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REVIEW

Water Quality Impact on Fish Behavior: A Review From an Aquaculture Perspective

Kaisheng Zhang[1] | Zhangying Ye[1,2] | Ming Qi[3] | Wenlong Cai[4] | João L. Saraiva[5,6] | Yanci Wen[1] | Gang Liu[2] | Ze Zhu[7,8] | Songming Zhu[1,2] | Jian Zhao[1]

[1]College of Biosystems Engineering and Food Science, Zhejiang University, Hangzhou, China | [2]Ocean Academy, Zhejiang University, Zhoushan, China | [3]Zhejiang Fisheries Technical Extension Center, Hangzhou, China | [4]Jockey Club College of Veterinary Medicine and Life Sciences, City University of Hong Kong, Hong Kong, China | [5]Fishethogroup Association, Olhão, Portugal | [6]Centre of Marine Sciences (CCMAR/CIMAR-LA), Faro, Portugal | [7]Zuckerberg Institute for Water Research, Jacob Blaustein Institutes for Desert Research, Ben Gurion University of the Negev, Midreshet Ben Gurion, Israel | [8]Biometris, Wageningen University and Research, Wageningen, Netherlands

Correspondence: Jian Zhao (zhaojzju@zju.edu.cn)

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ABSTRACT

Changes in water quality significantly shape fish behavior, a crucial index reflecting the growth and welfare status of fish. Given the centrality of this relationship to aquaculture practices, a comprehensive understanding of how water quality dynamics influence fish behavior is imperative. While there have been some summaries of the effects of water quality parameters on fish physiology and growth, few reviews on their effects on fish behavior have been reported yet. This article reviews several water quality parameters which are of great concern in aquaculture from multiple facets of actual production, including physical parameters (water temperature and turbidity), chemical parameters (dissolved oxygen, salinity, pH, and inorganic nitrogen), and chemical pollutants (microplastics and crude oil), which have gained increasing attention from the researchers and aquaculture practitioners over the past decades. Variations in these water quality parameters can exert profound effects on fish physiology, metabolism, internal tissues and organs, and sensory perception, which influences fish behaviors such as swimming, schooling, feeding, predation, anti-predation, aggression, courtship, as well as adaptive and stress-related behaviors such as exploration, avoidance response, and anxiety-like behavior. By synthesizing the behavioral changes caused by specific water quality parameters, this review aims to provide strong support for further water quality-related research, thereby fostering environments conducive to both fish welfare and aquaculture productivity.

1 | Introduction

As a crucial source of high-quality animal protein and micronutrients for human consumption, fish make significant contributions to global food supply and nutritional security, which therefore making fish industry thrive [1]. For the past two decades, significant changes have been made in aquaculture production and management, which include the maintenance of traditional extensive aquaculture systems (e.g., pond, cage, reservoir, offshore and nearshore aquaculture), alongside the development of numerous innovative intensive aquaculture models (such as intensive cage, integrated aquaponics,

polyculture, and recirculating aquaculture systems [RASs]) [2–7]. In all types of these aquaculture systems, fish interact with the water environment directly, highlighting the significance of maintaining optimal water quality for efficient fish farming, which plays an essential role in enhancing product quality and yield as well as fulfilling fundamental fish welfare necessities [8–10].

Water quality profoundly influences fish behavior and shapes their intricate adaptations and responses aimed at optimizing survival strategies [11–14]. For example, uneven temperature gradients can prompt fish to abandon their schools in search of preferred thermal areas, trading the safety of the advantages of schooling for individual comfort [15]. Such intrinsic drive based on environmental preferences underscores how water quality fundamentally shapes fish behavior [16–19]. On the other hand, from a physiological standpoint, suboptimal water quality can lead to stress, such as osmoregulatory imbalance, impaired organ function as well as hindered sensory systems [20–25], among other issues, all of which can directly or indirectly impact fish behavior, such as irregular feeding, hindered courting patterns, reduced exploration, increased aggression, and even anxiety-like behavior [26–31]. Such impacts can also have implications for fish welfare, including poor overall health and the inability to perform normal behaviors freely. By monitoring fish behavior, the aquaculture industry can optimize resource utilization, regulate water quality, and assess the welfare of farmed fish [32, 33]. Therefore, comprehensively examining the relationship between water quality parameters and fish behavior is crucial for improving aquaculture practices.

Given this, this review centers on water quality parameters of importance in aquaculture, and categorizes them into three broad groups: physical parameters (water temperature and turbidity), chemical parameters (dissolved oxygen [DO], salinity, pH, and inorganic nitrogen), and emerging its scope to address emerging chemical pollutants (microplastics and crude oil). Building upon these classifications, the review then directs attention to the diverse behaviors exhibited by fish in response to these factors (Table 1), aiming to provide a robust scientific foundation for the linkages between fish behavior and sustainable aquaculture.

2 | Methods

Databases including ScienceDirect, Scopus, Web of Science, Google Scholar were used for literature research in this review, following the combinations of the keywords: aquaculture AND/OR fish farming; climate change; behavior; welfare; water temperature AND/OR thermal effect; turbidity; DO AND/OR hypoxia; salinity; pH AND/OR acidification; ammonia AND/OR nitrate AND/OR nitrite; chemical pollutants; microplastics AND/OR nanoplastics; crude oil; swimming AND/OR locomotion; schooling AND/OR group behavior; courting AND/OR spawning AND/OR breed; exploratory behavior; anxiety-like behavior; antipredator behavior AND/OR forage; aggressive behavior. The publication year of the references mainly range from 2000 to 2024 and a small number of references related to the fundamental researches of fish behavior need to be traced back to the literature published in the last century.

This review categorizes aquaculture systems into two broad types. The first encompasses extensive outdoor aquaculture, including freshwater pond/reservoir aquaculture along with nearshore/offshore marine aquaculture; the second category comprises indoor, intensive aquaculture systems, with a primary focus herein on the increasingly popular RASs in recent years [54]. Marked by high densities, this mode of cultivation underscores the critical importance of collective behaviors and interindividual interactions as pivotal behavioral indicators. While the majority of aquaculture practices involve monoculture, it is pertinent to acknowledge the existence of polyculture in certain non-intensive outdoor systems, particularly prevalent in East and Southeast Asian regions, where multiple species are reared concurrently. Although the text primarily focuses on general implications, the inclusion of behaviors such as predation and antipredator strategies necessitates this acknowledgment. To preserve coherence and comprehensiveness, the discussion refrains from singling out specific aquaculture models, aiming instead to issue a broader alert relevant to the aquaculture sector and endeavors concerning fish welfare. Notably, not only aquaculture species were reviews here, some ornamental and wild species were also adopted to supplement the relevant views, which then provides valuable and comprehensive insights applicable to aquaculture.

3 | Physical Water Quality Parameters

Physical water quality parameters constitute a set of indices used to assess the physical characteristics of water bodies. This chapter consolidates a review of the profound impacts that water temperature and turbidity exert on fish behavior, underscoring their critical roles in determining fish welfare and ecosystem dynamics.

3.1 | Water Temperature

Fish, as ectothermic animals, rely on the aquatic environment for thermoregulation, making water temperature one of the most crucial physical water quality parameters [55]. Their sensitivity to even minute variations in external water temperature is remarkable, with some species, like teleostean fishes, capable of detecting fluctuations as minor as 0.03°C [56]. Water temperature fluctuations are common phenomena in aquaculture, even in the most controllable environment like indoor intensive aquaculture systems, where water temperature can still be disturbed by unexpected reasons like power failure and equipment malfunctions, let alone in extensive outdoor systems which are subject to the weather and climatic change; such variations in water temperature can impact fish to varying degrees, affecting behaviors such as swimming, schooling, aggressive behavior, exploratory behavior, courtship, spawning, and predator–prey relationships, as detailed in the following section, reflecting the stress responses of fish to temperature changes (Figure 1).

3.1.1 | Swimming

Water temperature can affect fish swimming by altering the water viscosity, which can affect the drag force experienced by

TABLE 1 | Definition of fish behaviors and their role in aquaculture.

Behavior	Definition	Behavioral measurements	Role in aquaculture
Swimming	Referring to fish using their body with each fin for locomotion, the patterns of which mainly include steady swimming, burst-and-coast swimming, hovering [34].	Encompassing trajectory, velocity, acceleration, activity, frequency, and amplitude of tail beat, turning angle and direction [35].	The basis for fish to move, feed, escape, and hunt.
Schooling	Referring to swimming as a group with the same direction and synchronized manner [36].	Including group structure and cohesion, measured in polarity, synchrony, nearest-neighbor distance (NND), inter-individual distance (IID), and the horizontal and vertical distribution of fish individuals [37].	1. Reducing swimming cost, which can influence fish growth and feed conversion rate [38]; 2. A crucial role in predation and anti-predation, as well as group activities such as courting [39].
Feeding	Referring to actions of searching, selecting, and consuming of food [40].	Mainly including duration time, and feeding intensity.	Directly impacting fish health, growth, and the overall productivity.
Predation and anti-predation	Referring to the behavioral response of predator to prey, and the behavioral response of prey to predator [41], respectively.	Including fast-start and rapid locomotion, which are based on the capacity to sense preys/predators as well as excellent swimming performance [41].	The vitally adaptive responses ensuring the survival of predators and preys in outdoor aquaculture and multi-trophic aquaculture.
Aggressive behavior	Referring to the aggressive interaction and response, which is expressed to secure resources such as food, territories, mates [42].	Mainly manifesting in various forms including pursuit, biting, tail-slapping, territorial disputes, and even cannibalism [43].	1. Increasing energy expenditure of fish [44]; 2. Easily leading to injuries, diseases and even death.
Exploratory behavior	Referring to the actions to investigate and interact with their environment in order to gather information and learn about their surroundings [45].	Including behaviors that individual is willing to investigate new environments [46].	A key indicator of adaptability to the new environment [21, 45].
Avoidance response	Referring to responses facing environmental stimuli based on their preference [47].	Mainly manifesting a tendency of getting close to or keeping far away from a particular area [47].	A crucial role for fish making tradeoff between preference and discomfort.
Anxiety-like behavior	Referring to the actions under the state with sustained apprehension of the environment and elevated vigilance [48].	Including freezing, increased dark preference, hiding and avoidance, reduced exploration, or staying at bottom or outer area of the tank for a long time [49].	The key indicator of compromised welfare for fish.
Courting and spawning	Courtship is the process by which fish attract potential mates; spawning is the release of gametes or of developing young to the external environment [50].	Including emitting sound signals, displaying colorful body, or communicating with their species-specific signal [51–53].	Courting and spawning aim at reproduction, which affect the success rate in breeding more fish fry in aquaculture.

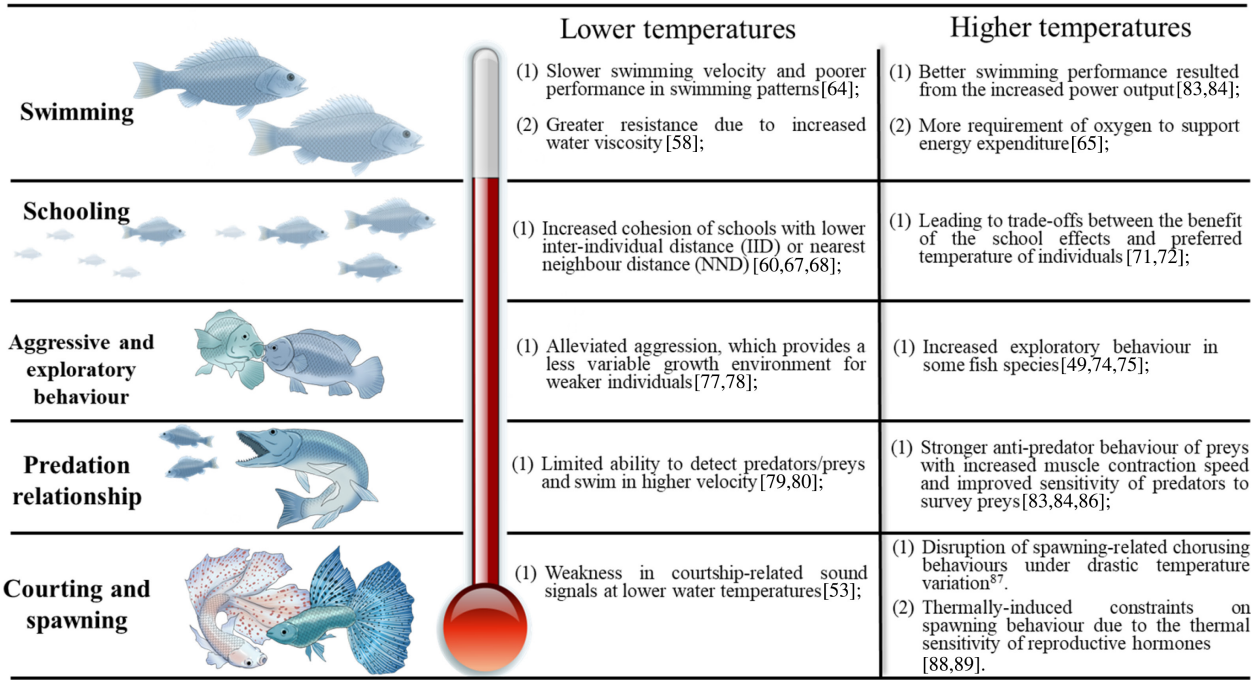

FIGURE 1 | Effects of water temperature on fish behavior.

the fish [57]. At low Reynolds numbers (i.e., low flow speed or low temperature), the viscosity of water is high, resulting in a greater drag force on fish and greater energy expenditure during swimming [57]. While this may not be significant for streamlined, adult fish, it can have a substantial impact on juvenile fish whose bodies deviate from the typical streamlined shape owing to the viscosity-related hydrodynamic effect caused by low temperatures and its magnitude of influence increases with decreasing temperature [58]. However, the effects of temperature on swimming performance through physiological changes may outweigh those mediated by changes in water viscosity for larger fish or those in higher-temperature environments [59].

Although fish may generally tolerate slow and rapid variation of water temperature in aquaculture environment due to seasonal or daily changes, fish inevitably alter behavior to ensure their swimming performance under this condition by changing their tail beat frequency, amplitude, and turning angle [60, 61], suggesting that temperature can regulate their behavior to maintain optimal swimming performance, potentially driven by intrinsic needs. Considering fish as ectothermic animals, water temperature exerts a profound influence on their metabolic rates and energy allocation [62, 63]. Existing research indicates that lower water temperatures can reduce fish swimming velocities. Zebrafish (*Danio rerio*) acclimated to 28°C showed reduced swimming speeds at 24°C, while exposure to 30°C decreased immobility duration and turning angles without significantly altering speed [64]. On the other hand, when water temperature increases and surpass the optimal range for fish, increased oxygen consumption ensues, prompting fish to adopt a strategy of swimming slower to conserve energy [65]. The alteration of swimming strategies in fish due to temperature changes reflects their adaptive capabilities in response to environmental shifts, yet it also indicates a compromise where they must adjust to maintain optimal conditions, thereby constraining their behavioral freedom and potentially impacting their welfare. It is noteworthy that the swimming strategies adopted by fish in response to temperature fluctuations are heavily influenced by the species under investigation and their inherent thermal adaptation, highlighting the significance of considering species-specific and environmentally contextual factors in such research.

3.1.2 | Schooling

Schooling refers to a group of fish swimming in the same direction in a polarized and synchronized manner [38]. Schooling relies on cooperation among individuals and has a significant impact on normal activities. The benefits of forming a school include facilitating foraging and better predator resistance. In addition, compared with individual swimming, swimming in group can significantly reduce swimming cost [36, 38], leading to a greater proportion of daily intake allocated for growth, which is critical in aquaculture production.

To keep the benefits of fish schools, the cohesion of schools must be maintained. A decline in cohesion within fish schools may reduce hydrodynamic drag leading to increased energy expenditure during swimming [36, 38]. This, in turn, can impact the daily energetic budget of individuals and potentially impair the collective response of the group when confronted with stressors. Some researchers use interindividual distance (IID, referring to the mean distance between the focal fish and any other ones) and nearest neighbor distance (NND, referring to the distance between the focal fish and its closest neighbor) to quantify fish school cohesion [37, 66]. At lower temperatures, fish schools exhibit higher cohesion in many species, which show smaller values of IID or NND. For example, giant danio (*Devario aequipinnatus*) show smaller average NND at 25°C (average

NND = 4.04 cm) compared with 28°C (average NND = 9.34 cm) [67], delta smelt (*Hypomesus transpacificus*) exhibit larger average IID at 21°C (average IID = 37.36 cm) than at 17°C (average IID = 30.69 cm) [60], and juvenile walleye pollock (*Theragra chalcogramma*) have 32% shorter NND under colder conditions (2°C) than under warmer conditions (9°C) [68]. Such effects allow them to maintain higher school cohesion in cooler environments, which, for juveniles, can offset the increased energy expenditure caused by the higher water viscosity associated with lower temperatures to some extent [59]. Conversely, as temperature increases, school cohesion may decrease slightly. For example, brown trout (*Salmo trutta*) fry showed increased IID with rising temperatures (4°C–10°C), with the NND increasing most significantly [66]. Such effects mean that swimming in warmer water regions may prevent them from effectively utilizing the hydrodynamic benefits of schooling, thus requiring them to expend more energy, although muscle contractility and efficiency are better in the warmer waters [59].

Fish have the ability to use a neural thermoregulatory system to sense thermal signals from the environment, helping them avoid harmful temperatures and occupy preferred zones for growth and performance [69]. This spatial preference under temperature gradients or fluctuations significantly affects individual distribution within schools [70]. When the environmental temperature is close to the preferred temperature, individuals spend more time in school [15]. Conversely, if the temperature is not preferred, the fish balances the benefits of schooling against its temperature preferences, potentially leaving the school to seek a more favorable environment for metabolism and feed conversion [71, 72], which then results in a unique spatial distribution of fish schools in areas with varying temperatures.

3.1.3 | Exploratory and Aggressive Behavior

Exploratory behavior is used to evaluate the emotion state and stress response of fish [21, 45], and aggressive behavior in aquaculture cannot only increase energy expenditure, but also easily lead to injuries, diseases or death among the cultured fish [26, 43, 44], thereby causing loss in aquaculture production. Both of these two behaviors are important indicators to assess fish welfare level. It is believed that exploration and aggression are associated with fish personality (including aggressiveness, exploration-avoidance, boldness-shyness [73]), and water temperature can pose influences on them to some extent.

Exploration is a relatively complex behavior, involving physical capabilities and personality traits [45, 49, 74] related to boldness and shyness, primarily manifested as more time in risky areas like the top and bright open spaces, and keeping away from groups. In a study on mosquitofish (*Gambusia affinis*), newborn fish raised at a lower temperature (25°C) showed different behavioral traits in adulthood: female fish exhibited repeated shyness and exploration, while male fish showed marginal repeated shyness, suggesting that environmental factors influencing fish in the early stage may shape behavior traits in adulthood; and mosquitofish reared at higher temperatures (30°C) were more exploratory than those raised at lower temperatures, with no difference in shyness trait [29]. The promotion of exploratory behavior by higher temperature may be due to alterations in the central nervous system and modifications in protein synthesis and ATP production, as was pointed out in a serious of studies on zebrafish [49, 74, 75]. While it is inconclusive whether an increase or decrease in exploratory behavior is advantageous or detrimental to fish, as an increase in exploratory behavior may imply a higher likelihood of successful foraging despite a greater risk of predation in more complex outdoor or multi-trophic aquaculture systems and may also increase the feeding rate in normal feeding process in aquaculture. From the perspective of fish welfare, to promote exploratory behavior, for instance by adding enrichment of aquaculture aquatic environment, signifies an increased freedom to display most normal behavioral patterns and enhancement of cognition and brain physiological functions [21, 76].

In terms of aggressive behavior, as one of the traits of fish personality as well, it mainly manifests in various forms including pursuit, biting, tail-slapping, territorial disputes, and even cannibalism [43]. In most aquaculture production, although aggression is a part of natural fish behavior, excessive aggressiveness is considered detrimental to production. That is because aggression implies extra energy expenditure and even lead to injuries and death, causing reduction in profit [26, 43, 44], and fish that lose fights in the aggression may be unable to escape from their victors, in which case they will suffer from chronic stress, causing impairments in welfare. Decreasing temperature can alleviate the aggressive behavior of some fish species. In neotropical cichlids (*Cichlasoma paranaense*), which can tolerate temperatures up to 39°C, gradually reducing the water temperature by 6°C from an initial 27°C was found to decrease aggressive behaviors in both individual fish and groups; conversely, when the water temperature was gradually increased by 6°C from the same starting point of 27°C, no significant change in aggressive behavior was observed among the fish [77]. Similar conclusions were drawn in matrinxã (*Brycon amazonicus*) juvenile fish, where compared with the control group temperature (28.33°C ± 0.12°C), lower temperature (24.09°C ± 0.15°C) reduced the aggression of juvenile fish [78]. In general, alleviating the aggressive behavior of fish provides a less variable growth environment for fish individuals and decreases disease to some extent, which is beneficial for fish welfare in aquaculture [26].

3.1.4 | Predator–Prey Relationship

Predation and anti-predation affect production in polyculture fish farming, a culture mode with more than a single species. Predators and prey often exhibit similar responses to temperature changes under lower temperature condition for the reason that most fish species tend to swim more slowly for the requirement of maintaining optimal swimming performance [79, 80], and low temperatures can constrain their ability to detect cues of predators or preys, making preys more vulnerable to predator attacks and predators more difficult to acquire food [81]. In addition, considering that both predators and prey in the water are affected by increased water viscosity due to low temperatures, smaller-bodied or deformative fish with odd body shapes experience greater resistance and energy expenditure during swimming, placing them in a disadvantageous position in the predator–prey relationship [58]. However, in some cases, the impact of low temperature on predators may be greater than

that on prey because the neural performance of fish may be affected, which affects the coordination and perception of complex tasks such as rapid movement during predation, whereas escape movement, which displays some degree of directional randomness, requires relatively lower neural performance [82]. When it comes to warmer waters, the antipredator behavior of fish would become stronger than that in colder waters, mainly because of the increase of muscle contraction speed, which affects the muscle performance and power output, resulting in greater power output and higher escape swimming performance [83, 84]. Likewise, this increased activity and swimming speed also improve the sensitivity of predators to prey and benefit pursuit and attack [85, 86].

3.1.5 | Courting and Spawning

Courting, the process by which fish attract potential mates, can involve emitting sound signals in some species. Sound signals emitted during courting, which are closely related to season and water temperature, are stronger during warmer periods from early spring to early autumn and difficult to detect during colder winters [53]. Spawning, the process of releasing eggs, exhibits diverse behaviors across species. In meagre (*Argyrosomus regius*), spawning-related chorusing is strongest at an average water temperature of 15°C–25°C, peaking around 18°C, with drastic temperature changes causing the chorus to stop [87]. Furthermore, water temperature impacts fish spawning through its effects on reproductive hormones. For example, high temperatures can reduce spawning capacity in clownfish (*Amphiprion melanopus*) due to the thermal sensitivity of reproductive hormones [88], and low-temperature stress can lower reproductive behavior in guppy (*Poecilia reticulata*) due to a reduction in reproductive-related traits [89]. Thus, for aquaculture aimed at increasing production, effectively regulating water temperature to ensure proper courtship and spawning of fish is crucial for the advancement of aquaculture development.

3.2 | Turbidity

Turbidity, characterized by the degree to which suspended particles obstruct light penetration, is a key physical indicator of water quality [90]. In aquaculture, the accumulation of feed and fish waste is a major contributor to water turbidity. Researchers have classified turbidity into organic and inorganic turbidity based on the underlying causes: organic turbidity is mainly caused by eutrophication, which leads to the proliferation of algae and increases the water turbidity; inorganic turbidity is primarily caused by precipitation or suspended particles [91]. An increase in water turbidity leads to reduced visibility, significantly influencing behaviors that are reliant on visual cues, especially among fish that mainly depend on sight for activities [23], which then affects their feeding [27], predation, antipredation, courting, and mating, as well as the overall efficiency of fish schooling behavior [92] (Figure 2).

3.2.1 | Feeding and Predation Relationship

Turbidity can affect fish feeding behavior (predation efficiency and feeding rates) primarily by affecting the visual perception of fish, resulting in a lower success rate of predation [30]. In largemouth bass, primarily a visual predator, only 15% caught prey in a 250 nephelometric turbidity units (NTU) environment compared with 100% in a 0 NTU environment [93]. In addition, the low availability of visual cues, mainly in polyculture

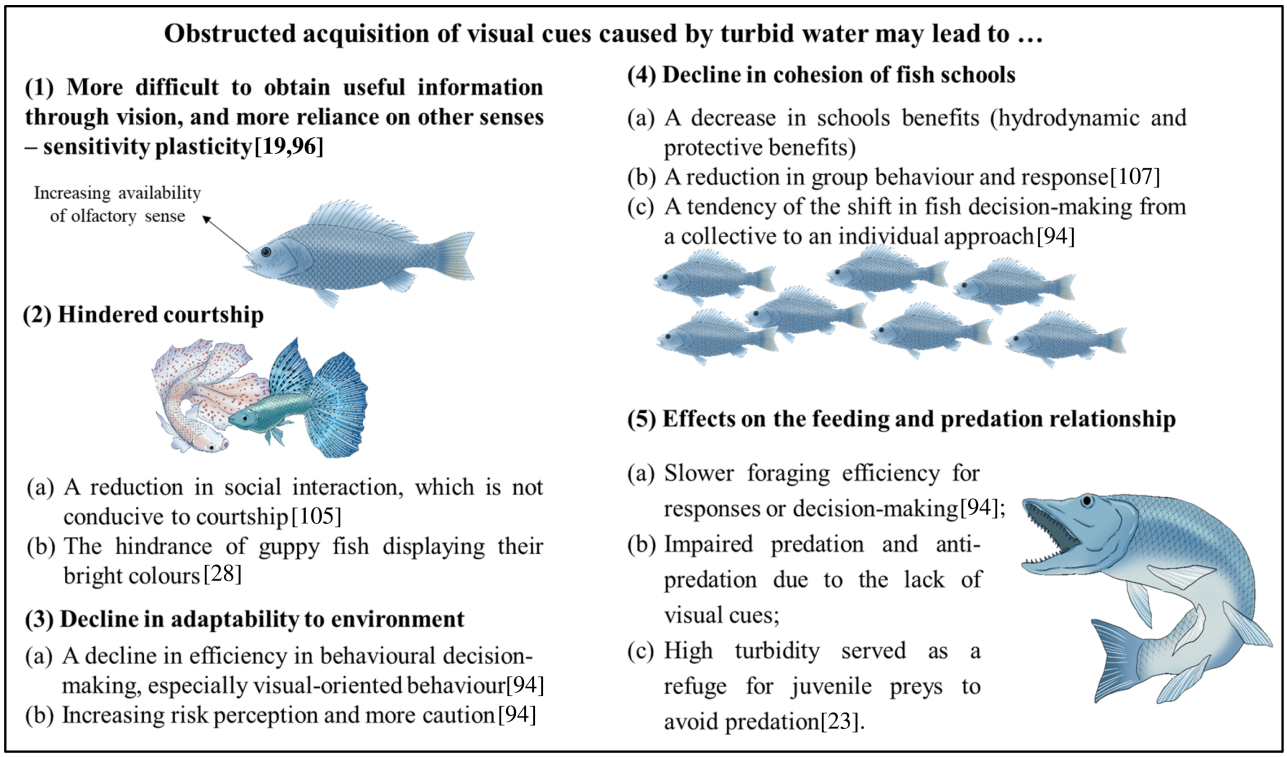

FIGURE 2 | Negative influence caused by obstructed acquisition of visual cues in turbid water.

systems and outdoors systems, can also slow certain responses or decision-making processes [94], leading to a slower foraging speed and declined efficiency [30], as seen in Picasso triggerfish (*Rhinecanthus aculeatus*), which linger with a slower search rate and take more time to find food [95]. Reduced predation efficiency and feeding rates, which can lead to declining yields, are undesirable in aquaculture. Fortunately, some fish have developed strategies to cope with the challenges posed by high turbidity. When visual information acquisition is limited by increased turbidity, some fish rely more on their olfactory senses to detect chemical cues, known as sensitivity plasticity [19, 96]. For example, zebrafish exposed to a turbid environments showed a weaker response to visual stimuli but a stronger response to olfactory stimuli, indicating a shift in their primary sensory mode [19]. However, for predation, chemical cues may persist long after the prey leave, making them somewhat inaccurate, whereas visual signals can accurately and quickly grasp the position of prey [97]. Therefore, for the fish that rely on olfaction, lack the visual cues can lead to more cautious decision-making as well due to the sense of fear [97]. Losing the freedom from fear can severely compromise their welfare in normal life.

Although turbid water affect fish that rely on visual cues for predation, excessive low turbidity can also lead to poor feeding performance for some species. For example, pikeperch (*Sander lucioperca*) at low turbidity (0 FAU) had a 25% lower feed intake with slower feeding response than pikeperch at high turbidity (38 FAU) and a 10.5% lower compared with pikeperch at intermediate turbidity (15 FAU) [98]. Such slower feeding response in low-turbidity water may not be due to visual impairment but rather to low turbidity stress, as pikeperch naturally prefer dimmer environments for foraging [98]. From a fish welfare perspective, this underscores the importance of adjusting the aquaculture environment based on specific species' inherent turbidity preferences during the farming process.

Antipredator behavior, which rely on prompt responses to predator cues [99], is similarly impacted by turbidity. In polyculture models rearing several species of fish, especially in traditional pond aquaculture, turbidity can affect the predation and antipredation behaviors of fish, which is related to the natural growth of mixed fish and affects the stability of the aquaculture ecosystem. In turbid water, visual cues are hindered, prompting some fish to behave more cautiously and increase their risk perception [94]. For example, mosquitofish reduced their activity and exploration in response to predator cues in turbid environments [100], and Stymphalia minnow (*Pelasgus stymphalicus*) exposed to turbid environment exhibited hesitancy and reduced activity when leaving artificial refuges, even in the absence of predator cues [101]. These studies suggest that turbidity may elevate perceived predation risk and decrease exploratory behavior in prey species. However, the effect of turbidity on the prey is not always negative. Juvenile fish can benefit from high turbidity because suspended particles can form a protective cover, which allows them to conceal themselves and reduce predation pressure [23]. A study has found that Japanese anchovy (*Engraulis japonicus*) larvae in the high-turbidity group (300 mg/L kaolin) showed significantly higher survival rate when exposed to predators jack mackerel (*Trachurus japonicus*) compared with the ones in the low-turbidity groups (0, 50 mg/L kaolin) [102]. Additionally, it should be noted that whether turbid water can act as a protective cover depends on the habitat of the fish [103]. If fish live in water with almost no shelter, high turbidity may be beneficial and their survival rate may be increased. To some extent, these phenomena reflect the diverse effects of turbidity on predation.

3.2.2 | Courting

Beyond predation and anti-predation, turbidity also affects fish courting behavior. Some fish species use colorful appearances to attract mates, such as guppy [28] and cichlid [104]. However, excessive turbidity can impair visual cues, affecting the courting process. For example, male guppy displayed bright colors to court females but exhibited less frequent courting behavior in turbid water compared with clear-water conditions, which hinders female mate selection [28]. Turbidity negatively impacts visual acuity and the effectiveness of visual communication in aquatic systems by obscuring visual cues, leading to reduced social interaction time between male and female individuals within the fish group [105]. While visual cues become limited in turbid water, some fish still can use olfactory signals to compensate during courting. In a mate selection experiment with three-spined sticklebacks (*Gasterosteus aculeatus*), females relied more on visual cues than olfactory cues in clear water but shifted to relying more on olfactory cues in organic turbid water containing algae (*Isochrysis* sp.) [106]. This finding may suggest that fish can adjust their reliance on different cues based on environmental conditions when conducting courting behavior, choosing the most informative cues available.

3.2.3 | Schooling

Increasing turbidity also negatively impacts fish schooling behavior. For example, yellowtail (*Seriola quinqueradiata*) juveniles demonstrated increased NND and separation angles, indicating weakened cohesion and polarity within schools [92], and guppies displayed reduced activity and formed smaller schools in turbid conditions compared with clear water, showing a tendency toward more solitary behavior [107]. Furthermore, in another study using a V-shaped decision arena (an arena is a well-designed device or tank with a particular shape to reach for the need of the experiment where fish take part in), three-spined sticklebacks under turbid conditions shifted from collective decision-making to more individualistic approaches, a behavioral adaptation that could exacerbate issues such as uneven food allocation and diminished safety in numbers [94]. This behavioral shift also entails heightened caution, suggesting that fish in turbid environments behave more like isolated individuals than as cohesive groups. Consequently, the inherent energy conservation benefits typically associated with schooling behavior may be diminished in highly turbid waters. The synthesis of these findings reveals profound implications of turbidity on fish behavior, particularly regarding social dynamics and behavior strategies. Notably, this section mainly synthesizes the impacts of inorganic turbidity on fish behavior, particularly on visual-oriented behavior. However, in scenarios of organic turbidity caused by the presence of algae and other organisms, there is potential for decreased or fluctuating DO levels in

the water, which introduces additional behavioral alteration resultant from oxygen deficiency [108] (Such behavioral alterations can be further explored in Section 4.1).

3.3 | Summary

In summary, the effects of water temperature and turbidity on fish behavior are multifaceted and significant. As vital physical water quality parameters, temperature can alter water viscosity and influence metabolism, while turbidity can affect visibility, leading to behavioral variations or stress in fish. Maintaining water temperatures within ranges that support optimal metabolic efficiency can maximize growth rates and feed conversion ratio and controlling turbidity levels ensures normal behaviors, both of which are crucial for minimizing stress and improving overall fish well-being, contributing to more sustainable aquaculture productivity.

4 | Chemical Water Quality Parameters

Chemical water-quality parameters are indicators used to describe the characteristics and contents of chemicals in water bodies. The chemical water quality parameters discussed in this chapter include DO, salinity, pH, and inorganic nitrogen, which are of great concern in aquaculture.

4.1 | Dissolved Oxygen

DO is vital for the survival of aquatic organisms and is influenced by various complex factors. In aquaculture production, large inputs of feed, excessive stocking density, failure to use aerators can lead to a decrease in DO [109]. DO is more uncontrollable in extensive aquaculture systems than that in intensive mode, given the impact of weather changes. As an example, in the rainy season, extensive pond aquaculture experiences reduced water solubility of oxygen, a consequence of inadequate sunlight exposure [110]. Additionally, seasonal environmental conditions such as summer thermal stratification and winter ice cover affect the distribution of DO in open water as well [111]. Under condition with oxygen deficiency, or hypoxia, fish maintain their oxygen uptake at the level of the standard metabolic rate (SMR), the minimum required for basic functions [112]. This may lead to respiratory difficulties, impaired movement, reduced appetite, and physiological responses, which then results in behavioral changes (Figure 3). Noted that, oxygen supersaturation, or hyperoxia, has been proved that it can pose a risk of physiological issues or diseases such as bubble gas disease in salmon [113, 114], highlighting the necessity for the appropriate DO management on species-specific (freshwater or marine) and system-dependent (intensive or extensive environments) condition. However, due to the less common discussions of the impacts of hyperoxia on fish behavior and the more focused concerns in aquaculture over the effects of hypoxia, this section has focused on the influence of hypoxia on fish behavior.

4.1.1 | Swimming and Avoidance Response

Fish can perceive the level of oxygen in their living environment and whether it is suitable for their activities [115]. In coping with a low DO environment, fish exhibit two strategies to enhance survival under hypoxic conditions [116–118]. First, they reduce activity levels, exemplified by diminished swimming behavior, to curtail oxygen demands [117]. This strategy encompasses the adoption of burst-and-coast swimming, a highly efficient energy conservation mechanism characterized by intermittent bursts of vigorous motion (the burst phase) followed by motionless intervals with a streamlined posture (the coast phase) [119]. For example, hypoxia frequently prompted species like the Atlantic cod (*Gadus morhua*) and red drum (*Sciaenops ocellatus*) to increase the frequency of burst-and-coast swimming, enabling

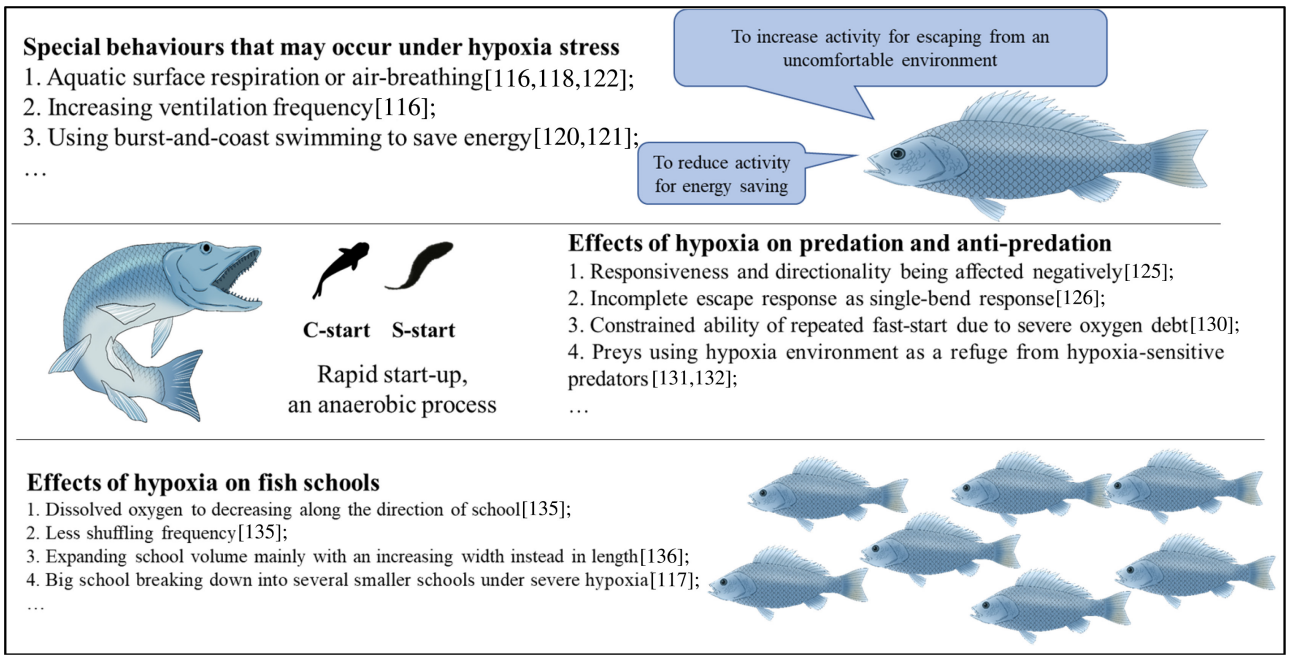

FIGURE 3 | Effects of hypoxia on fish behavior.

them to sustain swimming velocities with reduced energetic expenditure [120, 121]. Second, fish may elevate their activity to rapidly locate regions with higher oxygen concentrations. This includes behaviors such as swimming to the water surface for aquatic surface respiration (ASR) [116, 118, 122]. The golden grey mullet (*Liza aurata*) has demonstrated a substantial rise in ventilation frequency upon exposure to reduced oxygen saturation levels, ranging from 10% to 40%; when oxygen saturation plummeted to 15%, they engaged in ASR, illustrating an adaptive strategy to mitigate oxygen deprivation [116]. Similarly, the Nile tilapia (*Oreochromis niloticus*) has been observed to initiate ASR when the oxygen partial pressure in the culture water decreased below 2.1 kPa [122], highlighting a comparable threshold of different species for adopting compensatory mechanisms under hypoxic conditions.

Both strategies employed by fish in response to hypoxic conditions involve different "considerations." The pursuit of potentially oxygen-rich areas may inadvertently guide fish into further hypoxic zones or expose them to different stressors [123, 124], such as somewhere with suboptimal temperatures, light intensities or even stress from predators. Conversely, confining activity within zones of marginally tolerable DO, though limiting spontaneous swimming, conserves vital oxygen and energy resources for alternative physiological processes [123], although it does not fully alleviate the detrimental consequences of hypoxia. It follows that the strategic modulation of activity levels represents a pivotal adaptive response to hypoxia, underscoring the complex interplay between environmental challenges and fish survival strategies.

4.1.2 | Predation Relationship

In predator–prey relationship, hypoxia influences both the predation of the predators and the anti-predation responses of the prey by constraining their swimming abilities and fast-start process, encompassing responsiveness and directionality [125]. Fast-start happens at the point of preys sensing predator signals and predators starting to hunt after finding targets. Most researchers divide fast-start into two stages: (1) First body bend (C- or S-shaped) caused by muscle contractions. This stage begins at the start of the sensing signals and ends when the head stops turning or changes direction. (2) Second body bend, which begins at the end of stage one and ends when the head stops turning or changes direction [126]. Fast-start movements, executed under anaerobic metabolism, rely on anaerobic muscle energy for sudden acceleration to maximum speed, and it was previously believed that hypoxia does not affect this escape movement [127]. However, certain performance-related escape behaviors, such as responsiveness and directionality, are related to brain and sensory functions and are negatively affected by hypoxia. This not only affects the capacity to perceive predators (i.e., vigilance against predators) [128], but also the capacity to judge direction during the escape process. For instance, the avoidance and approach responses of sea bass (*Dicentrarchus labrax*) were random when escaping responses occurred when the oxygen level dropped to or below 50% oxygen saturation, suggesting impaired direction discrimination mediated by mechanosensory systems [129]. Furthermore, escape responses are often incomplete under hypoxia, favoring single-bend responses due to their lower energy costs, which have been suggested to be more common under conditions of reduced swimming performance [126]. Noted that, although escape is powered by anaerobic metabolism, it requires an aerobic recovery phase, which may be limited by hypoxia in fish, resulting in severe oxygen debt and constraining the ability to perform repeated fast-starts [130].

In predator–prey relationships, hypoxia also challenges the low-oxygen tolerance of fish, which enables preys to use hypoxic environments as refuges to evade predators, as demonstrated in red drum [131, 132], and enables predators to forage in hypoxic areas when prey abundance is low in oxygen-sufficient surface waters, as revealed in yellow perch (*Perca flavescens*) [133]. Despite this, while hypoxia may not necessarily increase the probability of fish being preyed upon by other fish, predators unaffected by water oxygen levels, such as birds and aquatic mammals, may exploit the disadvantages of fish escaping under hypoxic conditions to hunt them [84, 125], such as when fish engaging in ASR. To mitigate this risk, some fish adopt strategies as part of their antipredator behavior, such as surfacing irregularly or synchronously with other fish to reduce predation risk [134]. Fathead minnows (*Pimephales promelas*), for instance, dive swiftly below the surface upon detecting alarm signals while engaging in ASR and quickly return to the surface without reducing their activity [111]. This indicates that fish have strategies to cope with the risks of hypoxia, despite suffering from impaired response and weakened swimming capacity.

4.1.3 | Schooling

Although the formation of schools has many advantages for fish, uneven distribution of DO remains prevalent within fish schools, with the consumption of oxygen by fish at the leading edge of the group causing a decrease in DO along the direction of schooling movement, making fish positioned toward the rear more prone to hypoxia [135]. Thus, schooling involves a tradeoff between individual oxygen demand and interest demand such as hydrodynamic benefits. In fish schools, different individuals occupy distinct positions in the school at different times as shuffling frequently occurs during school movement [135], thus enabling hypoxic individuals to move to areas with relatively more oxygen. Under this circumstance, hypoxia has a great impact on fish school size. As water oxygen concentration decreases, the volume of the school expands particularly in width instead in length, because fish at the same horizontal level can obtain hydrodynamic advantages, by which fish can save swimming cost more easily and the phenomena that fish at the rear become increasingly hypoxic may be prevented [136]. As the oxygen concentration decreases further, the schools continue to expand until they reach a certain point, at which point they may disperse and break down into several smaller schools to better cope with hypoxia [117]. These findings suggest that oxygen continually regulates fish schooling and is an important factor in determining schooling capacity.

This section has focused on reviewing the impacts of hypoxia on fish swimming, predator–prey relationships, and schooling. Related behavioral alterations reflect the adaptive strategies in response to hypoxic environments. Considering these effects of hypoxia on fish behavior as evidenced in multiple studies,

the further adverse impacts under severe hypoxia underscore the detrimental influence on normal activities and lives of fish, which necessitates careful consideration and management in practical aquaculture systems.

4.2 | Salinity

Salinity is used to measure the total concentration of inorganic ions in water. With global atmospheric changes and elevated anthropogenic pollutants entering natural open waters, varying degrees of salinity pollution occur in many water areas [137, 138]. This negatively affects the growth of aquatic organisms and ultimately disrupts outdoors aquaculture systems, both in ocean water or fresh water areas [139]. Fish inevitably experience salinity stress due to frequent variability in salinity levels, particularly in nearshore areas or in brackish water inland regions, where freshwater inputs cause salinity to fluctuate, necessitating tolerance of wide salinity ranges. Otherwise, living in an environment with inappropriate salinity or frequent salinity fluctuations has been found to lead to an osmotic imbalance between the fish body and the external environment [140], and to impair the sensory system [20], particularly the olfactory system, affecting in fish behavior (Figure 4).

4.2.1 | Osmosis Imbalance-Induced Behavioral Changes

When confronted with salinity stress, fish have to adopt physiological strategies to cope with osmotic imbalance [22, 140]: ions transportation occurs in fish to maintain osmotic balance, where the reactions can be found in the aquaporins and ion channels/pumps in their gills and intestines [141, 142]. However, some of these ion transport pathways consume considerable energy and can influence energy allocation and the metabolic rate [143–145]. Therefore, as a compensatory strategy to cope with the cost of osmoregulation, some fish reduce activities, or have a higher cost of energy expenditure to move under salinity stress, which is not conducive for swimming, predation, anti-predation, and spawning [146–148].

Some fish are able to make a tradeoff between their preferred salinity range and potential stress. For example, smolts, known as the salmonid in a particular life stage when they undergo physiological changes for the migration from fresh habitat to the ocean, experience dynamics salinity fluctuations and tend to prefer shallow ocean areas with lower salinity (< 20 psu) to avoid sea lice [149], which inhabit environments with salinity higher than 20 psu [149]. When confronted with inappropriate salinity, fish need to balance the requirement to maintain their current osmotic balance with the need to relocate in order to alleviate stress, based on their adaptive osmoregulation strategies [150]. To mitigate salinity stress, fish must have an accurate perception of their surroundings, such as the ability to sense changes in ambient sodium and chloride levels, and the capacity to migrate away from high-stress areas promptly [151, 152]. However, when the water salinity exceeds the tolerance threshold of fish, the dehydration and declined swimming capacity come to fish so that they may not be able to migrate from high-stress areas to preference location [145], even if they are able to sense the salinity stress in this case.

4.2.2 | Impaired Olfaction-Induced Behavioral Changes

In addition to impairing osmotic imbalance, salinity can affect fish behavior by impairing olfactory sensory fish [20, 153]. Inappropriate ambient salinity may interact with the olfactory receptors of fish or act on the alarm cues directly, leading to a decrease in the availability of olfaction [146], which can limit the

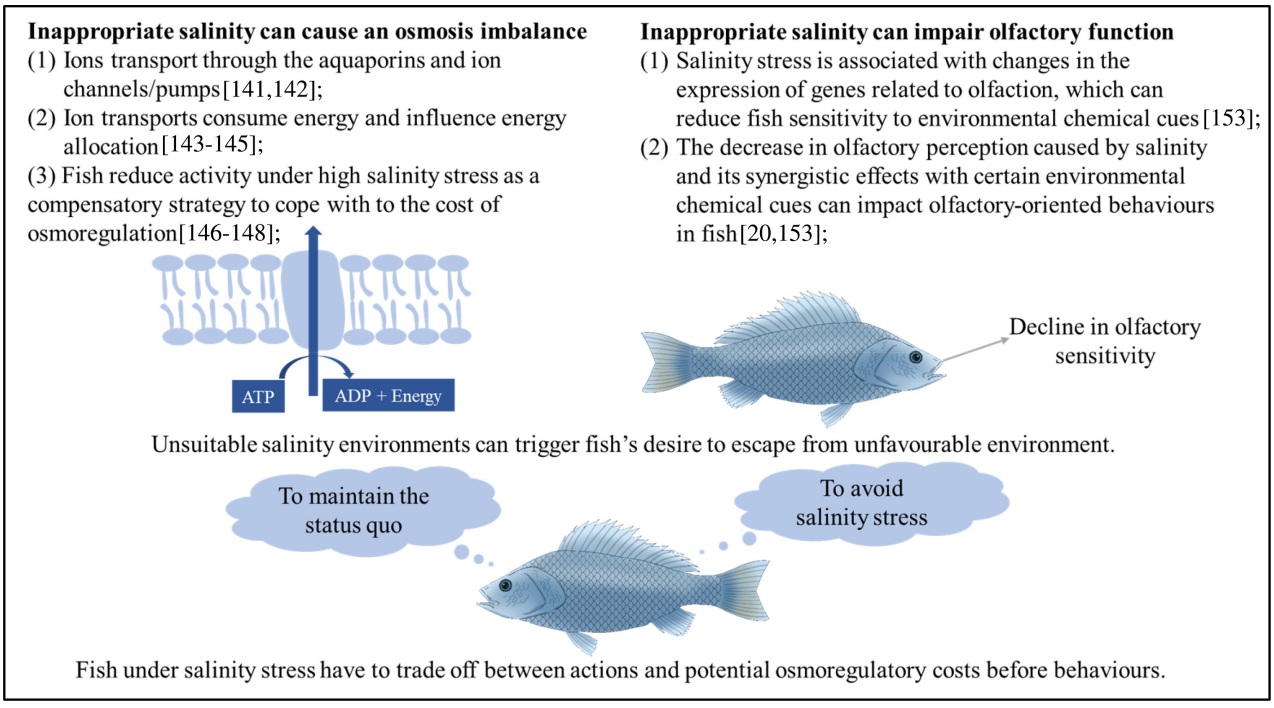

FIGURE 4 | Abnormal behaviors caused by inappropriate salinity.

capacity of fish to perceive environmental chemical cues such as certain ions [154] and endocrine disruptors [20], potentially impairing their antipredator responses, such as detecting risk cues. For instance, fathead minnows undergoing high-salinity treatment (8000 ppm) reduced the response of antipredator behavior compared with low-salinity treatment (1000 ppm), reflected in a decreased percent change in movement distance before and after predator stimuli ((poststimulus–prestimulus)/prestimulus) [146]. Without the ability to sense risks, fish may be subjected to constant stress and find it difficult to display normal behavior freely [76]. Moreover, salinity not only interact with the olfactory receptors but also be associated with the change in the expression of genes related to olfaction, demonstrated in a study on salmonid fish migration [153]. Salinity plays a vital role in this important life cycle due to its influence on spawning related physiological activity, encompassing the release of related hormone, such as cortisol, and the olfactory-related memories during migration [153]. Significant fluctuations in salinity during this process can impact migration, indirectly affecting the spawning success. This phenomenon provides insights for aquaculture practices, emphasizing the necessity for rigorous control of water salinity for species that are highly dependent on specific salinity regimes.

From a welfare perspective, chronic stress from exposure to inappropriate salinity can lead to reduced fitness and compromised welfare with osmosis imbalance or impaired olfaction, which highlight the importance of maintaining stable and optimal salinity levels in aquaculture systems, especially in aquaculture systems characterized by fluctuating water salinity, such as marine and offshore operations. Additionally, understanding the behavioral responses of fish under different salinity conditions can assist farmers in implementing better management practices, ensuring healthier and less stressed fish populations.

4.3 | pH

Water pH is used to measure the acidity and alkalinity of water. Intensive aquaculture systems, notably RAS, maintain stable control over water quality, minimizing pH fluctuation impacts. Conversely, outdoor aquaculture, both in freshwater and marine, is more susceptible to external environment, such as more solution of atmospheric additional emission of carbon dioxide due to human activities [155]. These factors collectively challenge the stability of outdoor extensive aquaculture systems.

The suitable range of pH for farmed fish is species-specific for optimal physiological activities, and deviation from this range can alter fish behavior, such as swimming. For example, the critical velocity of rainbow trout (*Oncorhynchus mykiss*) at water pH4, 5, and 10 was only 55%, 67%, and 61%, respectively of that in water of pH7, and fatigue occurred earlier in fish swum to exhaustion in acid or alkaline condition, compared with fish in neutral condition [156], both of which indicated that fish in inappropriate range of pH might expend more energy on swimming, resulting the potential problem that fish divert energy away from growth to normal activities. Some species are highly sensitive to environmental pH levels; for example, land-locked sockeye salmon (*Oncorhynchus nerka*) will attempt to avoid areas with pH levels below 6.0 during their upstream migration, even in response to slight pH changes [157]. Furthermore, Brook Char (*Salvelinus fontinalis*) and Arctic Char (*Salvelinus alpinus*) were also found that they exhibited avoidance responses to unsuitably low pH environments (< 5.5) [158, 159]. Thus, it has been speculated that salmon may be able to perceive the pH of their surroundings and respond accordingly [157]. Nevertheless, the impact of pH on fish behavior extends beyond these direct effects: acidified water can impair the olfactory senses to response to chemical cues in most fish species, consequently altering behaviors that are ordinarily guided by olfaction [24, 160, 161].

Fish can use olfactory function to discriminate chemical cues [162], which is crucial in shaping their olfactory-mediated behavior, including their responses to risks [163], feeding [160, 164], and habitat selection [165]. For example, due to the potential issue that olfactory neurones are impaired and olfactory sensitivity to chemical cues is reduced under acidic conditions, orange clownfish (*Amphiprion percula*) were found to be unable to effectively use olfactory cues to locate their habitat under simulated acidified conditions (pH7.6), compared with conditions under seawater (pH8.15) [165]; similarly, fathead minnows, finescale dace (*Phoxinus neogaeus*), and rainbow trout struggled to detect conspecific alarm cues under mildly acidic conditions (pH6.0), compared with normal pH conditions (pH7.0–7.2) [166]. Importantly, such olfactory dysfunction may persist over extended durations, even after leaving from the acidic areas, observed in a study in which fathead minnows failed to exhibit feeding responses typically elicited by strong chemical stimuli after returning to their original habitat (pH8.1) after exposure to an acidic environment (pH6.0) for 72 h, indicating a lingering effect on their chemosensory capabilities [160]. These phenomena occur not only in acidic water but also in water that experiences pH fluctuations caused by precipitation, which can temporarily lead to a sluggish response of fish to alarm signals, as found in Atlantic salmon (*Salmo salar*) [163]. In addition to impaired olfactory neurons, fish in acidic environments may experience degraded chemical cues [24] or reduced affinity of these cues for odorant receptors [167], which can transmit incorrect information or obstruct information transmission, leading to a loss of the capacity to make correct decisions. For instance, when eggs and larvae of clownfish were exposed to simulated acid seawater (pH7.8), they lost the capacity to distinguish between predators and non-predators and were strongly attracted to the smell of predators [161], which alters antipredator behaviors and elevates the likelihood of predation, profoundly disadvantaging their healthy development.

The disruption of chemical signals by pH, in addition to affecting olfactory perception related to predation and anti-predation, also impacts gustatory sensitivity of fish [25, 168]. pH may alter the binding kinetics of specific amino acids to available taste cell receptors, changing their perceived intensity and quality, thus inhibiting or enhancing the effect of particular amino acids [169], which in turn affects fish appetite. Furthermore, studies have shown that lower pH can stimulate the release of cholecystokinin and peptide in the intestine, substances that inhibit appetite, leading to reduced feeding in fish [170]. Therefore, it is believed that lower pH significantly impacts fish appetite, decreasing their feeding rate, which has substantial implications in aquaculture systems that require feeding [169]. In Atlantic salmon, lower pH has been observed to decrease feeding

response and reduce food intake, to the detriment of growth [171], with significant implications for nutritional status and overall health. Moreover, similar results was found in yellowtail kingfish (*Seriola lalandi*) reared in RAS: fish in water with a pH of 6.58 ate significantly less food than those in waters with pH7.16 [172]. Given the impact of pH on fish behavior, particularly on olfactory and gustatory responses, researchers predict that decreasing open-water pH levels may impair fish ability to respond to chemical sensory signals [165]. This impairment could reduce rapid responses to food [173], potentially leading to reduced feeding efficiency, which may result in slower growth, malnutrition, and increased vulnerability to disease, ultimately causing significant losses in aquaculture.

4.4 | Inorganic Nitrogen

Nitrogen in water exists mainly in the forms of ammonia, nitrite, and nitrate [174]. In aquaculture, excess feed and fish excrement are the primary causes of increased nitrogen levels in the water, which often result from high stocking densities or poor water quality management [175]. In this article, we review the effects of these three types of inorganic nitrogen on fish behavior like swimming and feeding.

4.4.1 | Ammonia

Ammonia (NH_3) is a common pollutant in aquaculture due to decomposition of biological waste [176]. Intensification and high-density can easily lead to increased ammonia production in aquaculture systems [177]. When it comes to open water bodies, excessively much ammonia can even result in acidification or eutrophication of oceans or rivers [174], served as a typical aquaculture stressors (Figure 5).

Ammonia, in its free (NH_3) and ionized (NH_4^+) forms, poses significant threats to fish health, with the unionized form being particularly hazardous due to its greater permeability across gill membranes [176]. Although the capacity to tolerate high ammonia levels varies between fish species and depends on the duration of exposure, exposure to elevated ammonia levels triggers a cascade of detrimental effects on fish, for example, yellowfin tuna (*Thunnus albacares*) exposed to ammonia levels of 5–10 mg/L for over 24 h experience severe oxidative stress [178], rainbow trout exposed to approximately 1 mg/L of ammonia for more than 24 h show a significant reduction in feeding [179], and Indian carp (*Labeo rohita*) exposed to 3 mg/L of ammonia for an extended period suffer gill damage and experience a significant increase in oxygen consumption rate [180]. These negative effects are likely to manifest in fish behavior, like swimming and aggression, even at sublethal dose. Following paragraphs will present these behavioral effects of fish subject to acute as well as chronic exposure to ammonia.

In some aquaculture systems, such as RAS, operational disturbances may periodically cause similar irregularities, such as low efficiency in biological filtration, leading to short-term and high levels of ammonia, which can typically be attributed to improper water quality management [181, 182]. Such irregularity may lead to the result that fish acutely or chronically expose to ammonia. Acute exposure of fish to environmental ammonia (short-term exposure to high concentration of ammonia) leads to adverse effects, and fish need to undertake a series of

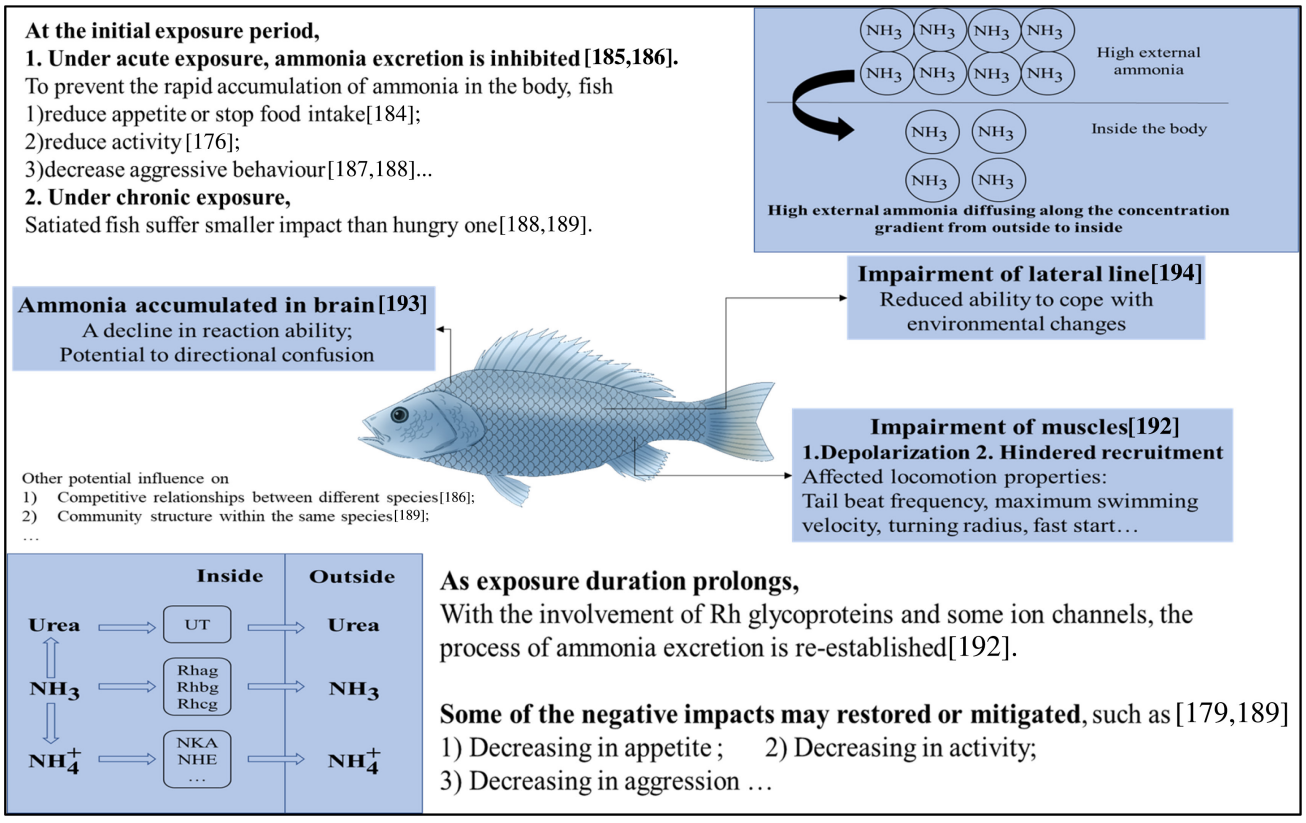

FIGURE 5 | Negative influence fish suffer in the environmental ammonia.

behavioral responses or strategies to cope. The initial behavioral responses of fish acutely exposed to excessive ammonia levels include reducing or stopping feeding [176, 183]. Loss of appetites have been observed in fish exposed to external ammonia, such as rainbow trout [179] and Mediterranean barbel (*Barbus meridionalis*) [184]. This may be because the decomposition of ingested proteins can lead to a sudden increase in ammonia levels inside the body. Under excessive ammonia, the excretion of ammonia through the gills is inhibited and ammonia may even diffuse into the fish body from the outside [185], resulting in the rapid accumulation of ammonia inside the body [186]. Therefore, reduced food intake as an efficient strategy could protect fish from significant further increases in postprandial blood ammonia level to minimize toxic effects [183]. In addition to food intake, ammonia production in fish can be also attributed to stress and increased metabolism caused by stress and exercise [176, 187]. In this situation under acutely excessive environmental ammonia stress, another strategy for fish to prevent the rapid accumulation of ammonia is to reduce exercise [176]. For example, rainbow trout and zebrafish exposed to excessive ammonia levels exhibited reduced activity levels and decreased aggressive behavior [188, 189]. However, the effects of acute exposure to environmental ammonia in fish contrast with those of chronic exposure, wherein the stress persists over an extended period. Unlike acute exposure, when chronically exposed to environmental ammonia, satiated fish demonstrated higher efficiency in excreting ammonia than hungry fish and experienced relatively less ammonia stress during exercise, with less accumulation of ammonia in the blood, compared with starved fish [190, 191]. This may be attributed to the possibility that feeding increases the metabolic rate of fish and leads to an elevated oxygen consumption rate, ultimately promoting ammonia excretion [191]. Such mechanisms indicate that fish have behavioral strategies to reduce ammonia toxicity when exposed to acute or chronic nonlethal ammonia levels. As exposure time prolongs, the involvement of Rh glycoproteins and certain ion channels helps re-establish the process of ammonia excretion [192]. This physiological regulation facilitates the recovery of ammonia excretion capability [185], thereby mitigating behavioral changes observed under ammonia stress, such as reduced appetite [179], decreased activity levels, and diminished aggression [189].

Exposure to ammonia environments can lead to the accumulation of ammonia in various tissues or organs within fish. The accumulation of ammonia in muscle tissue, especially in white glycolytic muscles which enable fish to acquire a large amount of energy within a short time through anaerobic metabolism, can cause muscle damage and affect energy supply [186]. And the accumulation in the brain can significantly impair the reflex arc neural function and related sensory systems in fish [193], which can greatly result in a reduction in the response ability as well as directional confusion during movement [186]. In addition, it was also observed that ammonia can damage the lateral line sensory system which is essential for perceiving environmental information. All these effects mentioned above can lead to difficulties in maintaining optimal behavior performance, including normal swimming performance, predation and anti-predation [194, 195], placing fish at a disadvantage in competitive relationships between different species (or inter-species relationship), as observed in a study on brown trout, where a decrease in swimming performance after ammonia exposure led to a significant reduction in capture success [186]. Notably, ammonia cannot only affect inter-species relationships but may also have an impact on community structure within the same species, which manifest as hierarchical structures within the same species group [186, 189]. This is evident in a study on rainbow trout, where hierarchical structure could be maintained at relatively low ammonia concentration, with a decline in activity levels manifested as reduced aggression, but the stable structure no longer existed at higher ammonia concentration [189]. Although these sublethal effects mentioned above may not directly lead to death, fish may loss the capacity to cope with or adapt to environmental variations.

4.4.2 | Nitrate

Nitrates (NO_3^-), a common and widespread stressor within various aquatic environments, mainly originate from the aerobic chemoautotrophic bacterial oxidation of ammonia. As the most stable form of inorganic nitrogen, nitrate represents a concern for water quality management within aquaculture systems [196, 197]. In cases where water quality maintenance is inadequate, long-term exposure of fish to nitrate can induce chronic stress on fish [198].

Chronic exposure to high or low concentration of nitrate may contribute to fish vulnerability to hypoxia stress [199], as demonstrated in European grayling (*Thymallus thymallus*) [200] and silver perch (*Bidyanus bidyanus*) [199], showing that fish chronically exposed to varying nitrate concentrations utilized the aquatic surface respiration earlier and increased ventilation rates in environments with progressively decreasing oxygen levels, due to the histopathological changes in the gills induced by nitrates, which limits oxygen uptake [200]. Furthermore, nitrate-induced stress has been implicated in the manifestation of anxiety-like behaviors in fish, characterized by prolonged dwelling near the tank bottom, resulting in more time spent on decision-making behavior and weaker associative learning capabilities [31, 201]. These phenomena were observed in zebrafish exposed to nitrate with a concentration of 606.9 mg/L. Yet, in high-density aquaculture settings, elevated nitrate levels are common. Although these impacts are generally species-specific, it is worth underscoring the need to be vigilant about the potential implications of such increases on fish health and welfare.

Nonetheless, the influence of nitrate on fish behavior may not always be adverse outcomes. An research has indicated that sustained exposure to nitrates below 100 mg/L did not give rise to any abnormalities in swimming behavior of post-smolt Atlantic salmon cultured in replicate freshwater RAS [202], suggesting a species-specific threshold exists beneath which nitrate may not impose detrimental effects. Furthermore, moderate levels of nitrate have been found to bring about some beneficial effects, including increasing the supply of metabolic fuels by promoting the use of less oxygen-demanding energy sources [203], and decreasing the oxygen demand during exercise by enhancing muscle metabolic efficiency [204]. These adaptations can potentially translate into positive behavioral

outcomes, such as increased activity levels and improved performance during exercise. Despite these potential benefits, the consideration surrounding nitrate in aquaculture predominantly centers on its detrimental impacts, rendering the practical application of its positive aspects in aquaculture contexts challenging.

4.4.3 | Nitrite

While nitrite (NO_2^-) levels seldom exceed the tolerance limits of fish in traditional extensive aquaculture systems, high nitrite levels are often encountered in intensive aquaculture system [205]. Nitrite, usually produced in oxygen-deficient locations like bottom muds [205], is much more harmful to aquatic organisms than nitrate and is recognized as one of the most toxic inorganic nitrogen substances [206]. Abundant studies focus on the factors that influence the toxicity of nitrite and its effects on fish physiology, but its impact on fish behavior remains unclear [205, 207].

Studies on Chinese perch (*Siniperca chuatsi*) [208], rainbow trout [209], and goldfish (*Carassius auratus*) [210] indicated that long-term exposure to low nitrite concentrations can reduce fish appetite and affect feeding behavior. One of the reasons is that nitrite exposure can impact the olfactory system and ability to detect food [210], leading to a slow feeding rate and, in some cases, cessation of responses to food [209]. In addition, exposure to nitrite can impair the oxygen uptake capacity of fish as well [205]. The most noticeable behavioral manifestations in aquaculture include gasping at the water surface, with excessive respiration, and frequent gill covers flipping [205, 211], resulting from nitrite converting hemoglobin into methemoglobin, which cannot transport oxygen as hemoglobin does [206]. Consequently, even when the DO content in aquaculture water reaches optimal levels, affected fish may frequently exhibit signs of hypoxia [206]. These physiological effects can significantly affect health and can manifest through behavioral performance [212], such as decreased swimming speed, as observed in striped catfish (*Pangasianodon hypophthalmus*) [213], catla (*Labeo catla*), rohu (*Labeo rohita*), and mrigal (*Cirrhinus mrigala*) [211].

4.5 | Summary

The chemical water quality parameters attract attention of farmers in both intensive and especially extensive outdoor aquaculture due to their multifaceted influences on fish behavior. While the mechanisms by which various parameters influence fish behavior are distinct, ranging from DO affecting metabolic processes and energy supply, to salinity influencing osmoregulatory balance and olfactory perception, and pH affecting olfaction and gustation, and inorganic nitrogen impacting accumulation within the fish body, fish show an inherent ability to adapt to environmental changes through behaviors. Certain chemical water quality factors are perceived by fish, which then force fish to conduct behavioral strategies to maintain their physiological state. In conclusion, this section underscores the critical role of chemical water quality parameters in shaping fish behavior and their adaptive responses.

5 | Chemical Pollutants

Chemical pollutants, such as those from industrial waste and oil spills resulting from human activities, have become increasingly common in aquaculture and can have direct and indirect effects on multiple tissues, ultimately affecting fish behavior. However, unlike other water quality parameters, chemical pollutants have the potential to cause bioenrichment, accumulating within organisms and transferring negative impacts to other organisms along the food chain [214–216], thereby drawing increasing attention from relevant researchers in this area.

5.1 | Microplastics

Microplastics (MPs) are insoluble synthetic solid particles or polymer matrices with a regular or irregular shape that range in size from 1 to 5000 μm [217]. Nowadays, MPs are widely distributed globally and difficult to degrade, and some break down into smaller, harder-to-detect particles known as nanoplastics [218, 219]. Owing to their small size, MPs easily attach to parts of fish such as gills, skin, and be taken in through respiration and digestion [214, 220, 221]. As is reported, microplastic particles have been found in the digestive systems of captive and wild-caught fish in the ocean [222], even in the stomachs of polar cods in the Arctic ecosystem [223]. Once inside the fish body, MPs may spread through the bloodstream to various body areas, leading to stress from oxidation, metabolic problems, weakened immune function and hindered growth [219, 224, 225]. More concerning, MPs in fish bodies can be transferred through the food chain from low to high trophic level organisms [226, 227], causing negative impacts and posing serious health risks and ecological security issues (Figure 6). The wide range of these impacts has made it a vital topic in the field of aquaculture [228, 229].

5.1.1 | Feeding and MPs Intake

The main route for MPs uptake in fish involves inadvertent ingestion, either by mistaking MPs as food or through incidental consumption during feeding or respiration [220, 227]. Studies on zebrafish and common goby (*Pomatoschistus microps*) [230, 231] reveal that the presence of MPs alongside food reduces fish discernment, leading to increased MPs consumption, especially as food abundance rises. Feeding habits also influence MPs intake; fish that swallow whole prey consume more MPs compared with those fed by filter or suction feeders [232], and piscivorous fish are more prone to MPs ingestion than those feeding on crustaceans or gelatinous zooplankton [233]. Furthermore, personality of individual fish affects MPs uptake as well, as exemplified by bolder zebrafish consuming more MPs than their shyer counterparts [234]. However, some fish possess mechanisms to minimize the ingestion of microplastics. Species relying on chemosensory cues for feeding can better discriminate against nonedible particles [220] and some fish, like hybrid groupers, utilize both visual and taste senses to distinguish MPs from edible items [235], although fish that specialize in visually hunting small prey-like plankton may confuse MPs for food, especially under starvation conditions [220]. Notably, certain fish exhibit reflexive expulsion

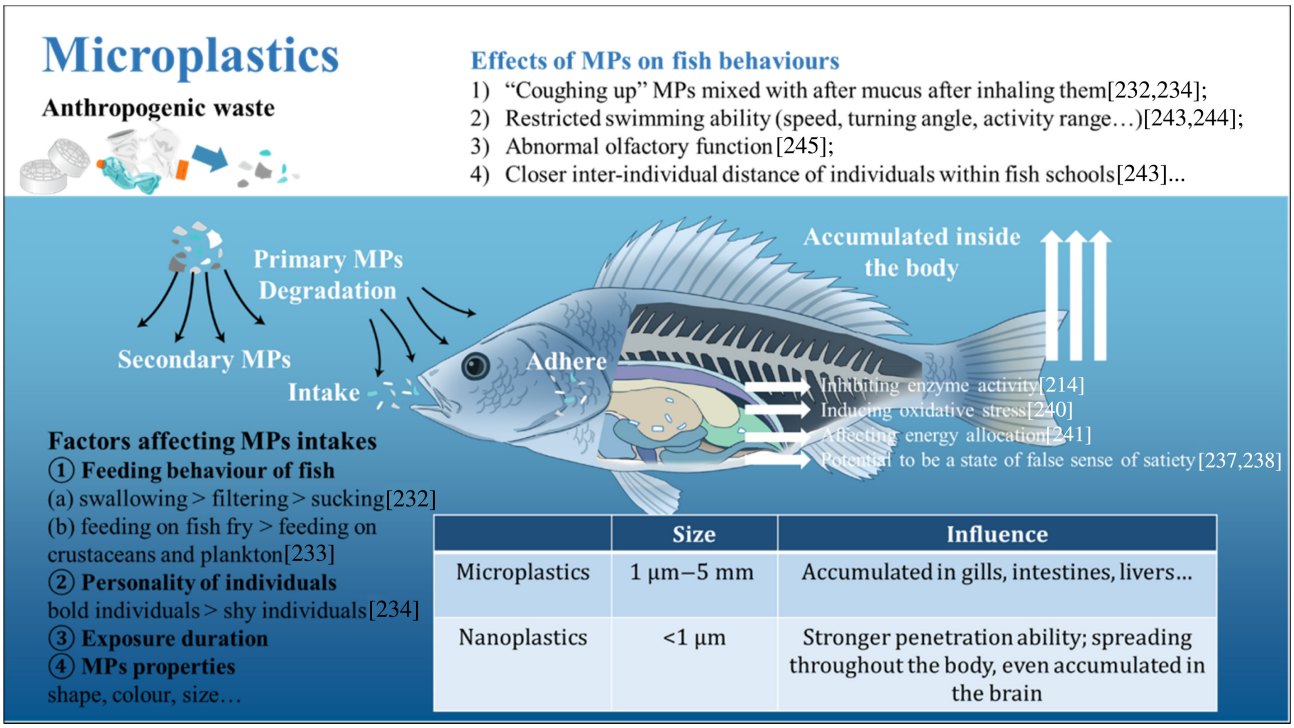

FIGURE 6 | Interaction between MPs and fish.

of ingested MPs, as seen in largemouth bass, yellow catfish (*Pelteobagrus fulvidraco*), goldfish and zebrafish, which can help reduce MPs accumulation within their bodies by spontaneously coughing up MPs mixed with mucus [232, 234], although this rejection mechanism may also damaging oral tissue and disrupting normal feeding [236].

The accumulation of MPs in fish digestive systems can obstruct feeding and intestinal transit, leading to malnutrition and starvation or a state of a false sense of satiety which hinders growth and development [237, 238]. This accumulation impacts appetite, feeding behaviors, and energy allocation across various physiological functions [239]. The severity of these effects correlates with MP size, with smaller MPs having greater impacts. Micron-sized plastics can be ingested and expelled [227]. However, smaller MPs, or even nanoplastics, can accumulate in the organs like gills, liver and intestines [214], causing various damage, inducing inhibiting enzyme activity, oxidative stress metabolic changes, and affecting energy distribution [214, 240, 241], severely compromising multiple physiological functions and leading to alterations in fish behavior to varying degrees as following.

5.1.2 | MPs Intake-Induced Behavioral Changes

MPs accumulation in the digestive tract stimulates the gut and impacts digestion, leading to reduced food intake and altered feeding behavior [242]. This results in energy deficits that constrain swimming speed, turning angle, and range of movement [243, 244], notably diminishing foraging efficiency, as observed in species like black rockfish (*Sebastes schlegelii*) [242]. Furthermore, MPs exposure impairs olfactory function in some fish, undermining their ability to detect environmental cues which are vital for prey localization and predator avoidance [245]. In response to MPs contamination, fish like black rockfish aggregate more closely to form compact schools, manifested as decreased IID [243], which may serves as a defensive strategy against predators and to facilitate essential tasks like foraging. These observations collectively highlight the adverse influence of MPs pollution on fish swimming, predator–prey interactions and social structures [246], thereby substantially reducing their adaptability within both natural and aquaculture ecosystems.

The severity of MPs impacts on fish behavior is related to multiple factors: MPs concentration, shape, size, and exposure duration [221, 247, 248]. Higher MPs concentrations provoke greater organ stimulation, such as in the eyes and gills [247], and increase the likelihood of accidental ingestion; irregularly shaped MPs have a more pronounced effect than spherical ones, causing a more significant decline in swimming ability, with shorter total movement and lower maximum swimming speed observed in sheepshead minnow (*Cyprinodon variegatus*) [247]. Smaller MPs, particularly nanoplastics, pose heightened risks due to their larger specific surface area (the ratio of surface area to volume) and enhanced penetration capabilities, facilitating cellular absorption and interaction with organisms [245], leading to potentially more severe outcomes, as demonstrated in a study, in which goldfish larvae exposed to 1000 μg/L nanoplastics for 3 days exhibited markedly reduced swimming speeds, with further decreases noted after 1 week at both 100 and 1000 μg/L exposure levels [214].

In general, MPs are widely distributed and capable of inducing multiple negative impacts on fish. These negative effects mainly stem from the ingestion of MPs by fish, which disrupts physiological activities at the tissue and organ levels, leading to oxidative stress or affecting energy distribution and other physiological

functions, thereby restricting certain behavioral patterns like swimming. Fish subjected to MPs stress experience decreased adaptability to their environment, highlighting the urgent need to address this issue in aquaculture.

5.2 | Crude Oil

The development of seabed oil exploration and shipping has led to the entry of crude oil into marine and freshwater aquaculture environment [249, 250]. After the Deepwater Horizon incident, a large number of studies on the impact of crude oil were conducted [251–253]. They showed that exposure to crude oil can have a destructive impact on fish because of impaired organ function, consequently leading to behavioral changes. It is worth noting that crude oil contains complex mixtures of components, and most current researches on the effects of crude oil on fish behavior focuses primarily on the impacts of polycyclic aromatic hydrocarbons (PAHs).

5.2.1 | Swimming

Impairments in fish swimming ability have been observed due to exposure to environments contaminated with crude oil, mainly as a result of cardiovascular and muscular dysfunctions [254–258]. Red drum and cobia (*Rachycentron canadum*) exposed to PAHs showed reductions in stroke volume and cardiac output, accompanied by increased heart rate [256, 257]. Mahi-mahi (*Coryphaena hippurus*) embryos and juveniles exposed to PAHs for 24 h suffered severe cardiovascular dysfunction [258], highlighting the consistent detrimental impact across developmental stages. These findings collectively illustrate the profound disruption of cardiovascular health in fish exposed to crude oil, with implications for their overall swimming endurance and survival [255, 256]. Specifically, mahi-mahi exposed to a mix of PAHs at 8.4 μg/L displayed a 14% drop in critical swimming speed, a 10% decrease in optimal swimming speed, a 20% reduction in maximum metabolic rate, and a 29% decline in aerobic scope [251]. Atlantic haddock (*Melanogrammus aeglefinus*) larvae exposed to crude oil at 10 and 80 μg/L for 8 days experienced a 30%–40% decrease in swimming speed [259]. European sea bass larvae exposed to weathered crude oil and dispersant at 80 mg/L for 1 month showed reduced hypoxia tolerance and swimming capacity [260]. Moreover, crude oil exposure also alters calcium cycling in skeletal muscles [261, 262] and decreases muscle mitochondrial function [254, 255], constraining swimming ability and impacting social competition [263].

Noted that, fish exposed to oil pollution often experience a delayed recovery of their cardiorespiratory functions, with sublethal effects potentially lingering [264]. This means that if exposed to oil in early life, especially during the embryonic and larval stages, negative effects on cardiac function may persist as fish as they grow. Nearly a year after embryonic oil exposure, adult zebrafish showed abnormal changes in heart shape during growth and significantly reduced swimming capacity [265]. A similar phenomenon was observed in mahi-mahi [264], as exposure of embryos and larvae to 1.2 ± 0.6 μg/L ΣPAHs for 48 h and then developing them to juveniles or directly exposure juveniles to 30 ± 7 μg/L ΣPAHs for 24 h led to significant 37% and 22% decreases in the critical swimming speed, respectively. And the suppression of swimming capacity can impair a wide range of normal critical exercises, such as schooling.

5.2.2 | Schooling

It has been documented that exposure to oil can disrupt the schooling behavior of fish: the cohesion and performance of Atlantic croaker (*Micropogonias undulatus*) schools were significantly impaired following acute oil exposure at a concentration of 32.9 ± 5.9 μg/L ΣPAHs, as indicated by an increase in inter-individual distance and decrease in movement speed [266]. Similarly, zebrafish schools exposed to 100 μM PAH benzo[a]pyrene showed increased IID (10.0 ± 0.3 cm) compared with control group (7.6 ± 0.4 cm), and decreased total movement distance (5204 ± 120 cm) compared with control group (5898 ± 226 cm) [267]. Furthermore, it was found that even if only one fish suffers from crude oil exposure, other fish in the school will also be affected, thus compromising the cohesion of the entire school [266].

5.2.3 | Exploratory and Anxiety-Like Behavior

A syndrome-like condition can be resulted from exposure to crude oil [268], which may lead to a wide range of behavioral changes, such as abnormal exploratory and anxiety-like behaviors and avoidance responses. Active and exploratory behavior represents boldness, which often emphasizes rewards rather than risks; in contrast, spending more time swimming in situ, staying closer to the habitat, and exhibiting low activity represent anxiety-like behavior, which emphasizes safety rather than potential rewards [269]. In a series of studies, researchers observed that zebrafish exhibited decreased anxiety-like behavior and engaged in more exploratory behavior after exposure to crude oil or its components, suggesting an increase in boldness. For example, zebrafish preferred to stay in the center of the arena after exposure to benzo[a]pyrene [267]. However, exposure to crude oil does not always promote exploratory behavior and inhibit anxiety-like behaviors. Some studies have shown that exposure to different components of crude oil mixtures can increase anxiety-like behavior in fish and decrease exploratory behavior. For example, zebrafish exposed to two PAH mixtures (one from pyrolysis and one from light crude oil) [270] and the water-soluble fraction (WSF) of crude oil [271] showed increased anxiety-like behaviors. In addition, Trinidadian guppies from crude oil-contaminated sites had lower exploratory behavior than those from uncontaminated sites, indicating that exposure to oil suppressed exploratory behavior [272]. These experimental differences underscore the complexity and species-specific nature of crude oil impacts.

5.2.4 | Avoidance Response

Similar to responses elicited by other environmental stressors, fish may exhibit behavioral changes, such as an avoidance response, to escape from crude-oil-polluted environments [273]. Avoidance responses help reduce the time fish come into contact with oil-polluted water [274], thus alleviating stress. Avoidance responses are dependent on the species, oil composition, and oil concentration. Some fish initiate avoidance responses when

encountering even very low concentrations of environmental oil pollutants, such as the European sea bass, which shows significant avoidance responses to 8.54 μg/L ΣPAH [274]. Caspian roach (*Rutilus caspicus*) can also detect and avoid the WSF of crude oil at a concentration of 2 mg/L [275]. However, not all fish can detect or avoid oil at extremely low concentrations. Gulf killifish (*Fundulus grandis*), sailfin molly (*Poecilia latipinna*), and sheepshead minnow, all estuarine fish, only showed significant avoidance responses to oil pollution at medium (20 mg/L) to high (40 mg/L) concentrations [276]. As crude oil exposure can impair vision, olfaction [277, 278], it may be more difficult for fish to avoid oil pollution following exposure. For instance, mahi-mahi, which can distinguish oil based on their olfactory senses, pre-exposed to 14.5 μg/L ΣPAH for 24 h were unable to avoid oil-contaminated areas, while unexposed fish were able to avoid it [252].

5.3 | Summary

The ubiquitous presence of chemical pollutants is indisputable, permeating various systems of aquaculture, with microplastics and crude oil contaminants no longer confined to marine culture alone [219, 238, 279, 280]. Studies and reports have highlighted the presence of microplastics even in intensive RASs, signifying their omnipresence across aquatic environments [280]. The impact of these pollutants on fish is profound, primarily stemming from ingestion or accidental consumption, leading to physiological disruptions that manifest in abnormal behavior. These include disturbances to energy regulation, feeding, swimming, schooling, and the induction of exploratory and anxiety-like behaviors in individuals [221, 225, 267, 268]. Against this backdrop of widespread chemical pollution, examining its impact on fish behavior serves as a cautionary note. The concern extends beyond microplastics and crude oil, as numerous other chemical pollutants similarly imperil aquaculture productivity and the welfare of fish populations. Analysis here aims to underscore the urgency for vigilance and mitigation strategies in safeguarding both the sustainability of aquaculture production and the welfare of aquatic life.

6 | Conclusions

This review summarizes the profound influence of water parameters—temperature, turbidity, DO, salinity, pH, inorganic nitrogen, microplastics, and crude oil pollution—on fish behaviors, encompassing swimming, schooling, feeding, predation and anti-predation, avoidance responses, exploratory behavior, aggression, anxiety-like behavior, and courtship (detailed in Supporting Information S1). While not all behaviors are reviewed within each respective water parameter section and not all the species referred in this review belongs to aquaculture species, the overarching intent is to underscore the profound and pervasive impact of these water quality parameters on fish behavior, thereby informing future research and facilitating advancements in aquaculture management practices.

Aquaculture systems require tailored water quality management. Outdoor extensive systems, due to their susceptibility to disturbance and environmental complexity, witness a wider array of behavior-modulating effects, necessitating intricate assessments of diverse water quality parameters and behaviors tailored to variable environments. In contrast, intensive indoor systems like RAS, with greater water quality management, the dynamics of these behaviors assume critical importance. Given the link between water quality and fish behavior, understanding these patterns is crucial for sustainable aquaculture management and fish welfare. While fish behavior holds a wealth of information regarding water quality and fish welfare in aquaculture systems, the practical implementation of behavior monitoring for enhanced production and welfare assurance currently faces notable challenges and incurs substantial costs. Nonetheless, propelled by technological advancements and the global emphasis on fish welfare and sustainability, the utilization of fish behavior as a tool for assessing water quality and estimating fish welfare in aquaculture is emerging as an increasingly prominent trend.

Author Contributions

Kaisheng Zhang: writing – original draft, writing – review and editing, data curation, conceptualization. **Zhangying Ye:** writing – original draft, data curation, project administration, supervision. **Ming Qi:** data curation, writing – review and editing. **Wenlong Cai:** writing – review and editing, data curation. **João L. Saraiva:** writing – review and editing. **Yanci Wen:** writing – original draft, data curation. **Gang Liu:** writing – review and editing. **Ze Zhu:** data curation. **Songming Zhu:** writing – review and editing, data curation. **Jian Zhao:** conceptualization, writing – review and editing, supervision, project administration.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.