food webs (de de Souza Machado et al., 2018).

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There are different categories of MPs present in the aquatic environment which are based on their origin, composition, and physical attributes. MPs are broadly classified into two categories in literature: primary and secondary MPs. Primary MPs are the result of particle emissions released during industrial manufacturing and the discharge of plastic dust from plastic items. Secondary MPs refer to plastic particles that are bigger in size, such as fragments, fibres, and films, which result from the breakdown of larger plastic debris due to environmental factors (Laskar and Kumar, 2019). Plastic debris in the environment has been classified into different categories that include macroplastics (100–2.5 cm), mesoplastics (2.5 cm to > 5 mm), microplastics (1 µm to 5 mm) and nanoplastics (< 1 µm) (Kershaw and Rochman, 2015). Currently, regulatory categorisations of MPs are in place in some countries, however these regulations are not yet fully harmonised. In the EU for instance, there is no regulation in place concerning MPs, but there are several regulations addressing MP-specific objectives (e.g. European Commission Marine Strategy Framework Directive (MSFD) or the amended Annex XVII of September 2023 (for intentionally added MPs).

In the laboratory, research has focused primarily on MPs that are polyethylene (PE), polystyrene (PS), polyvinyl chloride (PVC), polypropylene (PP), polyamide (PA) and polyethylene terephthalate (PET) (Guo and Wang, 2019). A significant chemical characteristic common to all MPs is their capacity to absorb and accumulate environmental pollutants, including heavy metals and organic contaminants (Menéndez-Pedriza and Jaumot, 2020). Moreover, MPs contain various types of chemical additives, such as plasticizers and flame retardants, suggesting they can be a “carrier” and “source: for other chemicals. MPs are typically resistant to chemical reactions, although they may undergo photochemical deterioration when exposed to UV light, resulting in higher rates of fragmentation. In addition, the hydrophobic properties of MPs can dictate their interactions within aquatic habitats and organisms (He et al., 2023; Li et al., 2024). Taken together, MPs exhibit unique properties as environmental pollutants that affect their distribution, uptake, and toxicity in aquatic species.

Fishes play essential roles in maintaining the health and balance of aquatic ecosystems. They are integral components of food webs, occupying various trophic levels and serving as both predators and prey (Lynch et al., 2016). They are also important for human health because humans often get exposed to persistent contaminants by eating contaminated fishes (Huang et al., 2021). MPs enter fish tissues primarily through direct ingestion (Li et al., 2021). Zooplanktivorous fishes may inadvertently swallow MPs, as the size of MPs mirrors their prey in water (Ory et al., 2018). MPs can also be transported into the body through the gills via passive filtration during respiration (Liang et al., 2023). These uptake methods for MPs into a fish vary based on the species, their habitat, diet, and the level of pollution in their environment (Jovanović, 2017).

The ingestion of MPs by fishes and other aquatic organisms can lead to a range of toxic effects, such as inhibition of growth, histopathological alteration of target organs, oxidative stress, neurotoxicity, metabolic interference, hepatotoxicity, and inflammation (Batel et al., 2018; Dong et al., 2022; Lee and Kim, 2023; Soliman et al., 2023; Xie et al., 2021; Zaman et al., 2024). Some other toxic substances, such as heavy metals, polycyclic aromatic hydrocarbons, antibiotics, and different organic compounds, may also be absorbed by MPs, which can result in synergistic toxicity in fishes and other aquatic organisms (Batel et al., 2018; Tien et al., 2020; S. Wang et al., 2022). Furthermore, the negative impact of MPs on fish reproduction also has become a growing concern (Wang et al., 2019). For example, MPs can have serious implications for the endocrine systems of fishes (Han et al., 2022) and different bisphenol analogues and phthalates, which are well-known plasticizers and notable endocrine disruptors, can leach into the environment from MPs (Mathieu-Denoncourt et al., 2015). These chemicals can mimic or cause hormonal imbalance, leading to low fertility rates, altered growth in progeny, or even changes in sex ratios (Faheem and Bhandari, 2021).

Several studies have found that MPs can affect female reproductive

systems by inducing oxidative stress, apoptosis, and hormonal imbalance (Cao et al., 2023; Gupta et al., 2023; Qiang and Cheng, 2021; Xia et al., 2023). MPs can cause adverse effects on fertilization, gonadal morphology, steroidogenesis, and the function of the hypothalamic-pituitary-gonadal (HPG) axis (Batel et al., 2020; Liu et al., 2023; Qiang and Cheng, 2021). The HPG axis regulates reproductive functions in animals by maintaining the balance reproductive hormones, and MPs may disrupt the HPG axis and delay ovarian development (Maradonna and Meccariello, 2023).

In addition to the reproductive system, the central nervous system of fishes may also be negatively impacted by MPs, resulting in altered reproductive behaviour (Rahman et al., 2022). The overall fitness of an organism, including its survival and reproductive success, is closely related to its behaviour. Beyond direct physical and chemical effects, MPs can induce neurological and behavioural changes in individuals. MPs can also disrupt normal feeding (Carrasco et al., 2019; Coppock et al., 2019; Van Colen et al., 2020), social (Takai et al., 2022), and swimming behaviours of fishes. Modifications in behaviour can influence vital activities like feeding, escaping from predators, or reproduction and can subsequently reduce the fitness of an organism within the ecosystem, popularly known as ‘ecological death’ (Scott and Sloman, 2004). For instance, swimming ability and social behaviour in fishes are often employed as indicators to assess chemical toxicity at concentrations that do not cause mortality (Audira et al., 2021). In addition, MP exposure can cause increased anxiety or stress, prompting some modifications in natural behaviours, thus making these individuals more vulnerable to adverse outcomes (Félix et al., 2023). Moreover, exposure to MP can disrupt the olfactory-mediated behaviour of goldfish, *Carassius auratus*, through the interruption of olfactory neural signal transduction (Shi et al., 2021).

1.1. Objectives of review and search strategy

Over the past several years, review articles have summed up the harmful effects of MPs, with a focus on the cellular and physiological responses of fishes and other aquatic organisms (Choi et al., 2023; D’Costa, 2022; Desai et al., 2023; Huang et al., 2023). However, these reviews do not focus on the impaired reproductive mechanisms underlying MPs exposure in fishes, by assessing neurobehavioural and physiological changes. Here we provided an overview of the toxic effects of MPs on neurobehaviour, physiology, and reproduction in fishes. We aimed to summarize what is known about the underlying mechanisms that mediate such abnormalities in fishes. We also highlighted the role of hormones and neurotransmitters, as well as their signaling pathways, when discussing mechanisms of MP-induced neurobehavioural, physiological, and reproductive toxicity through the perturbation of these pathways. Lastly, future research directions are proposed to understand how MPs affect fish behaviour in their natural habitats.

Our search strategy involved entering keywords for “microplastics” and “fish”, along with a specific endpoint (i.e., “behaviour”, “neurotoxicity”, “reproduction”) in Google Scholar, Web of Science, PubMed, and Scopus database (over the last ten years from January 2013 to April 11th, 2024) in the title, abstract, or keywords. We retrieved 2039 publications with these keywords. Most papers were within the field of “Environmental Sciences”, “Agricultural and Biological Science”, and “Pharmacology, Toxicology and Pharmaceutics” (Fig. 1A). We systematically filtered these results using predefined inclusion and exclusion criteria. To be included, studies had to involve fish as the subject and focus on the effects of MPs on neurobehaviour, physiological changes, or reproductive impacts. We manually screened the titles of the 2039 publications to exclude studies that did not meet the inclusion criteria. This step reduced the number of relevant articles to 156. The full texts of these 156 articles were then assessed for eligibility. Articles that did not provide sufficient data or focus on our areas of interest (neurobehaviour, physiology, reproduction) were excluded. We then manually selected 78 articles for our review that had the following criteria: (1) The study

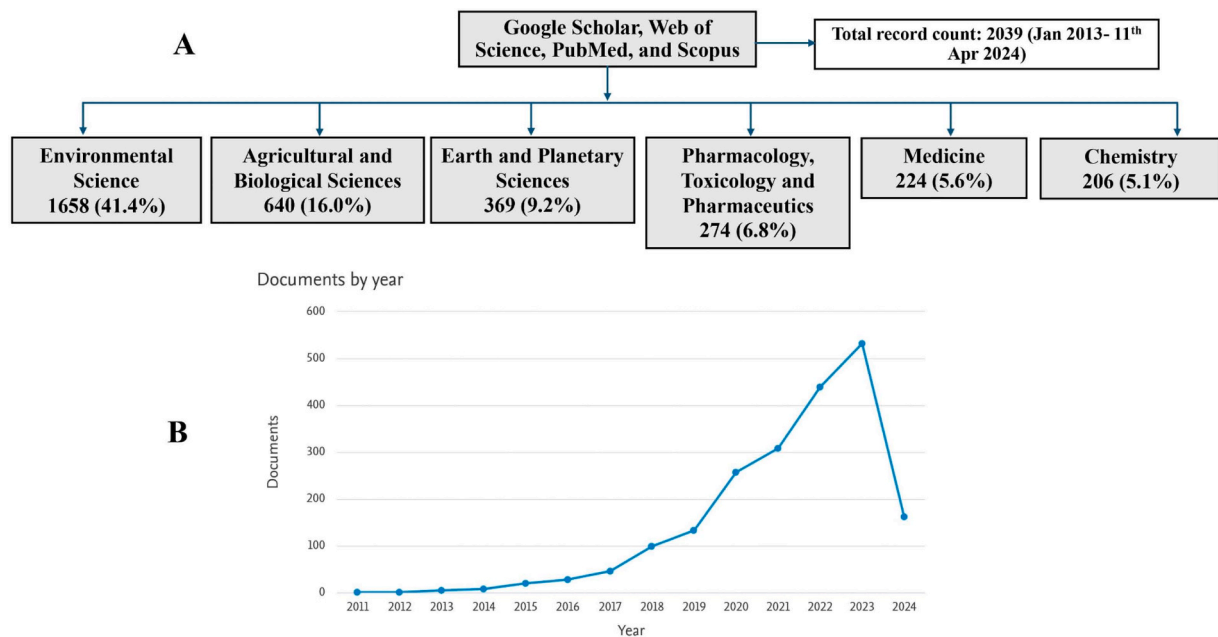


Fig. 1. (A) The total count of papers published between January 2013 and April 11th, 2024, along with the six categories that have the highest publication records. The information was obtained by conducting a search on Google Scholar, Web of Science, PubMed, and Scopus by entering key words “microplastics” and/or + “fish”, along with a specific endpoint (i.e., “behaviour”, “neurotoxicity”, “reproduction”) applied to the title, abstract, and keywords. (B) The number of published papers from 2011 to April 11th, 2024.

reported the effects of MPs on fish behaviour (15 papers); (2) The study evaluated the physiological impacts to MPs exposure to fish (37 papers) and (3) the investigation related to the reproductive effects of MPs in fish (26 papers). Over the past several years (2015–2023), there has

been increased attention regarding the impact of MPs on fishes (Fig. 1B).

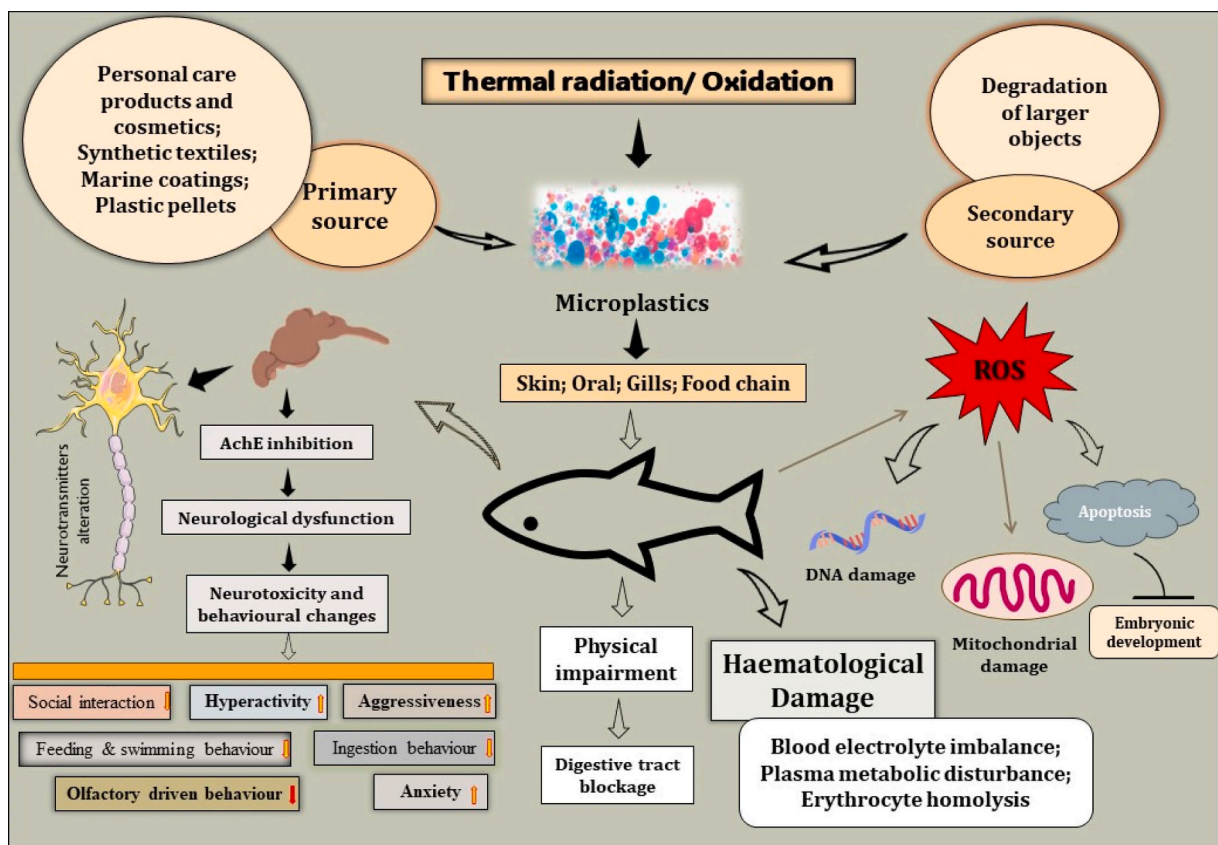


Fig. 2. The figure shows the different toxic effects of MPs in fishes.

2. Behavioural effects of MPs in fishes

The effect of MPs on fish behaviour is of significant concern as it impedes their normal function in natural habitats (Fig. 2). Different behavioural abnormalities and their possible causes are outlined in Table 1.

2.1. Hyperactivity and hypoactivity locomotion

Locomotion of fishes reflects their ability to utilize energy efficiently for essential activities such as migration, feeding, and predator avoidance (Domenici et al., 2007; Langova et al., 2023). MPs have been noted to increase the locomotor activity of fishes under certain conditions. For example, adult zebrafish exposed to polystyrene MPs (PS-MPs) (5 µm) for 7 days across a broad concentration range (0.001–20 mg/L, equivalent to 14.5–2.9 × 10⁵ particles/mL) exhibited hyperactive swimming behaviour, increased swimming distance, and prolonged manic and active states (Chen et al., 2020). In this study, the hyperactivity was associated with decreased glucose and acetaldehyde levels and increased amino acids in liver, indicating energy depletion. However, the effect of MPs on locomotor activity is not consistent from study to study and may be reflected by the time of exposure, size of particle, uptake, or type of MPs. For example, hypoactivity was observed in 5-day zebrafish larvae after exposure to 50 nm polystyrene nanoparticles (Browne et al., 2008). Other investigations have also reported changes in activity levels of fishes with MP exposure. Im et al. (2022) reported that the early life exposure to PS-MPs in zebrafish for 10 days led to hyperactivity in adulthood, which was associated with gene expression changes related to oxidative stress (*nrf2a* and *sod2*) and the nervous system (*nrbf2*, *slc6a4b*, and *npy*) (Im et al., 2022). Yu et al. (2022) also noted that, after exposing adult zebrafish to both waterborne (40–47 µm, 0.1–10 mg/L) and foodborne (0.01±0.01 µg/mg; 0.1±0.1 particles/mg) PE-MPs for 7 days, fish exhibited more pronounced hyperactive behaviour due to alterations in the cholinergic system and changes in dopamine and 5-HT neurotransmitter concentrations in brain (Yu et al., 2022).

2.2. Aggressive behaviour

Aggression significantly impacts the social dynamics and well-being of animals and includes a range of actions and interactions directed towards conspecifics or other objects (Holekamp and Strauss, 2016). Based on mammalian literature, biochemical indicators of aggression include decreased dopamine activity in the nucleus accumbens region of the brain and levels of adrenaline and noradrenaline in brain areas like the cortex, amygdala, and hippocampus. Additionally, imbalances in excitation and inhibition mechanisms of the brain have been characterized by reduced GABA levels and increased glutamate levels in the cortex (Ende et al., 2015). In addition, hormones such as testosterone, melatonin, vasopressin, and oxytocin are all implicated in influencing aggression by impacting stress hormones in the body and altering hormonal systems, which can modulate male territorial behaviour (Koop and Oster, 2022). In zebrafish, vasotocin and isotocin regulate aggression, in a similar way to their counterpart's vasopressin and oxytocin control aggression in rodents. These hormones also play a role in establishing social hierarchies in fishes (Lema et al., 2015).

Studies show that MPs can affect aggression behaviour via several mechanisms. Hollerova et al. (2023) treated rainbow trout, *Oncorhynchus mykiss*, to a six-week exposure to PS-MPs (0.5 %, 2 % and 5 % with diet). This resulted in increased aggressive behaviour and activity. It was speculated that this behavioural change may be attributed to starvation resulting from the replacement of regular food with non-nutritious plastics. The results of the study highlight the importance of considering both direct and indirect mechanisms by which MPs can influence behavioural responses in aquatic organisms. While direct interactions with MPs may induce physiological or neurological changes

affecting behaviour, indirect effects such as reduced food intake or nutrient absorption can also play a significant role. Thus, the altered behaviour may be related to the substitution of essential nutrients. Aggressive behaviour can also be caused by stressors other than MPs, such as pathogens, which can lead to skin damage and subsequent changes in behaviour and hunger-related responses, as observed in rainbow trout (Martins et al., 2012).

2.3. Feeding and swimming behaviour

The methods by which organisms consume food directly impacts their nutrient intake for growth, development, and maintenance of biological functions. It has been proposed that fishes ingest plastics as readily as they do their prey under controlled conditions. Indeed, there are several reports documenting plastic consumption by fishes (da Costa Araújo and Malafaia, 2021; Markic et al., 2020). It is important to quantify ingestion behaviour, particularly if we consider that behaviour can be disrupted by chemical additives on the MPs. Zebrafish tend to eat particles (247.5 µm; ranging from 0.5, to 9.4 %) when mixed with their food (Kim et al., 2019). However, when zebrafish ingest MPs, the individual can expel them from the oral cavity, suggesting that zebrafish can distinguish MPs as non-food items. One outstanding question related to food intake involves whether there can be intentional uptake of MPs over food in wild fish, which may subsequently lead to starvation. While it remains difficult to definitively state the uptake was intentional, it remains an intriguing possibility.

Zebrafish are known for their vision and adaptive movements in response to prey. When presented with either food or MPs, they displayed increased turning behaviours, indicating their frequent attempts to consume them. Manipulating the ratio of food to MPs allowed to show that zebrafish could differentiate between food and MPs (Kim et al., 2019). When exposed to 20 mg of MPs, the zebrafish exhibited escalated spitting behaviour- a response commonly associated with food items- indicating their ability to recognize and reject MPs. In a similar study, McCormick et al. (2020) examined consumption of microplastic spheres by larval Ambon damselfish, *Pomacentrus amboinensis*. In the study, forty polystyrene spheres were added to 0.8 L glass beakers that contained groups of 4 fish. After 1 h, the fish were dissected and the spheres in the gut were quantified. All but 9 out of 60 fish had consumed plastic spheres (85 %), with ingestion rates ranging between 1 and 33 particles with a mean of 4.5 spheres per fish.

Other types of feeding behaviour can be modified with MPs exposure. Yin et al., (2018) studied the impact of PS-MPs on jacobever, *Sebastes schlegelii*, and found that, when fish were exposed to a concentration of 1 million polystyrene microspheres per litre of water, the individuals exhibited changes in behaviour, energy reserves and nutritional composition. Notably, the presence of MPs extended the time spent foraging, suggesting an inhibitory effect on feeding activity. Exposure to MPs also decreased swimming speed and range of movement, which resulted in the fish becoming more susceptible to predators. Fish exposed to MPs also showed lower propensity to explore within their tank compared to control fish, indicating an adverse impact on hunting behaviour and curiosity. These observed behavioural changes may be attributed to factors such as alterations in brain composition due to increased water content caused by exposure to MPs. It can also be due to the breakdown of larger particles into smaller ones within the digestive system which can affect organ functions, oxidative stress, or stimulation of the gastrointestinal tract impacting digestion and food intake (Yin et al., 2018). Several other studies have investigated potential reasons for such alterations associated with exposure to MPs (Kolandasamy et al., 2018; Lu et al., 2016; Pang et al., 2014). However, combinations of biological mechanisms can affect the behaviour of fishes but may not necessarily affect their feeding habits. For example, MP exposure may lead to physical impairments in marine organisms, affecting their locomotion, swimming performance, agility, and overall mobility, which may impact predator-prey relationships in marine

Table 1
Effects of microplastics on behaviour of fishes.

Species	Developmental stage	Exposure duration	MPs types	MPs sizes	Concentration	Behavioural effects	Possible causes of behavioural effects	References
Common goby (<i>Pomatoschistus microps</i>)	Juvenile	96 hours	PE	420–500 μ m	-	Confusion with prey. Predatory efficiency and performance decreased.	Developmental factors may affect fish prey selection.	(Cunningham et al., 2021)
Gilt-head bream (<i>Sparus aurata</i>)	Juvenile	21 days	PE	100–500 μ m	4.52 \pm 2.30, 4.06 \pm 1.52, and 4.05 \pm 1.58 % diet	More assertive in social interactions. Low feeding activity.	Activation of antioxidant enzymes. Elevated SOD and CAT activity. Lipid peroxidation.	(Rios-Fuster et al., 2021)
Zebrafish (<i>Danio rerio</i>)	Adult		PE	247.5 μ m	0.5–9.4 %	Showed spitting behavior. Ingestion behaviour changes by various food volumes. (Feeding behaviour).	-	(Mitchell et al., 2020)
Zebrafish (<i>Danio rerio</i>)	Adult	20 Days	PE and PS	90 and 25 μ m	90 % and 10 %	Altered locomotion activity.	Up-regulation of the circadian clock gene <i>nr1d4b</i> in liver transcripts.	(Limonta et al., 2019)
Spiny chromis (<i>Acanthochromis polyacanthus</i>)	Juvenile	6 weeks	PET	2 mm	0.055–0.16 mg/L	No significant effect behaviour.	Lower number of plastics found in the gastrointestinal tract.	(Critchell and Hoogenboom, 2018)
Crucian carp (<i>Carassius carassius</i>)			PS	24–27 nm	9.3 \times 10 ¹² particles/mL	Impacts feeding and shoaling. Reduced activity, longer periods of feeding, closer together, and less explorative.	Effect on metabolism.	(Mattsson et al., 2015)
Goldfish (<i>Carassius auratus</i>)	Juvenile	28 days	PS	500 nm and 30 μ m	25 mg/mL	Olfactory responses to L-cysteine and taurocholic acid significantly impaired.	Hampered odour detection, action potential production, transmission of olfactory brain signals, and information processing. Suppression of <i>GFA2</i> , <i>GFA28</i> , <i>GFB1</i> , and <i>GFB8</i> genes.	(Shi et al., 2021)
Jacopever (<i>Sebastes schlegelii</i>)	Juvenile	14 days	PS	15 μ m	1 \times 10 ⁶ microspheres/L	Reduced feeding and increased shoaling. Decreased swimming and exploration ability.	Stimulates digestion and the gut and reduces food intake due to changes in appetite and behaviour. Respiratory stress and lesions. Change in ion regulation and oxygen consumption.	(Yin et al., 2018)
Rainbow trout (<i>Oncorhynchus mykiss</i>)	Juvenile	6 weeks	PS	52.5 \pm 11.5 μ m	0.5, 2 and 5 % of diet	Feeding behaviour reduced. Individual fish were more aggressive and active.	Skin injuries. Serum ammonia changes. Oxidative stress, hematological changes and severe liver and gills lesions with negative impacts on pro-inflammatory genes detected.	(Hollerova et al., 2023)
Zebrafish (<i>Danio rerio</i>)	Adult	7 days	PS	5 μ m	0.001, 0.01, 0.1, 0.25, 0.5, 1, 2, 10, and 20 mg/L	Hyperactive and remained in manic and active moods for extended periods of time.	Attributed to particulate matter stimulation and estrogen up regulation. Overactivity lowered glucose and acetaldehyde metabolites and raised amino acid levels, confirming the energy shortfall.	(Tien et al., 2020)

(continued on next page)

Table 1 (continued)

Species	Developmental stage	Exposure duration	MPs types	MPs sizes	Concentration	Behavioural effects	Possible causes of behavioural effects	References
European seabass (<i>Dicentrarchus labrax</i>)	Juvenile	96 hours	Fluorescent red polymer microspheres	1–5 mm	0.26 and 0.69 mg/L	Reduced swimming speed and resistance. Lethargic and erratic swimming behavior.	Potentially attributable to adverse effects induced by MPs on the metabolic, endocrine, and nervous systems.	(Barboza et al., 2018a)
Zebrafish (<i>Danio rerio</i>)	Adult	21 days	Naturally weathered MPs	5 mm	0.1 and 1 mg/L	Induced anxiety-like behaviour.	Brain catalase activity enhanced, but lactate dehydrogenase activity suppressed following exposure of 1 mg/L. Glutathione levels increased without changing their ratio. Mitochondrial respiratory chain complexes II and IV reduced significantly without affecting mitochondrial function.	(Félix et al., 2023)
Chichlid (<i>Chindongo demasoni</i>)	Juvenile	30 days	PET	5 mm	-	Altered swimming behaviour.	-	(Li et al., 2024)
Gibel carp (<i>Carassius gibelio</i>); Crucian carp (<i>Carassius carassius</i>)	Adult	60 days	PE and Tire wear particles	-	0.1 %	Altered swimming behaviour.	-	(Gorule et al., 2024)
Medaka (<i>Oryzias latipes</i>)	Adult	42 days	PS-MP	2- μ m	0.1 mg/L, 2.5×10^7 particles/L	Reduced shoaling behaviour. Caused social behaviour disorders.	Brain-gut bacteria system alteration.	(Tamura et al., 2024)

ecosystems (Yin et al., 2018).

The swimming performance of fish is one of the most widely used behavioural responses utilized in toxicity evaluations and can provide valuable insight about fish health (Hamed et al., 2024a). Swimming speed, for example, has been used to evaluate behavioural alterations in fish exposed to MPs. Juvenile African catfish, *Clarias gariepinus*, exposed to low-density polyethylene (LDPE) MPs (50–500 μ m) at concentrations of 0.5, 1.0, 1.5, and 2.0 g/L for 4 days, exhibited reduced swimming speed (Tongo et al., 2024). Such behavioural change may be associated with physiological disturbances in metabolism or neuromuscular systems, as MPs can inhibit acetylcholinesterase (AChE) activity, which impairs nervous and neuromuscular functions (Bonansea et al., 2016). Other studies also reported changes in swimming patterns. For example, larval zebrafish exposed to 1000 μ g/L PS-MPs from 4 hours post-fertilization (hpf) to 5 days post-fertilization (dpf) exhibited decreased swimming competence in the alternating light-to-dark stimulation assay. These responses were associated with the upregulated expression of genes related to inflammation (*il1b*) and oxidative stress (*cat*) (Qiang et al., 2019), however it is unknown if such responses are directly related. In another study, Yin et al. (2019) evaluated the effect of 15 μ m PS-MPs on black rockfish, *Sebastes schlegelii*, over a 21-day period and observed a reduction in swimming speed and range of movement. These behavioural changes may be related to respiratory stress, as the adherence of PS-MPs to gills and skin can alter oxygen consumption and ion regulation, thereby affecting swimming behaviour (Abdel-Tawwab et al., 2019; Kolandhasamy et al., 2018).

There is also evidence that plastic particles can directly enter the central nervous system, potentially causing direct molecular or physical damage to its structure. In a study conducted by Yu et al. (2023), plastic nanoparticles penetrated the blood-brain barrier in Crucian carp, *Carassius carassius*, resulting in changes in foraging behaviour. The mechanisms underlying changes in the activity are not yet elucidated. Moving forward, omics-based techniques such as transcriptomics will be useful

for discerning the mechanisms of toxicity, and such techniques will provide new insight into gene expression changes associated with MPs exposure. This will help establish a direct connection between molecular responses and subsequent behavioural alterations. However, it is noted that behavioural changes are influenced by complex interactions involving physiological, neurological, and environmental factors, and transcript abundance alone does not necessarily translate into direct observable behavioural alterations.

2.4. Social interactions

The gathering of fish in shoals reflects a balance between the disadvantages, such as competition for resources and disease transmission, and the benefits, like improved defence against predators and foraging opportunities (Ward and Webster, 2016). This equilibrium significantly affects the well-being of fish (Senior et al., 2012) and any disruption to this balance can have consequences. For example, factors that decrease shoal cohesion may impede the exchange of information among fish, hindering their ability to respond promptly and accurately to threats and reducing their anti-predator behaviours (Sbragaglia et al., 2022). Based on a study by Rios-Fuster et al. (2021), exposing *Sparus aurata* to dietary MPs ranging from 100 to 500 μ m for 21 days can result in alterations in social interactions. In this study, the control group of fish displayed shyness during interactions and showed reduced activity during feeding compared to those exposed to MPs. Similar studies conducted on fish species have shown altered movement patterns, decreased hunting behaviour, and changes in predatory performance after exposure to nanoparticles or MPs. These changes can potentially impact population dynamics and ecosystem health (Guimarães et al., 2021; Yin et al., 2018). There are conflicting findings regarding the impact of MPs exposure on behaviour, with some studies reporting no change in behaviours (Chen et al., 2020). Nevertheless, slight behavioural alterations, such as in species interactions or altered feeding habits, can have

far-reaching consequences for populations and ecosystems. These changes can affect growth rates, survival rates and overall fitness levels (Ferreira et al., 2018).

2.5. Anxiety like behaviour

Anxiety is a response that occurs when an organism encounters unfamiliar environments or potential threats (Graeff et al., 2010). While moderate anxiety can increase alertness and protect individuals from danger, extreme levels of anxiety can have effects on survival and social interactions (Champagne et al., 2010). When studying anxiety symptoms, researchers often use the dark-light preference test. This test determines if fishes prefer exploring areas or avoiding others based on light or darkness. In adult male zebrafish, increased anxiety has been observed due to cortisol levels and disruptions in neurotransmitter pathways such as serotonin, dopamine, and gamma-aminobutyric acid (Tu et al., 2020). In another study, Félix et al. (2023) investigated the impact of weathered MPs on adult zebrafish after being exposed to concentrations of 0.1 mg/L and 1 mg/L for 21 days. The results showed changes in anxiety-related behaviours, such as time spent entering areas and increased time spent in those zones. Zebrafish are inclined towards spots and tend to avoid well-lit areas. Observing an increase in their activity in the dark can suggest that the anxiety-like behaviour in fish may be related to the presence of MPs (Mansur et al., 2014). While there is no information on how propylene affects zebrafish, previous studies on amphibian larvae exposed to polyethylene MPs have also reported anxiety-inducing effects of MPs, implying potential disturbances in the nervous system (Araújo and Malafaia, 2020).

2.6. Olfactory-driven behavioural responses

Aquatic organisms heavily rely on their sense of smell for survival; however, their olfactory systems are susceptible to pollutants (Braubach et al., 2009). Shi et al. (2021) demonstrated impacts of PS-MPs on the ability of goldfish to detect and process scents after exposure to 0.26 and 0.69 mg/L of PS MPs for a duration of 28 days. The findings could result from changes in gene expression, enzyme activities, neurotransmitter levels and/or injury to the olfactory bulb. The study revealed that MPs disrupted the binding process of G protein-coupled receptors (*gpcrs*), which are vital for olfactory signalling (Shi et al., 2021). Notably, two *gpcr* gene families, *gfa* and *gfb*, are responsible for encoding these receptors and play roles in food and pheromone sensing and were determined to be suppressed in the goldfish exposed to MPs. This suppression of *gpcrs* may potentially explain the decline in olfaction-driven behaviour in both mammals and fishes (Williams and Yoshida-Honmachi, 2013).

3. Effect of MPs on fish physiology

3.1. Neurotoxicity

MPs can cause neurotoxicity in fishes by interfering with enzymes involved in nerve function and lipid peroxidation (Fig. 2). MPs have the potential to suppress the levels of several neurotransmitters, including dopamine, aminobutyric acid, melatonin, vasopressin, serotonin, oxytocin, and kisspeptin (Table 1). AChE is one of the most prominent neurotransmitters and is useful for measuring neurotoxicity as it provides information on the possible loss of cholinergic signalling in neuromuscular system pathways (Barboza et al., 2018b). AChE plays a crucial role in maintaining appropriate neuromuscular function by inactivating acetylcholine which is essential for junction and synaptic cholinergic neurotransmission (Hamed et al., 2024c). There is evidence that MPs exposure can cause neurotoxicity by decreasing AChE and causing lipid peroxidation in the brain of European seabass (Barboza et al., 2018b). Exposure to MPs for 14 days at concentrations of 1, 10, and 100 µg/L, resulted in the inhibition of AChE activity in the brain of

Nile tilapia, *Oreochromis niloticus*, which has the potential to impact other biochemical responses, inducing neurotoxicity (Ding et al., 2018). Acetylcholine may accumulate in the synapse following exposure to MPs, which dramatically reduces activity of AChE in the brain (Ding et al., 2018; Hamed, et al., 2022a). The suppression of AChE activity is indeed one of the mechanisms by which neurotoxicity can occur. Motor dysfunction can result from disruption in nerve signaling, leading to symptoms such as muscle weakness, tremors, and coordination problems (Chen et al., 2017). Multiple studies have documented that exposure to MPs results in the inhibition of AChE in many fish species, including Common carp, *Cyprinus carpio* (Banaee et al., 2019); zebrafish larvae (Chen et al., 2017; Umamaheswari et al., 2021); juveniles of common goby, *Pomatoschistus microps* (Fonte et al., 2016; Miranda et al., 2019); African catfish (Hamed et al., 2022c; Iheanacho et al., 2020); Amazonian cichlid, *Symphysodon aequifasciatus* (Wen et al., 2018); and goldfish (Yang et al., 2020). This inhibition leads to disrupted neurotransmission, motor function, and behavioural patterns. The alterations in AChE activity that occurred in fishes after exposure to MPs are displayed in Table 2, which provides supporting evidence of neurotoxicity following MPs exposure.

3.2. Immunotoxicity

The intestinal immune system consists of three categories of cells: myeloid cells, innate lymphoid cells, and T cells, all of which are found in the intestinal lamina propria and mesenteric lymph node (Leone and Powell, 2020; Hamed et al., 2024b). The immune system is continuously inundated with different pollutants including MPs which can lead to dysfunction. There are several examples of adverse effects in fishes. For example, exposure to one of 100 nm, 5 µm and 200 µm PS-MPs for 21 days can cause a malfunction in the intestinal immune cells of zebrafish to promote a higher abundance of harmful bacteria, potentially leading to health concerns (Gu et al., 2020). In another study, PE-MPS exposure (250 and 500 µg/L) for 30 days resulted in disruption of the complement system and immunity-related enzyme activity in the plasma of common carp (Banaee et al., 2019). The interruption of phagocytic capacity and respiratory burst of head-kidney leukocytes were also noted when exposed to the PVC-MPs for 21 days at a concentration of 1–500 mg/kg (Espinosa et al., 2018). The interferon-induced transmembrane protein (*ifitm1*) and leukotriene B4 receptor (*ltb4r*) are two prominent genes, which were decreased in the liver after exposure to the high-density of 100 and 1000 µg/L PE or PS particles in zebrafish for 20 days (Limonta et al., 2019).

MP exposure can cause neutrophil extracellular trap release, primary granule degranulation, and oxidative damage in cells, which can ultimately impact fish immunity. MP absorption in fishes can disrupt immune response through the interception of oxidative and inflammatory intestinal balance, and interference with the permeability of the gut epithelial cells (Hirt and Body-Malapel, 2020). Fish have an innate immune response that supplements the adaptive immune system, defending the individual from foreign toxins (Kim and Kang, 2016). Such processes can be perturbed by MPs. Choi et al., (2023) investigated the effect of PA-MPs at concentrations of 0, 4, 8, 16, 32, and 64 mg/L over a 2-week period in Crucian carp, and reported a decrease in immunoglobulin M (IgM) levels. In addition to immunoglobulins, lysozymes are an essential component of the innate immune system in fishes, which splits the glycosidic connections into the peptidoglycan layers of bacterial cell walls. The presence of MPs has been reported to alter the quantity of lysozymes in fishes (Zhang, et al., 2022). Similarly, Hamed et al. (2022b), noted that the lysozyme activity decreased after common carp were exposed to 100 mg/L of PE-MPs for 15-days. Conversely, during the same period and under the same conditions, there was a substantial increase in the total myeloperoxidase activity in common carp (Hamed et al., 2022b). After being exposed to MPs, common carp showed a considerable decrease in both its lysozyme, complement C3 and C4, and immunoglobulin levels (Banaee et al., 2019). The drop in

Table 2
Summary of physiological toxicity of microplastics in fishes.

Species	MPs types	Concentration	MPs size	Exposure duration	Physiological and molecular effects	References
Zebrafish (<i>Danio rerio</i>)	HDPE & PS	100 and 1000 µg/L	25–90 µm	20 days	Increased xenobiotic metabolism genes. Decreased AChE activity.	(Limonta et al., 2021)
Gilt-head bream (<i>Sparus aurata</i>)	LDPE	0.5–10 % of diet	200–500 µm	90 days	Antioxidant enzyme and glutathione s-transferase, pro-inflammatory enzymes, myeloperoxidase, and the level of oxidative damage markers-MDA and protein carbonyls increased.	(Solomando et al., 2020)
Nile tilapia (<i>Oreochromis niloticus</i>)	PA	10 mg/L	500 µm–4 mm	15 days	Nuclear and cellular abnormalities, histological damage of gill and intestine.	(Hasan et al., 2023)
Zebrafish (<i>Danio rerio</i>)	PA	1, 10 and 20 mg/L	~32.50 µm	10 days	Disrupted lipid metabolism and genes involved in digestion, transmission, and absorption.	(Zhang et al., 2022)
Common carp (<i>Cyprinus carpio</i>)	PE	250 and 500 µg/L	-	30 days	Decreased AChE and GGT, and elevated AST, ALT, LDH, and ALP.	(Banaee et al., 2019)
Common goby(<i>Pomatoschistus microps</i>)	PE	0.184 mg/L (25°C)	1–5 µm	96 hours	Caused 33% mortality and 28% predation inhibition after exposure.	(Fonte et al., 2016)
Common goby(<i>Pomatoschistus microps</i>)	PE	18.4 and 184 µg/L	1–5 µm	96 hours	Reduced aerobic energy production. MPs inhibit AChE activity.	(Oliveira et al., 2013)
European seabass (<i>Dicentrarchus labrax</i>)	PE	100 and 500 mg/kg	40–150 µm	21 days	Reduced antioxidant enzyme activity, indicating oxidative stress.	(Espinosa et al., 2019)
Flatfish (<i>Solea senegalensis</i>)	PE	1, 10 and 100 particles	125–250 µm	128 hours	Increased antioxidant defenses, neurotransmission, and energy expenditure and histological changes observed.	(Santana et al., 2021)
Walking catfish (<i>Clarias batrachus</i>)	PET & LDPE	-	-	60 days	Liver, kidney, intestine, and gills exhibits morphology alteration.	(Fatema et al., 2023)
Zebrafish (<i>Danio rerio</i>)	PE	10 and 40 mg/L	100–150 µm	-	Higher neurotoxicity and oxidative stress.	(Zhang et al., 2021)
European seabass (<i>Dicentrarchus labrax</i>)	PP	-	-	-	Stimulate intestinal inflammation.	(Montero et al., 2022)
Blue discus (<i>Symphysodon aequifasciatus</i>)	PS	50 and 500 µg/L	32–40 µm	30 days	SOD and GPx activity increased.	(Wen et al., 2018)
Brown trout (<i>Salmo trutta fario</i>)	PS	105 and 106 particles/L	50 µm	60 days	Neither affects fish growth, oxidative stress, or AChE function.	(Schmiege et al., 2020)
Common carp (<i>Cyprinus carpio</i> var. Jian), Grass carp (<i>Ctenopharyngodon idella</i>), Largemouth bass (<i>Micropterus salmoides</i>),	PS	0.02, 0.2 and 2 mg/L	8 µm	48 hours	Abnormalities in the intestine, mRNA abundance fluctuates.	(Zhang et al., 2023)
Marine medaka (<i>Oryzias melastigma</i>)	PS	10 mg/L	2, 10, and 200 µm	60 days	Small PS causes hepatic inflammation. Larger PS-MPs caused lipid metabolism disorders and gut microbiota dysbiosis.	(Zhang et al., 2021)
Nile tilapia (<i>Oreochromis niloticus</i>)	PS	5 mg/L	9 µm	28 days	SOD, GPX and MDA levels increased significantly.	(Ahmadifar et al., 2021)
Yellowhead catfish (<i>Pelteobagrus fulvidraco</i>)	PS	0.115 and 11.5 µg/L	20 µm	15 days	Immune response stimulation.	(Li et al., 2021)
Zebrafish (<i>Danio rerio</i>)	PS	10 and 100 µg/L	100 nm	35 days	ROS production impairs neurotransmission, hepatic enzymology, and the antioxidant defense system. Substantially increased <i>gstp1</i> , <i>hsp701</i> , and <i>ptgs2a</i> gene expression and decreased <i>cat</i> , <i>sod1</i> , <i>gp1a</i> , and <i>ache</i> gene expression. Brain and liver histopathology lesions observed.	(Umamaheswari et al., 2021)
	PS	1 mg/L	45 µm	120 hours	No significant impacts except elevated <i>zfrho</i> visual gene expression.	(Chen et al., 2017)
	PS	20, 200 and 2000 µg/L	70 nm	4 hours, 12 hours, and 1, 2, and 7 days	Liver inflammation and lipid build up. SOD and catalase significantly increased.	(Lu et al., 2016)
African catfish (<i>Clarius gariepinus</i>)	PVC	0.3 % in pellet	100 µm	45 days	Serum glucose and serum transaminases significantly elevated. Plasma protein, brain AChE and antioxidant enzyme activities substantially reduced, and MDA levels elevated.	(Iheanacho et al., 2020)
		0.5, 1.5, and 3.0 % in pellet	100 µm	45 days	Mean cell volume and hemoglobin decreased considerably. Gill and brain GPx activity significantly altered. SOD activity reduced the gill and brain, and higher lipid peroxide levels in the brain.	(Iheanacho and Odo, 2020)
Common carp (<i>Cyprinus carpio</i>)	PVC	10, 20, and 30 % of weight	100–200 µm	30 and 60 days	SOD and CAT showed inverse relationship, dose dependent downtrend in GPx activity. MDA significantly reduced.	(Xia et al., 2020)

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Table 2 (continued)

Species	MPs types	Concentration	MPs size	Exposure duration	Physiological and molecular effects	References
Goldfish (<i>Carassius auratus</i>)	PVC	0.1 and 0.5 mg/L	0.1–1000 µm	96 hours	Shorter villi. The liver showed inflammation, haemorrhaging, and necrosis. Greatest oxidative damage in liver.	(Romano et al., 2020)
Gilt-head bream (<i>Sparus aurata</i>)	PVC	500 mg/kg	40–150 µm	15 and 30 days	Head-kidney gene expression, <i>prdx5</i> , dropped substantially, <i>prdx1</i> and <i>prdx3</i> significantly increased. Liver <i>hsp90</i> and <i>ucp1</i> gene expression decreased and decreased, respectively.	(Espinosa et al., 2017)
Marine medaka (<i>Oryzias melastigma</i>)	PVC	-	-	-	Hypoxia.	(Xia et al., 2022)
European seabass (<i>Dicentrarchus labrax</i>)	MPs	0.26 and 0.69 mg/L	1–5 µm	96 hours	Caused neurotoxicity by inhibiting AChE increasing brain and muscle LPO and altering LDH and IDH activity.	(Barboza et al., 2018b)
Grass carp (<i>Ctenopharyngodon idella</i>)	MPs	100 and 1000 µg/L	-	21 days	Increased liver oxidative damage. Oxidative stress and metabolic disorders are connected by pathway enrichment.	(Liu et al., 2022)
Nile tilapia (<i>Oreochromis niloticus</i>)	MPs	1, 10, and 100 mg/L	>100 nm	15 days	SOD, CAT, total peroxides, OSI, LPO, and DNA fragmentation increased. Proteinogram alteration showed.	(Hamed et al., 2020)
Sheepshead minnow (<i>Cyprinodon variegatus</i>)	Green spherical PE	50 and 250 mg/L	150–180 µm	4 days	Intestinal distention created cellular ROS, but ROS related transcriptional and enzymatic alterations differed.	(Choi et al., 2018)
Guppy (<i>Poecilia reticulata</i>)	Green fluorescent PS	100 and 1000 µg/L	32–40 µm	28 days	Na ⁺ /K ⁺ -ATP activity declination. Increase of the MDA content. Caused peroxidative damage and oxidative stress.	(Huang et al., 2020)
Nile tilapia (<i>Oreochromis niloticus</i>)	Green fluorescent PS	1, 10, and 100 µg/L	0.1 µm	1, 3, 6, 10, and 14 days	AChE activity inhibited. SOD in the liver significantly induced. Potential role of CYP enzymes in MPs metabolism.	(Ding et al., 2020)
Zebrafish (<i>Danio rerio</i>)	Red fluorescent MPs	2 mg/L	1–5 µm	96 hours post fertilization	Increased ROS, CAT and GPx activities, oxidative stress, and neurotoxicity.	(Santos et al., 2020)
Medaka (<i>Oryzias latipes</i>)	PS	0.1 mg/L, 2.5 × 10 ⁷ particles/L	2 µm	42 days	Gut dysbiosis.	(Tamura et al., 2024)
Tilapia (<i>Oreochromis niloticus</i>)	PS	100 µg/L	2 and 20 µm	28 days	Upregulation of <i>egln3</i> and <i>nadk</i> . Downregulation of isocitrate. Respiratory dysfunction.	(Zheng et al., 2024)
Zebrafish (<i>Danio rerio</i>)	PS	0.05 mg/L	4.5 µm	21 days	Upregulation of <i>cyp1</i> gene. Liver vacuolization.	(Martínez-Álvarez et al., 2024)

Note: AChE, acetylcholinesterase; GST, glutathione S-transferase; SOD, superoxide dismutase; ROS, reactive oxygen species; CAT, catalase; GPx, glutathione peroxidase; GGT, gamma-glutamyl transpeptidase; AST, aspartate aminotransferase; LPO, lipid peroxide; ALT, alanine aminotransferase; LDH, lactate dehydrogenase; MDA, melondialdehyde; ALP, alkaline phosphatase; OSI, oxidative stress index; and DNA, deoxyribonucleic acid.

total immunoglobulin levels may be attributed to a decline in the quantity of fully developed B lymphocytes, their inability to produce immunoglobulins, or a reduction in the production of immunoglobulin subunits (Ercal et al., 2000). Cholinesterase inhibition also causes a reduction in total immunoglobulin levels in fish (Banaee et al., 2019). The immunological responses, particularly neutrophil and lysozyme levels, can be increased significantly after exposure to PS and PE-MPs (Ahmadifar et al., 2021; Limonta et al., 2021). In contrast, absorption of MPs can reduce the number of neutrophils in Nile tilapia, and this finding aligns with the broader understanding of the immunotoxic effects of MPs observed in different organisms (Hamed et al., 2020). This was accomplished by preventing the absorption of vital nutrients and causing impairment in the allocation of energy. MPs have been identified as foreign substances that could either stimulate immunological responses in fishes or decrease immune function by generating immune toxicity (Kim and Kang, 2016). Other environmental stressors or confounding variables could also influence immune responses, making it challenging to isolate the specific effects of MPs. Therefore, while MPs may have the potential to affect immune function, the contradictory findings highlight the complexity of assessing their impacts and emphasize the need for further research to elucidate the mechanisms underlying these effects and their potential interactions with other environmental factors.

3.3. Oxidative stress

MPs can accumulate in the primary tissues of fishes and induce oxidative stress (Fig. 2). MPs are known to induce the production of intracellular reactive oxygen species (ROS) and inhibit antioxidant defense mechanisms, resulting in oxidative stress, which is a fundamental mechanism underlying their neurotoxicity (Li et al., 2023). These impacts can occur across various species and ecological contexts, highlighting the pervasive and multifaceted nature of the threats posed by MP pollution to environmental and public health (Solomando et al., 2020). To be more specific, the toxicity of MPs in fish cells is primarily caused by oxidative stress, which includes disruptions to the redox equilibrium, damage to the cellular mechanisms, and the formation of ROS (Solomando et al., 2020). Exposure to MPs may also result in a reduction in antioxidant enzymes because of the amount of energy that is expended in the process of defending against oxidative stress (Hamed et al., 2020). Santana et al. (2021) reported enhanced energy expenditure, disruption of neurotransmission, and reduced antioxidant defences after exposure to PE-MPs in flatfish, *Solea senegalensis*. Both the superoxide dismutase and catalase activity in the liver of European seabass that had been exposed to PE-MPs were shown to diminish, which was suggested to induce oxidative stress (Espinosa et al., 2019). Exposure to low MPs concentrations improved SOD activity of goldfish, *Carassius*

auratus, larvae to combat oxidative stress, while high concentrations reduced antioxidant capacity and superoxide dismutase activity (Yang et al., 2020). The activity of Glutathione S-Transferase (GST) in marine medaka, *Oryzias melastigma*, exposed to PS-MPs varied depending on the type of tissue, for example, GST increased in the intestine and the gills, but it significantly decreased in the liver and the testis (Wang et al., 2019). Moreover, the activity of GST in marine medaka changed with the size of the MPs, with increased activity at 50 nm and decreased activity at 45 µm according to Kang et al., (2021). In the guppy, *Poecilia reticulata*, exposure to PS-MPs resulted in a depletion of reduced glutathione (GSH), while simultaneously causing an increase in oxidized glutathione (GSSG), glutathione peroxidase (GPx), and glutathione reductase (GR) inside the organisms. Because it binds with ROS, GSH declines as the concentration of MPs increases, which causes GSSG levels to increase. The ensuing rise in GR activity may be caused by the MPs-induced production of ROS and consequent decrease in GSH to GSSG ratio (Huang et al., 2020). Elevated levels of ROS in fish cells result in oxidative stress, which can trigger inflammation and cellular apoptosis (Choi et al., 2018). Previous studies reported that the exposure of gilthead bream, *Sparus aurata*, to MPs resulted in protein degradation and elevated oxidative stress in the form of lipid peroxidation (LPO). These effects were observed even when the protective antioxidant responses, including superoxide dismutase, catalase, GST, and GSH, were activated (Solomando et al., 2020). After exposing catfish to MPs at a concentration of 500 mg/kg diet for a duration of 15 days, a decrease in the activities of several key enzymatic and non-enzymatic antioxidants were observed. Specifically, there were reductions in the activities of superoxide dismutase, catalase, total antioxidant capacity, and GST. These findings suggest a potential negative impact of MPs on the antioxidant defence system of catfish (Sayed et al., 2021). MPs possess a significant surface area and can potentially cause oxidative stress by releasing oxidizing substances that are deposited on their surface or by triggering the production of ROS during inflammatory response (Prata et al., 2020).

4. Reproductive and developmental effects of MPs in fishes

Hormones are responsible for reproductive activities in all vertebrates, including fishes, and are controlled by the complex endocrine systems, which involve the HPG and hypothalamus-pituitary-renal (HPR) axes (Faheem and Bhandari, 2021). Hypothalamus-pituitary-gonad-liver (HPG-L) interactions regulate reproductive processes, including gonad development, gametogenesis, vitellogenesis, steroidogenesis, and importantly, gonadal sex change in fishes (Borella et al., 2020). The hypothalamus secretes GnRH, stimulating the pituitary to release FSH and LH, which prompt gonads to produce dominant sex steroids (e.g., 17β-estradiol and 11-ketotestosterone in fishes) via specific receptor binding (Hachfi et al., 2012).

MPs can also contain additives or adsorb organic pollutants from the environment. When ingested by fish, these chemicals can disrupt their endocrine system, affecting hormone levels and reproductive functions (Hamed et al., 2020; Sayed et al., 2021). MPs are widely recognized as pervasive entities and potential carriers of endocrine-disrupting chemicals (EDCs). These chemicals can hinder reproductive functions in fishes by competitively binding to receptors for sex steroid hormones (Celino-Brady et al., 2021). For example, the upregulation of vitellogenin (Vtg) gene expression in male fish functions as an indicator of endocrine disruption induced by a pollutant. These EDCs either mimic estrogen (E2) or facilitate the aromatization process through the conversion of testosterone (T) to E2 with the help of CYP19A1, a member of the cytochrome P450 superfamily, leading to Vtg induction and feminization of male fishes (Coumaillieu et al., 2015; Molina et al., 2018). In another example, exposure of adult Japanese medaka, *Oryzias latipes*, to microfibers has been found to change the HPG axis-related genes and promote vitellogenesis in males, which is a clear indication of endocrine disruption and thus promotes irregular maturation patterns (Kim et al.,

2023). Among the various impacts of MPs on fish, there is evidence for the induction of early maturation and spawning, accompanied by reduced fecundity, gonadosomatic index, fertilization rates, and poor quality of gametes (Zhang et al., 2021).

MPs have also been reported to lead to diverse reproductive effects for fishes (Table 3). Prolonged exposure to environmental toxicants, including MPs, can impact the reproductive function and fertility of both males and females. In zebrafish, a concentration of 100 µg/L of PS-MPs exposure for 21 days elicited histological modifications in gonads, specifically manifesting as a reduction in the thickness of the testis basement membrane through the enhancement of ROS production (Qiang and Cheng, 2021). Early developmental exposure of zebrafish to a concentration of 50 mg/L of PE-MPs resulted in a significant reduction in hatching rate due to the teratogenic abnormality in juvenile fish (Malafaia et al., 2020). PE-MPs possess the capability to interfere with reproduction by influencing genes linked to the HPG axis. These interactions result in histological alterations, including compromised seminiferous lobule architecture, reduced sperm fluid in males, a decline in the number of mature spawning follicles, and an augmented presence of early vitellogenic oocytes in females marine medaka (Wang et al., 2019). Furthermore, parental exposure of marine medaka to PS-MPs was associated with heightened heart rates, premature hatching, and diminished growth in F1 offspring because of the disruption of sex steroid hormone biosynthesis and cytochrome P450 pathways (Wang et al., 2021). Karami et al., (2016) reported that exposure to polyethylene MPs (<60 µm) for a duration of 96 hours induced alterations in the transcription of reproductive-axis genes in African catfish. Additionally, dietary exposure to polyethylene MPs for a period of 60 days resulted in the downregulation of transcript levels of Vtg and choriogenin (Chg), which serve as precursors for egg yolk proteins and egg envelope proteins, respectively, in Japanese medaka (Rochman et al., 2013). Within the HPG axis, GnRH functions as a physiological regulator, orchestrating the release of gonadotropins (GtHs), which in turn, govern gonadal steroidogenesis and gametogenesis in vertebrates (Gutierrez-Hartmann et al., 2007). The downregulation of GnRH, Vtg, and Chg genes implies a potential involvement of MPs in disrupting reproductive processes (Sun et al., 2015).

The adverse effects of MPs on reproduction may be attributed to redox imbalance, as oxidative stress is widely recognized as an important factor in ovarian and testicular dysfunctions causing infertility, which is the imbalance between ROS and antioxidant production (Barati et al., 2020). Qiang and Cheng (2021) conducted sub-chronic exposure experiments on zebrafish using 1 µm PS, observing an increase in ROS generation in both the ovary and testis, particularly at concentrations of 100 and 1000 µg/L. This exposure also resulted in an elevated rate of spermatocyte apoptosis at 1000 µg/L. Furthermore, male gonads presented with elevated apoptosis, as indicated by the upregulation of p53, Bax, and Caspase-7, -8, or -9, coupled with a decrease in basement membrane thickness. In a parallel study involving zebrafish, an extended exposure period of 35 days to PS-MPs resulted in modifications to metabolic processes and gene regulation patterns. These alterations were suggested to be mediated by the generation of ROS (Umamaheswari et al., 2021).

The pollution of aquatic environments with MPs can directly impact the reproductive function of freshwater fishes, as demonstrated by studies on the African catfish. Consumption of diets containing 500 mg/kg of MPs for a duration of 15 days resulted in induced testicular damage, diminished sperm quality and viability, and suppressed hormonal profiles (Sayed et al., 2022). Similarly, exposure to PE-MPs at a concentration of 10 mg/L triggered hormonal disruption, testicular damage, and induced testis-ova in male tilapia (Ismail et al., 2021).

Effects on the reproductive system have the potential to perpetuate over multiple generations through epigenetic mechanisms. The toxic effects of MPs can transmit to the next generation through the germ cells causing intergenerational, multigenerational, or transgenerational reproductive effects on their offspring (Bringer et al., 2022; Wang et al.,

Table 3
Effects of microplastics on reproduction in fishes.

Species	Developmental stage	Size of MPs	Type of MPs	Exposure duration	Concentration of MPs	Reproductive effects	References
African catfish (<i>Clarias gariepinus</i>)	Juvenile	<60 µm	LDPE	96 hours	50 or 500 µg/L	Impact on gonadotropin releasing hormone.	(Karami et al., 2016)
	Adult	100 µm	PE	15 days	500 mg/kg	Resulted in diminished serum levels of LH, FSH, and sex steroids (T and E). Decreased sperm count, spermatocrit, viability and motility. Induced testicular histological and degenerative changes.	(Sayed et al., 2022)
Loach (<i>Paramisgurnus dabryanus</i>)	Adult	8–15 µm	PE	15 and 30 days	1 and 10 mg/L	Gonads antioxidant system parameters altered. Accumulation of PE in the gonads resulted in heightened gonadal pathological lesions, cell apoptosis, and adversely impacted the biological traits of semen, thereby affecting reproduction in the F0 cohort.	(Xia et al., 2023)
Marine medaka (<i>Oryzias melastigma</i>)	Embryonic-larval	4–6 µm	PE	12 days	10 mg /L	Resulted in decreased embryonic survival and hindered the hatching process.	(Le Bihanic et al., 2020)
	Adult	2.5 µm	PE	30 days	100 µg/L	Led to the presence of empty follicles and follicular atresia, along with alterations in the gene expression levels associated with HPG axis.	(Li et al., 2020)
Nile tilapia (<i>Oreochromes niloticus</i>)	Adult	10–63 µm	PE	12 weeks	0.065 and 0.65 mg/L	Resulted in diminished growth, reduced egg numbers, and a lower hatching rate.	(Chisada et al., 2019)
	Adult	100 µm	PE	15 days	10 mg/L	Resulted in a significant reduction in both serum LH and T levels. Histological degenerative changes in the testes and the presence of testis-ova observed.	(Das, 2023)
Zebrafish (<i>Danio rerio</i>)	Embryonic	38.26 µm ± 15.64 µm	PE	24, 48, 72, 96, 120, & 144 hours	6.2, 12.5, 25, 50 and 100 mg/L	Adverse impact on the hatching rate of embryos.	(Malafafia et al., 2020; Tarasco et al., 2022)
	Whole life cycles	20–27 µm	PE	30 days	1 % to feed.	Resulted in decreased relative fecundity in brooders, influenced the circular shape of eggs (egg circularity), and led to reduction in yolk area in eggs.	(Tarasco et al., 2022)
Marine medaka (<i>Oryzias melastigma</i>)	Adult	53–100 µm	PE and PP	5 months	1 % wet weight in food	Led to notable reduction in the quantity of eggs.	(Cormier et al., 2022)
Zebrafish (<i>Danio rerio</i>)	Embryonic	53–100 µm	PE and PP	96 hpf	1 or 10 mg/L	No changed in the hatching time and rate.	(Cormier et al., 2022)
	Adult	53–100 µm	PE and PP	5 months	1 % wet weight in food	Caused a notable decrease in reproductive success in offspring, revealing premature mortality after parental MPs exposure, along with hyperactivity observed in F1 unexposed larvae.	(Cormier et al., 2022)
Japanese medaka (<i>Oryzias melastigma</i>)	Embryonics	600 µm	PE, PP and PS	48 hours	100 µm	Caused lethal effects characterized by elevated embryo mortality and a diminished hatching rate.	(Pannetier et al., 2019)
Marine medaka (<i>Oryzias melastigma</i>)	Embryonic-larval	2-6 µm	MP-BaP, MP-PFOS, and MP-BP3	12 days	-	Decreased embryonic survival and prevented hatching.	(Le Bihanic et al., 2020)
Zebrafish (<i>Danio rerio</i>)	Larval	11–13 µm PE and 125–250 µm PVC	PE and PVC	4 months	1 % food weight	A delay was noted in the spawning, accompanied by a decrease in the percentage of successful spawning attempts.	(Cormier et al., 2021)
Japanese medaka (<i>Oryzias latipes</i>)	Adult	2 µm	PS	3 weeks	44 µg/L or (10 ⁷ beads/L)	No notable impacts on reproduction.	(Assas et al., 2020)
	Adult	10 µm	PS	10 weeks	500, 1000, or 2000 µg/L	Mature females exhibited dose-dependent reductions in egg numbers.	(M. Zhu et al., 2020)
Marine medaka (<i>Oryzias melastigma</i>)	Embryonic	10 µm	PS	28 days	0, 2, 20, and 200 µg/L	Reduced hatchability, prolonged hatching time, and inhibited growth.	(Li et al., 2020)
	Embryonic	6 µm	PS	3, 6, 9, 19 dpf	0.1, 1 × 10 ³ and 1 × 10 ⁶ particles/mL	MPs accumulation on the surface of the embryonic membrane and alters the expression of signal pathways. Delayed incubation time, changes in heartbeat, and a reduction in the hatching rate.	(Chen et al., 2020)
	Adult	157.68 µm	PS	21 days	500 and 1000 microfibers/L	Elevated VTG mRNA expression, disturbances in the mRNA expression of GnRH and LH receptors, and an increased mRNA expression of GnIH.	(Kim et al., 2023)

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Table 3 (continued)

Species	Developmental stage	Size of MPs	Type of MPs	Exposure duration	Concentration of MPs	Reproductive effects	References
Zebrafish (<i>Danio rerio</i>)	Whole life cycles	2- μ m	PS	150 days	0, 2, 20, and 200 μ g/L	Accumulation of MPs on the eggshell resulted in a decreased embryonic hatching rate. Adult fish exhibited a decrease in body mass and gonadosomatic index. Noticeable histopathological damages to gonads and decline in both egg production and fertilization rate.	(Wang et al., 2021)
	Adult	10 μ m	PS	60 days	2, 20, and 200 μ g/L	Led to decreased hatching rate, delayed maturation of gonads, and lowered fecundity in female fish. Induced negative regulatory effects in the female HPG axis.	(Wang et al., 2019)
	Embryonic	157 \pm 52 μ m	PS	72 hpf	250 item/ 50 mL	Induced an internal hypoxic microenvironment within the embryos, consequently resulting in delayed embryo hatching.	(Duan et al., 2020)
	Adult	1 μ m	PS	60 days	100 μ g/L	Significantly altered the expression of genes in HPG axis: <i>cyp19a1b</i> , <i>3βhsd</i> , and <i>17βhsd</i> were upregulated, and <i>gnrh3</i> was downregulated in females. Meanwhile, <i>cyp19a1a</i> , <i>17βhsd</i> , and <i>gnrh2</i> , <i>gnrh3</i> , <i>fshβ</i> , <i>era</i> , <i>cyp11a</i> , <i>17βhsd</i> , <i>fshr</i> , and <i>lhr</i> were downregulated in females.	(Lin et al., 2023)
	Adult	1 μ m	PS	21 days	10 and 10 μ g/L	Elevated levels of ROS in male and female gonads. In male testes, heightened apoptosis levels observed, concurrently associated with a decrease in the thickness of the testis basement membrane. Histological alterations were noted in both female and male gonads.	(Qiang and Cheng, 2021)
Common carp (<i>Cyprinus carpio</i>)	Adult	1 μ m	PS	10 and 21	100 μ g/L	Caused notable alterations in steroidogenic mRNA expression in gonads.	(Qiang et al., 2020)
	Larval	100–200 μ m	PVC	60 days	50, 100, and 150 mg/L	Vacuolation, necrosis, and breaking observed in emerging primary oocytes in the ovary, along with necrosis, cavities, sparse sperm cells, and fewer Sertoli cells in the testis. Significantly changes in the expression of HPG axis-related genes (<i>gthal</i> , <i>gnrh</i> , <i>fshβ</i> , <i>era</i> , <i>cyp19b</i> , <i>vgl1</i> , <i>sox9b</i> , <i>dmrt1</i> , and <i>cyp19a</i>), apoptosis-related genes (<i>bax</i> , <i>caspase3</i> , and <i>bcl-2</i>), and sex differentiation and sex steroid hormone-related genes (<i>dmrt1</i> and <i>cyp19b</i>).	(Liu et al., 2023)

2019). Transgenerational effects of MPs include increased embryonic mortality, delayed hatching, malformations, and developmental and behavioural anomalies (Zhou et al., 2020). Several fish species exhibited transgenerational effects of MPs, primarily attributed to the detrimental influence on the reproductive health of adult fish (Guo and Wang, 2019; Li et al., 2020; Tien et al., 2020; Wang et al., 2021)(Table. 3). These investigations highlight the notion that MP exposure to adult fish leads to alterations in the physiological, morphological, and behavioural traits of their offspring. Despite this understanding, a significant research gap persists regarding the transgenerational consequences of MPs in fishes. Notably, some studies have suggested that exposure to environmentally relevant levels of virgin MPs induces physiological stress in fishes but may not necessarily impact the reproductive output of their offspring (Qiang et al., 2020).

5. Conclusion and recommendations

MPs are tiny pieces of plastic fragments extensively present in various aquatic habitats throughout the world. The abundance of MPs in water bodies will continue to increase due to continuous emission and fragmentation of plastic products. As a result, fishes are becoming increasingly vulnerable to their toxic effects. From the present

understanding of MP-mediated toxicity, consuming such substances can result in bioaccumulation in the digestive system and transfer to other organs, causing various health issues. Different behavioural abnormalities such as altered activity, aggression, feeding, and social behaviour have been observed due to MPs-induced toxicity. Adverse physiological effects of MPs may be the result of the inhibition of AChE in the brain, causing neurotoxicity and alteration of IgM and lysozyme and oxidative stress in cells. This review also points to the disruption of the HPG axis in fishes as one mechanism leading to reproductive impairment.

Research into cognitive behaviour attempts to unravel how fishes process information. In recent years, this field has expanded significantly, revealing that fishes can have complex cognitive processes, more so than previously thought. However, EDCs can cause cognitive impairment in fishes. There is not enough information on MPs to definitively suggest exposure causes cognitive abnormalities in fishes. We are also required to examine the exact molecular pathways that can result in such behavioural deficits. The hypothalamus plays a vital role in behaviour, reproduction, and homeostasis regulation, and it is susceptible to toxicants such as MPs. The cellular and molecular mechanisms of MPs-mediated toxicity of the HPG axis are not fully characterized. Additional studies are needed to understand the hypothalamic function of MPs toxicity in fishes during developmental and

long-term effects. MPs also carry and absorb different metals and other toxic chemicals; thus, it is necessary to understand the synergetic effects of these chemicals combined with the MPs. Elucidating the epigenetic modifications due to toxicant exposure is a developing area of research, and knowledge of MPs-mediated epigenetics changes is limited. It is possible that some of the neurobehavioural, physiological, and reproductive toxicity of MPs are mediated by epigenetic modifications (e.g. alterations in DNA methylation). Thus, it is crucial to investigate the multigenerational and transgenerational effects of MPs in fishes and to elucidate the potential epigenetic changes that mediate such effects.

CRedit authorship contribution statement

A K M Munzurul Hasan: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization. **Som Niyogi:** Writing – review & editing, Supervision, Funding acquisition. **Douglas P. Chivers:** Writing – review & editing, Supervision, Funding acquisition. **Mohamed Hamed:** Writing – original draft, Writing – review & editing, Methodology, Investigation. **Jabed Hasan:** Writing – original draft, Writing – review & editing, Investigation. **Christopher J. Martyniuk:** Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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