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The Mechanism of Chemoreception in Fish under Low pH Condition

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Abstract

Studies in fresh water and marine ecosystem both have shown significant impacts that anthropogenic ocean acidification has on olfactory abilities of fish and other invertebrates' organisms, leading to impaired behavioral responses. This has led to far reaching consequences on population dynamics and community structure. In acidified waters, molecular change to chemical cues along with reduced olfactory sensitivity appears to be the primary cause of olfactory-mediated behavioral impairments. Many aquatic organisms, olfactory-mediated behavior is critical to maintenance of numerus fitness-enhancing activities such as homing, mate choice, predator avoidance, foraging, kin recognition and food odor source. Changes in olfactory-mediated behavior caused by elevated CO_2 in ocean, lakes or rivers could affect not only fish population but much more recruitment of fish as well. Recent research work has shown how fish behaviors have been potentially affected by acidification as carbon dioxide levels continued dissolving in ocean waters. In this paper I have tried to unpack potential consequences that befall on fish as chemosensory cells are impacted by acidified waters.

Keywords: Chemoreceptors • Chemoreception • Fish • Low pH • Carbon dioxide (CO_2) • Aluminum • Olfactory-mediated response

Introduction

Despite the recognition of the consequences of ocean acidification as a result of anthropogenic emission of carbon dioxide in the atmosphere, very little is known about the ability of the fish to respond efficiently to this acidification problem. The question to pose could be, are the acid-base regulatory mechanisms competent to respond to this acidic environment due to carbon dioxide emissions? What about the larvae (small fish) in their early stages of development could be particularly sensitive to many environmental factors that come into play in water? Their organs and physiological processes are still very tender and growing. The intensification of human activities globally has led to the rise in the atmospheric concentration of carbon dioxide and other oxides too like Nitrogen oxides and sulfur dioxides. This time around the concentration levels are in excess of 400 ppm, a level that has not been reached in the past 800, 000 years [1].

Literature Review

According to the Intergovernmental panel on climate change in 2014, the rate of CO_2 emissions then was projected to reach between 750 and 1000 ppm by the end of the twenty first century [2]. An aggressive scenario was projected that the emissions of carbon dioxide would reach 1500 ppm [3]. The corresponding increase in CO_2 dissolved in the ocean may cause a reduction in the pH of 0.3-0.4 units compared to current-day levels [3]. This deviation from the current day pH levels could take place at a faster rate than has been seen over the past few centuries, potentially limiting the capabilities of populations to adapt to such a rapid change [4]. The carbon dioxide that is emitted gets absorbed by the water in the oceans reacts with water to form carbonic acid which dissociates into bicarbonate ions (HCO_3^-) and Hydrogen ions (H^+). When the amount of hydrogen ions (H^+) increases in water, the water pH reduces and the term for that is ocean acidification. It is the reduced pH in water that directly affects the fish's physiology, leading to disruptions in signals [5,6], sensory processing [7], and metabolic function [8,9]. Sometimes indirect consequences can arise too, for example one species is injured to a degree, may lead to other trophic levels of other species being affected [10,11]. Species interactions are driven by physiological processes and the behaviors they result in. Further the strength of these interactions in turn drive community structure and function under chemical contamination [12-14]. Despite the fact that the low pH may affect the physiological functions of the fish, like respiratory system [15,16], circulatory system, central nervous system [17], metabolism, growth [18], and behavior, much of the effects seem to result from the acidification of the body fluids. Fish are bilaterally symmetric and possess an olfactory organ (nose) in the anterior portion of each side of the head. Water enters the nose and circulates over the nerve cells, where specialized receptors (Figure 1) detect specific chemicals dissolved in the water and transmit signals to the forebrain.

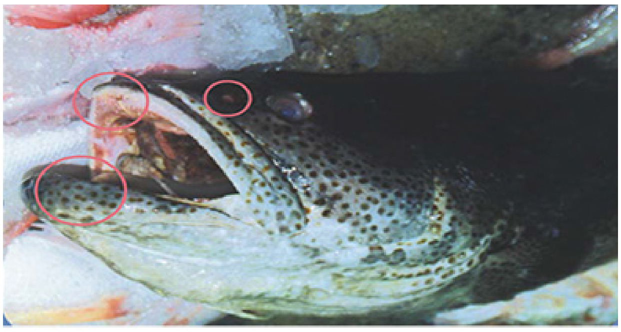

Figure 1. Fish "smell" by detecting wáter-soluble chemicals that enter their nostrils. They "taste" using taste buds on the lips, oral cavity and sometimes on their external body surface.

For taste, water circulates over the taste buds on the lips and within the oral cavity of fish. In addition, fish like catfish have taste buds that cover their entire external body surface. Due to this extreme specialization of the taste system, catfish have been termed "swimming tongues." This broad distribution of taste buds appears to function as a large antenna, enabling the fish to simultaneously contrast the concentration of the chemicals contacting its body surface, thus giving directional cues to the chemical (Figure 2).

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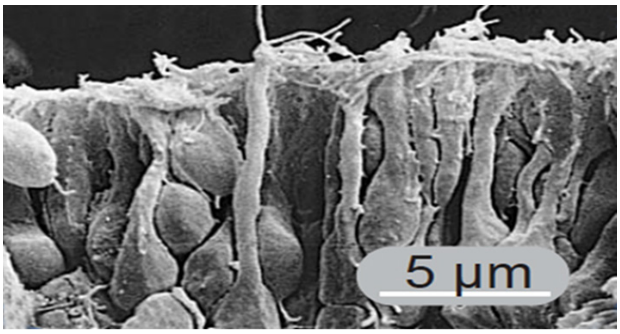

Figure 2. This scanning micrograph shows the olfactory epithelium of an adult zebrafish. Some of the receptor cells have long dendrites, while round receptor cells have short dendrites.

The reception of chemical signals in the aquatic environment, the subsequent processing and integration of the information in the fish's central nervous system, and the physiological and behavioral changes that subsequently occur together constitute a complex system that is vulnerable to the disruptive effects of toxicants at different levels of biological organization. The peripheral olfactory system is the more likely to be affected than other components of the nervous system because it is in direct contact with surrounding environment. The peripheral system is particularly vulnerable to environmental changes ranging from low pH to neurotoxic xenobiotics. Changes that can be accrued on the olfactory function could be

1. Anosmia, the inability of the fish to smell.

2. Hyposmia, reduced ability of the fish to smell.

3. Dysosmia which is the incorrect processing of the information by the fish.

Chemosensory receptors in fish allow organisms to perceive their environment. Perception of chemical, auditory and visual cues play a vital role in the daily life and survival of fishes by influencing homing [19], settlement [20], predator detection and evasion [21], foraging [22], conspecific social interactions [23] and mating [24]. Therefore, chemosensory perception (the ability to detect chemical cues) is the primary sense used by most fishes. Recognizing chemical cues is initiated by the binding of a chemical molecule to a receptor protein on a chemoreceptor neuron. This binding initiates a G protein based signaling cascade that transmits a signal to the central nervous system [25]. The morphology of chemoreception organs vary greatly in different species, but fish and cephalopods use specialized olfactory organs exposed to chemical cues through nasal cavities or olfactory pits [26,27]. To emphasize the point made earlier, chemosensory perception and communication are very critical in aquatic environments and relevant at all spatial scales [28]. The ability to accurately detect and respond to environmental chemical cues is critical for homing [29,30] settlement [31], foraging [21], and predator evasion. Dixson et. al. (2010) stated that settlement-stage of orange clownfish' (*Amphiprion percula*) larvae were attracted to the smell of a predator and could not distinguish between a predator and a non-predator odor cues [32,33], following exposure to elevated levels of pCO_2 (low pH) for a short period of time (11 days after hatching out), posing a danger to their survival [34].

The olfactory system in fish consists of three main features; source, signal and receiver. In fish the source or receiver can receive signals imparting directional, conditional, tactic and genetic information. Directional information may come from stationary or moving sources (Figure 3). According to K.B. Tierney et al. [33]. "The odorants are perceived by sensory neurons; the input is then processed and integrated with other sources, which can lead to physiological and /or behavioral response. Physiological and behavioral response can feedback on each other and be integrated into further processing [35,36]." Contaminants in this case acidified water can (a). Act as odorant or modify odorant perception and (b). Act on nervous system through other pathways and (c). Alter other physiological responses, all of which potentially translate into altered behavior. This altered behavior, for example if the altered behavior was failure to catch the odor of predators, can lead to the fish to be preyed up.

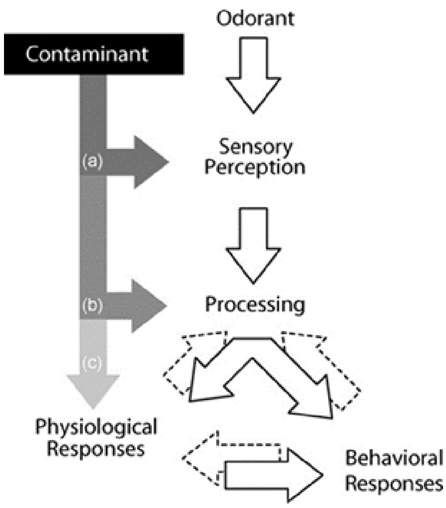

Figure 3. Odorants are perceived by sensory neurons, the input is then processed and integrated with other sources, which can lead to physiological and/or behavioral responses. Physiological and behavioral responses can feed back on each other, and be integrated into further processing. Contaminants can (a), act as odorants or modify odorant perception, and/or (b), act on the nervous system through other pathways, and/or (c), alter other physiologic responses, all of which potentially translate into altered behavior.

Sensory systems are involved in the feeding process in fish and involve, searching, detection, capture and ingestion of the food. Visual cues can in some cases be limited in aquatic environments as a result of turbidity from suspended sediments, low light conditions, and habitat complexity. In additional to all this the fact that water is a good solvent and the high persistence of chemical cues in water, render the sense of olfaction very useful in aquatic environments [37]. Therefore, cues other than visual ones, such as olfactory cues could increase in importance when visibility deteriorates. The value of olfactory cues depends however, on environmental factors such as water turbulence [38] and the pH value of the water [39].

Results and Discussion

Impact of acidified water on the chemosensory cells in fish

The sense of olfaction brings important environmental information to the fish, making activities such as locating food, mating, homing, discriminating kin, mate choice and avoiding predators be easily accomplished. But all these behaviors can be impaired or completely lost due to continuous exposure to toxic acidified ocean or sea waters. Acidified water has shown to negatively impact the olfactory cells and alarm cue responses of fish in two ways [40-45] (a). One of the chemical components of the alarm pheromone -hypoxan-thine-3(N)-oxide (H_3NO), the structure of this compound is altered at pH 6 becomes undetectable [38]. (b) The affinity or sensitivity of the olfactory receptors may be reduced at low pH as shown by the research done with fat head minnows. The fat head minnows showed a reduced feeding response to amino acids at pH of 6 [42-47]. Evidence is there including multiple sensory system impairment, cognitive alterations involving chemoreceptors, lateralization [48], learning and the observation that fish in acidified water received chemical cues but responded inappropriately, suggests a disruption in processing at the brain or neural level. Therefore, there must be a good research done to help us towards understanding the underlying mechanisms and functional significance of contaminant-mediated changes in the fish olfaction.

Acidified waters can impact response to alarm and predator cues, these behaviors have greater impacts on the fish's survival [49-51]. The physiological work on this phenomenon suggests that this behavioral response is due to changes in acid-base ion transport that work to prevent acidosis with downstream impacts on gama-aminobutyric acid (GABA) function in the brain [52,53]. Transgenerational experiments have been done in spiny damselfish (acanthochromis polyacanthus), to analyze into its parts and describe their syntactic roles and how plasticity in this behavioral response may be propagated across generations and how ocean acidification impacts the brain functions on a transcriptomic level. Individual fish that are sensitive or tolerant to ocean acidification, measured by their behavioral responses, were crossed with fish of similar phenotypes, and the progeny was reared at either control or high pCO_2 conditions [54]. Gene expression in the brains of these fish suggest that offspring from tolerant parents have flexibility in their ion regulation and can shift their physiology to avoid maladaptive response to acidic environment (high CO_2). A follow up study also finds differential expression of genes associated with behaviors, ion regulation and GABA pathways when fish were exposed to high pCO_2 acutely and throughout development, whereas these signatures returned to baseline levels when parents were previously exposed to high pCO_2 [55]. Differential gene expression signals of transgenerational plasticity in response to CO_2 varied between different parental genotypes, suggesting individual fish have different tolerances and sensitivities to how their brains regulate ion homeostasis, prevent acidosis and regulate GABA pathways [56]. The European sea bass too exhibited impaired sensory function under high pCO_2 conditions which was associated with differential expression of glutamate sensory pathways and genes associated with synaptic plasticity [57]. These findings strongly suggest that fish lose sensory acuity in their environment under high pCO_2 (low pH) conditions, an outcome that would have strong implications on fitness.

The hydrogen ion (H^+) in water can react with aluminum oxide or bauxite to release aluminum ions (Al^{3+}). The ionic form is least soluble at pH of between 5.7 and 6.2, above and below this range, aluminum tends to be in solution [58]. Aluminum in solution form has the most severe adverse effects on fish's life. Research has shown that a combination of pH less than 5.5 and dissolved aluminum concentration greater than 0.5 mg/L generally eliminates all fish and many macro– invertebrates. The concentration of aluminum is highest in acidified lakes, oceans and rivers and in these water bodies the number of fish has decreased. Aluminum affects the ion exchange across the gill membrane in fish in much the same way as hydrogen ion (H^+), resulting in a loss of body ions [53,59]. At a pH of 5-6, the presence of monomeric aluminum hydroxides and ongoing aluminum polymerization disturb normal respiration. The polymerization process of aluminum increases mucus secretion in fish which leads to clogging of the gill lamella, which in turn prevents effective respiration and gives rise to hypoxia [58,59]. These short-term effects may be magnified in heavily acidified environments (of pH<5.0 under which there is metallic ions e.g. of Al^{3+} and Cu) further interfering with olfactory epithelial cells leading to permanently chemosensory impairments [54,55].

Acid-base balance (compensation) in fish

Just like in other vertebrates' fish must maintain a constant intra and extracellular environment of the pH. Acidic environments (low pH) in which the fish live is responsible for fish death. The fish suffocates due to coagulation of mucus on the gills. This lowers the blood oxygen carrying capacity as blood pH is reduced. When arterial blood pH is low and there is a slow gradual increase in ventilation due to gills not functioning well, the fish suffocates and dies. Although the acid-base balance in fish is similar to that in animals, in animals the acid–base balance regulators deal with acids produced internally within the body and not in their environment as is the case with fish. When the rate of alveolar ventilation in animals fails to keep pace with the body's rate of carbon dioxide production, carbon dioxide accumulates in the extracellular fluid (ECF) and lowers the pH. This is respiratory acidosis; the kidney may take over by secreting H^+ in the filtrate until the acid-base balance is achieved. Since ventilation in fish is connected to the demand of obtaining oxygen from the gills of low oxygen content, the ability to make use of respiratory compensation of acid-base disturbance is insufficient [56]. Since the respiratory compensation is of limited value to the fish in acidic environment, the linchpin of acid-base regulation is the direct transfer of acid-base components between the acidic environment and the animal is primarily through the gills. The intake of the appropriate counter ion (Na^+ and Cl^-) from the environment is associated with the transfer of acid-base ions into the water. These acid-base transfers have a direct impact on the ion-regulatory requirements of the fish. The uptake of Na^+ or Cl^- from the environment by the fish in exchange for internal H^+ or HCO_3^- allows the fish not only make the acid-base adjustments but also to maintain ion and osmoregulatory homeostasis by obtaining NaCl from the water in the environment. Net acid-base transfers have been noted in a variety of research work that has demonstrated a remarkable ability of fishes to maintain internal pH homeostasis when faced with a range of internal and external challenges. The gills, intestine [57,58] and kidneys [59] have all been shown to be involved in acid-base transfers under some conditions, but the brachial epithelium is generally thought to account for the majority of the acid-base balance in fish. The extent to which the acids are removed from the gills in contact with external acids when the gills themselves are clogged with mucus is not very clear.

Conclusion

Therefore, the acid-base regulatory mechanism in fish may not adequate deal with the increasing ocean acidification until evolutionally changes take place to acid-base regulatory mechanisms which may be years in the future, mean time the fish will keep on dying. The low pH always leads to hypoxia and volume of oxygen in the blood falls. The reductions in both available blood oxygen capacity and gill oxygen transfer to other organs of the body, resulting in fish experiencing hypoxia and consequently dying.

The frightening conclusion is that if all these olfactory sensory cells impairments and acid-base balance can be observed in short-term experiments that are being done, what will the results be like for the fish to live in acidified environments forever? The fish have no other environment to live in except in water and therefore, the purity of water in rivers, seas, lakes and oceans is critical to their survival.

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