

Chemosensory-driven behavior in fishes

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Key points

- Fishes live in water; the chemicals detected by chemosensory systems are often different from terrestrial animals.
- Chemosensory systems of fishes include the olfactory and gustatory systems plus single chemosensory cells and CO₂ and O₂ detectors in the gills.
- Chemosensory systems are important in diverse behaviors including food-search, mate-choice, the alarm response, and migration.
- Kairomones and allomones are detected by both the olfactory and gustatory systems, and are involved in prey-search and identification, and predator avoidance.
- Pheromones are detected exclusively by the olfactory system; these are involved mainly in reproductive behavior and the alarm response, but—in some species—migration and habitat choice.
- Chemical cues, including pheromones, are often complex mixtures of different chemicals, the identities of which are only rarely fully understood.

Glossary

Allomone A semiochemical released by an individual of one species that affects the behavior and/or physiology of another species to the benefit of the originator but not the receiver

Kairomone A semiochemical released by an individual of one species that affects the behavior and/or physiology of another species to the benefit of the receiver but not the originator

Odorant A chemical detected by the olfactory system (the chemosensory system associated with cranial nerve I of vertebrates). A characteristic “odor” usually consists of a complex mixture of many different odorants. For terrestrial animals, odorants are necessarily both water-soluble and volatile; however, for aquatic organisms, such as fishes, an odorant only needs to be water-soluble

Pheromone A semiochemical released by an individual of one species that affects the behavior and/or physiology of members of the same species, conferring benefit to both sender and receiver. This is innate; it requires neither memory nor learning

Semiochemical A general term for a chemical, or mixture of different chemicals, released by one organism that affects the behavior and/or physiology of (an)other organism(s)

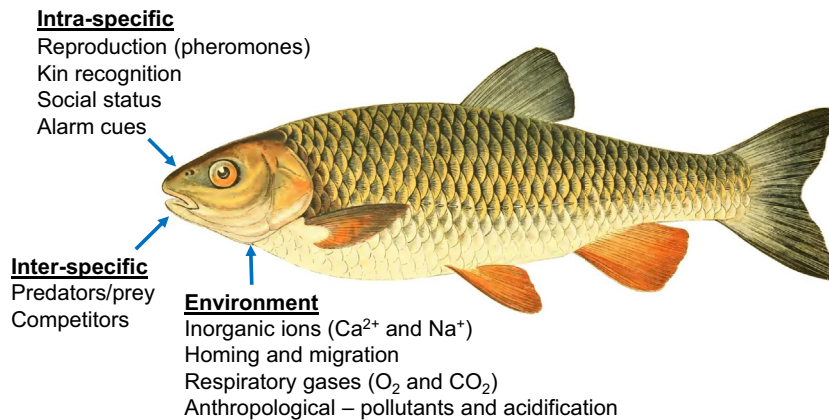
Tastant A chemical that is detected by the sensory cells of a tastebud. A tastant is necessarily water-soluble but does not need to be volatile; in fishes, there is much overlap between odorants and tastants

Abstract

Like most animals, but unlike humans, the chemosensory systems of fishes are vital for many important behaviors, such as food-search, predator avoidance and reproduction. However, as fishes live in water, the chemicals that they detect often differ from terrestrial animals, and many remain unidentified. In fishes, olfaction and gustation are more anatomically and functionally separate than in mammals, although still overlapping, and fishes also have single chemosensory cells and CO₂ and O₂ detectors in the gills. Given the diversity of fishes, and their life-histories and habitats, it is difficult to generalize about the role of chemosensory systems in their behavior. Nevertheless, this article will attempt to do so.

Teaching slide

- Fishes use olfaction and taste to detect chemicals in their environment.
- These chemicals can be from conspecifics (intra-specific), hetero-specifics (inter-specific) or the environment itself.



P. C. Hubbard. Chemosensory-driven behavior in fishes.

Introduction

As primarily audio-visual animals, us humans often under-estimate the importance of chemosensory systems, especially olfaction, to other animals, even to ourselves. These systems play a number of vital roles in the lives of most animals, including fishes. However, as aquatic organisms, the chemicals detected by the chemosensory systems of fishes need only to be water-soluble, rather than both water-soluble and volatile as in terrestrial animals. This means that odorants and tastants in fishes are often different types of chemicals from those of terrestrial vertebrates. Amino acids are one such example of important odorants for fishes (Hara, 1994; Kasumyan, 2004), that are undetected by the olfactory system of terrestrial vertebrates (as they are non-volatile); amino acids play many and varied roles in chemosensory driven behavior in fishes. Nevertheless, it is important to stress that characteristic odors—aquatic and terrestrial alike—are usually complex mixtures of many different odorants, the identities of which are not always known.

Fishes comprise the largest and most diverse class of vertebrates; as such, the roles of chemosensory systems in behavior are as many and varied as the life-histories and habitats of the fishes themselves. The most obvious is the role of olfaction and gustation in food-search and feeding behavior, but other roles include intra-specific chemical communication (pheromones), identification and avoidance of predators (kairomones), and migration and homing. This article will illustrate the range of chemosensory-driven behaviors in fishes with some well-studied examples.

Feeding behavior

In an environment that can be dark and/or turbid, fishes may rely heavily on olfaction to find and identify food. However, the odorants involved, and the exact roles of olfaction and gustation in feeding, depend on the types of food and means of capture involved; that is, feeding behavior is highly species-specific, and the roles of chemosensory systems in driving this behavior are also species-specific. An active piscivorous predator, such as tuna, will use olfaction for different purposes and at different stages of the feeding process from those of a bottom-feeder, such as carp, searching for invertebrate prey living within the substrate. As fish grow and/or migrate to different environments, their food preferences often change. Thus, the roles of chemosensory systems in feeding may also

depend on life-stage. Furthermore, fishes rarely rely solely on olfaction or gustation for feeding behavior; other sensory systems such as vision, hearing, touch and—in elasmobranchs—electroreception are also important. Again, the exact roles of these other sensory systems will depend on species and context. In contrast to olfaction, which is also involved in many other types of chemosensory-driven behaviors, the gustatory system is involved exclusively in feeding.

A detailed description of the physiology and morphology of the olfactory and gustatory systems of fishes is given elsewhere in this Encyclopedia. Here, it is only necessary to add that, in contrast to terrestrial vertebrates, the olfactory and gustatory systems are both anatomically and functionally more distinct. The olfactory system is anatomically separate from the respiratory system, and the gustatory system may also include external structures, such as barbels (for example catfishes), and tastebuds may be present on the lips and gills as well as inside the buccal cavity (mouth).

Nevertheless, there may be significant overlap both in the odors/tastants detected (amino acids are a good example) and in the modulation of feeding behavior by the two systems. Although there is surprising similarity in the olfactory sensitivity to amino acids among diverse fish species with widely different habitats and diets, there is more variability in the gustatory system; fish tastebuds seem to be more finely tuned to specific amino acids than the olfactory system. L-Proline and betaine, especially in marine fishes, are examples of tastants not well detected by the olfactory system. The main phases of feeding behavior in fishes are: (i) an initial arousal when the fish first detects a potential food item, (ii) an exploratory or search phase for the source of the stimulus, and (iii) a consummatory phase in which the fish decides to ingest (or not) the item. Whereas olfaction and gustation may be involved in the first two phases (along with other sensory systems), the final consummatory phase is driven exclusively by the gustatory system. Identification of the odors/tastants involved in all three phases has attracted much research interest, for obvious practical reasons in the fishing (both recreational and commercial) and aquaculture industries (for example, see: [Velez et al., 2011](#)).

Amino acids are ubiquitous odors for fishes, and can stimulate feeding behavior ([Braubach et al., 2012](#); [Hara, 2006](#)), but other small molecular-weight compounds such as nucleotides and polyamines are also detected ([Hara, 1994](#); [Kasumyan, 2004](#)). For example, L-cysteine, one of the most potent amino acids for many fishes, can evoke arousal in the same way as food extracts ([Hara, 2006](#)). The type of behavior evoked depends on the species and their normal mode of feeding; this can range from surfacing and jumping in salmonids that often feed on insects on the water surface, biting and snapping, to “pecking” gravel into the mouth in goldfish, a bottom-feeder ([Fig. 1](#)). Also, the effectiveness of amino acids other than L-cysteine to evoke feeding behavior differs among species. However, much of this work has been carried out on laboratory-reared fishes (for obvious practical reasons) fed artificial diets (zebrafish and goldfish, for example), and the behavioral responses to odors contained in these feeds may involve both memory and learning. How these studies relate to wild fishes feeding on natural prey items is a largely unanswered question.

Pheromones and reproductive behavior

Reproductive pheromones—and chemical communication in general—are thought to be involved in all stages of reproduction from initial mate-choice to parental care. However, given the wide variety of mating and reproductive strategies in fishes, the number of species that have been investigated in depth—to the identification of the pheromones involved—is vanishingly small, and largely confined to freshwater species (or those spawning in fresh water, such as salmonids and the sea lamprey). In general, reproductive pheromones in fishes ensure synchronicity; that is, the production and release of male and female gametes at the same time, an essential role in any broadcast spawners (such as many fish species). But many other roles have been proposed for chemical communication in a reproductive process, and these may be species-specific, in the wide range of reproductive strategies found in fishes.

The initial phase of reproduction is mate-choice; the identification of conspecifics of the appropriate sex and reproductive status with which to spawn. This may range from picking a suitable partner, from a limited range of suitors and based on input from different sensory modalities including—but not limited to—chemosensory systems (mainly olfaction in this context), to the mass school spawning of species, such as the herring. In cichlids, for example, well known for their dazzling colors and visual displays in mate-choice (for example “egg spots” on the anal fins), olfactory cues are also thought to play a role ([Keller-Costa](#)

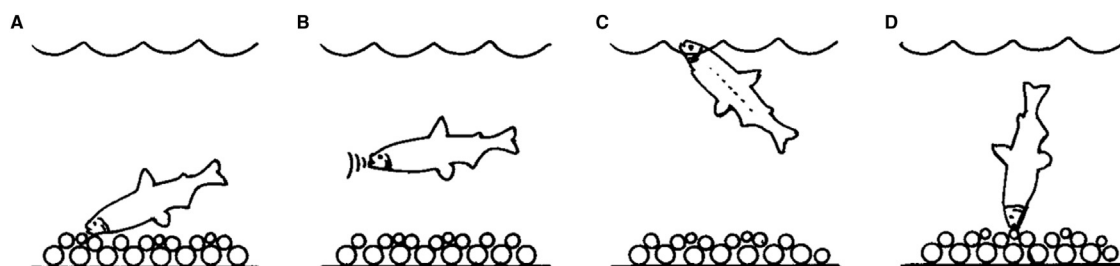


Fig. 1 Schematic presentation of feeding behavior elicited by chemosensory systems in fishes. Detection of food-related chemicals, initially by olfaction alone, causes arousal followed by increased locomotor activity and species-specific search behavior. As the fish nears the odor source, gustation (and other senses) plays more significant roles: (A) bottom searching in rainbow trout, (B) exploratory and escape behavior against the window in lake whitefish, (C) surfacing and jumping in lake charr, and (D) gravel “pecking” in goldfish. Reproduced from [Hara \(2006\)](#).

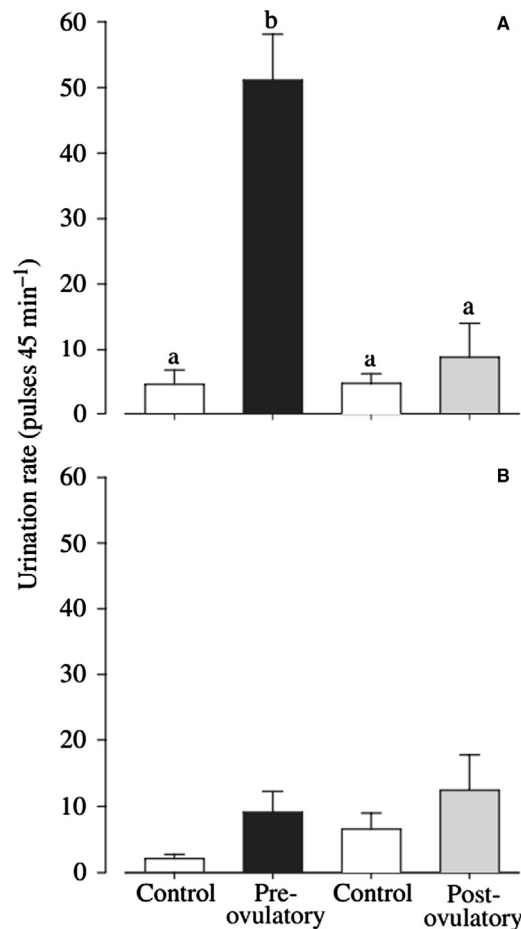


Fig. 2 Graphical representation of chemosensory-driven reproductive behavior in tilapia. Male Mozambique tilapia (*Oreochromis mossambicus*) signal their social status to females by urinating; urine from dominant males is much more potent than that from subordinate males. (A) Control males dramatically increase their urination rate in the presence of pre-ovulatory females (i.e., ready for spawning) but not in the presence of post-ovulatory females (already spawned). (B) Anosomic males (unable to respond to odorants) fail to increase their urination rate in the presence of either pre- or post-ovulatory females, although they show other forms of reproductive behavior. The implication is that males will only invest in urinary signaling if they can smell the female, as well as see her, and judge her as ready to spawn. From Miranda et al. (2005).

et al., 2015). In the Mozambique tilapia (*Oreochromis mossambicus*), a lek-breeding African mouth-brooder, the males use urinary cues to attract and stimulate oocyte maturation in females, essentially surrounding them in a cloud of pee (Keller-Costa et al., 2015). The male will only do this if—using olfactory cues—he judges that she is ready to spawn (Fig. 2; Miranda et al., 2005). However, the female has the last word; it is she that chooses which male with which to mate, usually the largest and/or most dominant male of the lek, again based in part on olfactory cues. In sticklebacks, females use major-histocompatibility (MHC) related olfactory cues released by the males to judge their relatedness (Milinski et al., 2005), thereby favoring males less closely related (and therefore increasing the genetic fitness of their offspring).

In the goldfish (*Carassius auratus*), the best-studied species with respect to reproductive pheromones, it is the males who are stimulated to increase milt production by a steroid hormone released by the females (Dulka et al., 1987). This pheromone (17 α ,20 β -dihydroxy-4-pregnen-3-one) was previously better-known as the maturation-inducing steroid, a hormonal role, leading to the concept of “hormonal pheromones”; that is, compounds with physiological (i.e., internal) hormonal roles that, when released to the water and detected by conspecifics, can give valuable information on the reproductive status of the emitter (Stacey, 2015). Over evolutionary time, this process gave rise to pheromonal roles for some hormones and/or their metabolites. But when the female goldfish has ovulated—that is, she is ready to release her eggs to the water—she evokes typical spawning behavior in the males (chasing, nipping, and encouraging the females to enter underwater vegetation) via prostaglandin F_{2 α} (another pheromone with well-established hormonal roles) and one of its metabolites released in her urine (Appelt and Sorensen, 2007; Sorensen et al., 1988).

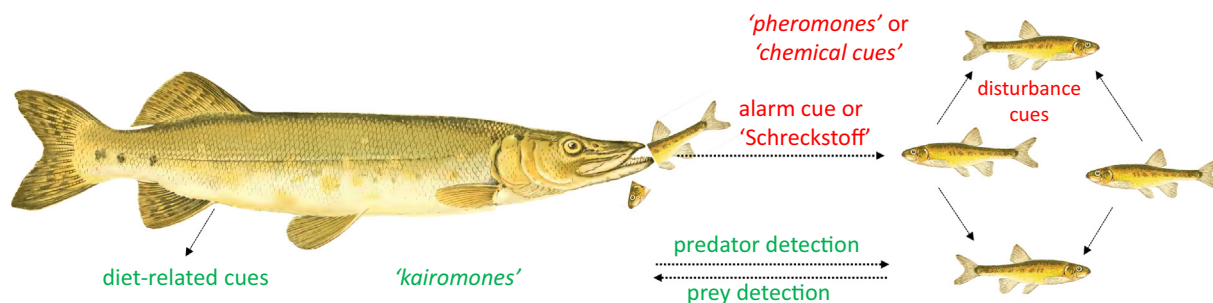


Fig. 3 Schematic representation of chemosensory systems and predator-prey interactions. A predator, here exemplified by a pike (*Esox lucius*; left), captures a prey fish (a minnow; *Phoxinus phoxinus*), damaging its skin and thereby releasing an alarm cue. Other minnows (right), when smelling this alarm cue, adopt behaviors such as tighter schooling, hiding in vegetation or freezing, all of which reduce the likelihood of predation. On becoming aware of the predator, either via vision and olfaction or by detecting the alarm cue, they also release “disturbance cues” (which do not require physical damage) which alert conspecifics of danger. Whether these cues can be called true “pheromones” remains controversial as they benefit only the receiver, not the emitter. On the other hand, kairomones emitted by the predator may alert prey fish to its presence, even to the extent that they can identify predators that have previously eaten conspecifics. Conversely, kairomones emitted by the prey fish may aid the predator in locating and identifying potential prey. Based on Wisenden (2015).

Alarm response

The other main behavioral category in which chemical communication plays an important role in fishes is the alarm response. This can be defined as the release of “alarm cues” by one individual which, on being detected by conspecifics, can alert them to the threat of potential predators, thereby altering their behavior (Fig. 3). Typical anti-predator behavior can include “freezing” (wherein the fish becomes immobile, usually on the bottom), tighter schooling, increased vigilance, and the use of shelter in dense vegetation, for example, all of which reduce the chances of predation (Maximino et al., 2019; Wisenden, 2015). This phenomenon was first observed by von Frisch in minnows (*Phoxinus phoxinus*), where he noticed that one minnow, having been captured—but then dropped—by a kingfisher, apparently alerted the school to the danger, and caused them to disperse (von Frisch, 1942). The explanation was that, upon damage, the skin released “Schreckstoff” (alarm substance) to the water, and the detection of this via the olfactory system of conspecifics led to the behavioral modification in conspecifics to reduce the likelihood of predation. As the release of alarm substance requires damage to the skin, and it does not necessarily imply the survival of the donor (unlike von Frisch’s original observation), some workers maintain that this cannot be viewed as a true pheromonal system, as it does not involve benefits to both sender and emitter. Nevertheless, this has not prevented interest in this system, evoking many behavioral studies in species other than the minnow (although this phenomenon was thought to be restricted to ostariophysan fishes, and is possibly not universal).

Early studies implicated the club cells of the skin as the source of the alarm substance, but this awaits confirmation. And, unlike reproductive pheromones, the alarm substance does not seem to be exclusively species-specific in that other species may detect, and respond to, alarm substance released by one species, including the attraction of other predators (Chivers et al., 1996). Again, unlike reproductive pheromones, the response to alarm substance may require an element of learning and memory; young fish learn to associate the detection of these alarm cues with a particular threat such as the smell of a predator (Kelley and Magurran, 2003). The alarm substance is thought to include hypoxanthine-3-*N*-oxide, but whether this is widespread among different species showing the alarm response requires confirmation. Another component could be chondroitin, a component of fish mucus, which acts as an odorant in zebrafish and induces antipredator behavior (Mathuru et al., 2012). However, one aspect of alarm cues is that they are—almost by definition—only temporary; their half-life in the water must be much less than reproductive pheromones (steroids, for example, are stable compounds). Another is that, like reproductive pheromones, they are likely to be mixtures of different compounds. This obviously makes chemical identification of such cues rather challenging.

Another type of alarm cue that does *not* require damage to the emitter has also been suggested to evoke behavioral changes in fishes; the so-called “disturbance cues.” These cues are released by fishes when exposed, for example, to a potential predator and evoke behavioral changes in other fishes that reduce predation risk, typically reduced movement and area use, and reduced foraging. These are less dramatic responses than those caused by damage-released alarm substances reflecting, perhaps, the lower intensity of threat or, perhaps, a lower concentration of active compound(s). The identities of disturbance cues are unknown; release of non-specific metabolites, such as ammonia, has been suggested but, again, this awaits rigorous confirmation.

Other conspecific-related behaviors

Olfactory cues are important in parent-offspring interactions, kin-recognition, and the formation of dominance hierarchies. Due to their popularity as aquarium species, and their well-documented parental care, much early work on parent-offspring interactions was done with cichlids. Chemicals released by larval jewelfish (*Hemichromis bimaculatis*), for example, induce parental coloration

and behavior including fanning and nipping (Keller-Costa et al., 2015). The parents can distinguish between their own young and other broods using chemical cues. While parents cannot distinguish between conspecific and heterospecific eggs, cichlids can often recognize conspecific young once hatched, even their own from other broods; this may involve learning and memory. As the larvae grow, however, the parents tend to rely more on visual, rather than olfactory cues.

Salmonids use chemical cues to distinguish between siblings and non-related conspecifics; they prefer water conditioned by siblings and tend to associate with familiar shoal mates. The source of the chemical cues may be feces and/or urine, but the identities of the cues are not yet known.

Social fishes commonly form dominance hierarchies to reduce aggression and violent interactions over competition for territory, mates, or food. Although less is known, it is clear that some species use olfactory cues to establish and maintain such hierarchies using “dominance pheromones.” One example is the Mozambique tilapia; high-ranking males signal to rival males by releasing pulses of urine, along with visual and auditory signals. The olfactory potency of dominant male urine is much greater than that of subordinate males, and the concentration of the steroid pheromone, 5 β -pregnane-3 α ,20 β -triol 3-glucuronate (and its 20 α epimer) that stimulates females is much higher. Rival males are able to estimate the social ranking of rival males, and will only risk an aggressive encounter if they have a good chance of winning. Thus, chemical communication of dominance can help establish and maintain social hierarchies by reducing the frequency of highly aggressive behavior.

Migration/homing

The long-range migrations of fishes such as the eel and salmon are well-known. It has long been suspected that fishes use olfactory cues to aid in these migrations. Many salmonids are able to “imprint” the smell of their native stream in order to return there to spawn themselves. This hypothesis was originally tested by exposing salmon parr to artificial odorants (morpholine and β -phenylethyl alcohol) during the critical parr-smolt transformation stage. Over 90% of adults that had been treated as parr returned to those streams to which either odorant had been added; those exposed to morpholine returned to the morpholine-scented stream whereas the β -phenylethyl alcohol-exposed fish returned to the β -phenylethyl alcohol-scented stream. Although this was an elegant proof of principal, the identity of the natural odorants was unknown; more recent work has suggested that the unique blend of amino acids of a given body of water may be involved, as well as the concentration of inorganic cations, such as calcium (Ueda, 2011). However, odorants other than amino acids may be involved; it is likely that salmon imprint to a complex mixture of chemicals unique to their natal stream, along with other, non-chemosensory cues. Once again, this makes the identification of such odorants more challenging.

Although other migratory species do not imprint to odorants in the same way as salmon, this does not negate the role of chemosensory cues in migration *per se*. A good example of the use of migratory cues is found in the sea lamprey (*Petromyzon marinus*). Despite its name, the sea lamprey spawns in fresh water. In the Great Lakes of North America—where it has become an invasive species—it lives its entire life-cycle in fresh water. The adults spawn in small, gravel-bottomed streams that flow into the lakes. However, they choose to enter (or not) these streams on the basis of chemosensory cues. The larvae release a mixture of bile acids, a class of steroidal compound produced by the liver, including (but not limited to) petromyzonamine disulfate; the adults have extremely high olfactory sensitivity to these bile acids (down to 10^{-14} M). Thus, the presence of detectable concentrations of these bile acids in down-stream water is indicative of larvae, and therefore a good spawning site. Then, as the males migrate upstream to find suitable spawning sites, they release another bile acid, 3kPZS (7 α , 12 α , 24-trihydroxy-5 α -cholan-3-one 24-sulfate) which, in turn, attracts the females to those spawning sites (Fig. 4).

Inorganic cations as odorants

The olfactory system of fishes has been shown to be sensitive to concentrations of inorganic cations, mainly calcium (Ca²⁺) and sodium (Na⁺), in both freshwater and marine species (Fig. 5: Bodznick, 1978; Hubbard et al., 2000, 2002; Nearing et al., 2002). Although this makes much sense in that movement from freshwater to seawater (and *vice versa*) requires changes in osmoregulatory physiology, the effects of this sensory input on behavior are less well studied. Sockeye salmon use calcium as one odorant among many by which to identify home waters (Bodznick, 1978), whereas larval zebrafish use olfaction to avoid high, and potentially lethal, concentrations of sodium (Herrera et al., 2021).

Single chemosensory cells

In addition to the olfactory and gustatory systems, fishes possess single chemosensory cells that resemble gustatory receptor cells over the surface of their body, referred to as the “common chemical sense”, often on the head and fin rays (Whitaker, 1992). Electrophysiological studies have shown that these cells respond to food-related chemicals, including amino acids or, in other species, non-amino acid odorants in the mucus of hetero-specifics. However, the contribution of the common chemical sense to food-seeking or predator avoidance behaviors is unknown. It is possible, of course, that the effects of this system on behavior depend on both species and context. Clearly, this is an area for future research.



Fig. 4 Chemosensory guided upstream migration in the sea lamprey (*Petromyzon marinus*). Male sea lamprey release a bile acid, 3kPZS (7α , 12α , 24-trihydroxy- 5α -cholan-3-one 24-sulfate), and females have extremely high olfactory sensitivity to this compound. Here, traps baited with 3kPZS were placed in the Ocqueoc River which feeds into Lake Huron (one of the Great Lakes where sea lamprey are a problem invasive species). Tagged females were released 70 m downstream, and their upstream migration tracked. Red lines illustrate ovulated females entering the left trap (Trap L) when the left trap was baited with 3kPZS. White lines illustrate ovulated females entering the right trap (Trap R) when the right trap was baited with 3kPZS. Green illustrates ground and black illustrates river. From Johnson et al. (2009).

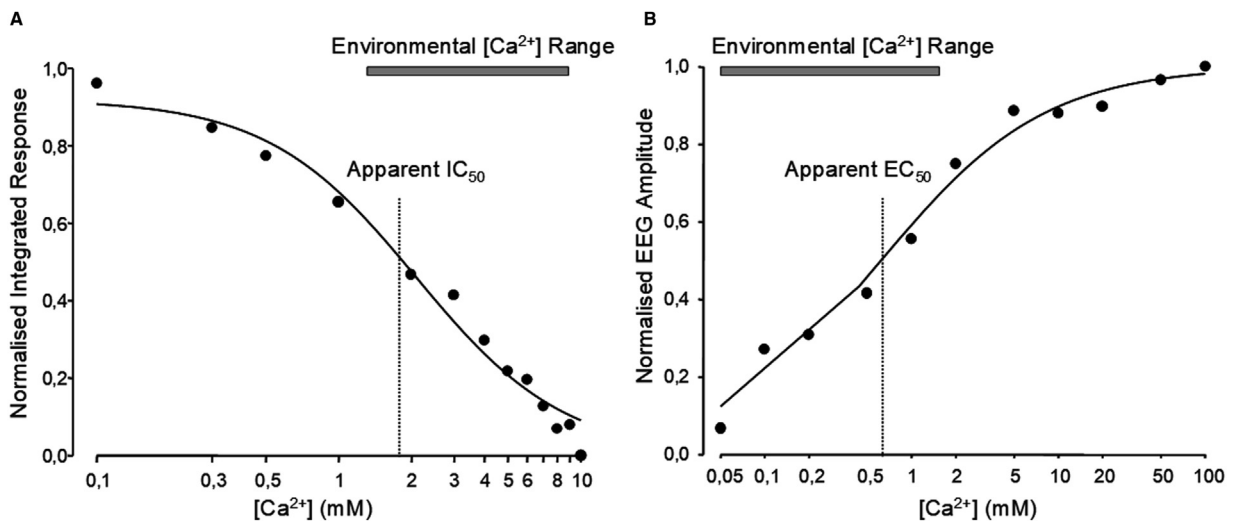


Fig. 5 Graphical representation of olfactory sensitivity to calcium. Fishes have olfactory sensitivity to inorganic cations such as calcium (Ca^{2+}) and sodium (Na^+); olfactory responses recorded from the olfactory nerve of a marine fish (the gilthead seabream, *Sparus aurata*; A), show how the olfactory system detects decreases in the calcium concentration [Ca^{2+}] in the seawater entering the nostril. A freshwater fish (the goldfish, *Carassius auratus*; B), on the other hand, responds to increases in environmental [Ca^{2+}]. In both cases, the linear (i.e., most sensitive) part of the curve falls within the range that the fish is likely to encounter in its natural environment. Fishes may use this sensory input to avoid entering water beyond their iono-osmoregulatory tolerance (Herrera et al., 2021), whereas salmon may use calcium as one odorant by which they identify home waters (Bodznick, 1978). Data redrawn from Hubbard et al. (2000, 2002).

CO₂ and O₂ sensing

As the level of oxygen dissolved in water is much more variable than its partial pressure in atmospheric air, fishes have evolved sensitivity to oxygen (O₂) as well as carbon dioxide (CO₂). These respiratory gases are detected by neuroepithelial cells in the gills and parts of the buccal cavity, rather than part of the olfactory or gustatory systems. The main role of this chemosensory system is the systemic regulation of ventilation frequency and cardiac output; that is, internal physiology (Milsom, 2012). However, in those fishes that can breathe air, hypercapnia (high CO₂) or hypoxia (low O₂) will increase the frequency of this behavior. Even in obligate water-breathers, such chemosensory input may alter behavior, by stimulating fishes to breathe water at the surface (where O₂ levels are likely to be higher) or seek better-aerated water. But such behavior may have costs; notably, the increased risk of predation from piscivorous birds, for example, due to the increased time fishes are obliged to spend close to the water surface.

Role of learning and memory

It has become increasingly clear that fishes are capable of learning and can retain memories for long periods (much more than the 7 s of popular myth!). How does such cognitive capacity affect chemosensory-driven behavior? As previously mentioned, many behavioral studies have been carried out on captive-bred populations that have been fed artificial diets. Therefore, fishes may learn to recognize the odor of such feed, and be less willing to accept something different. It is difficult to extrapolate such studies to the natural environment; do fishes have an innate ability to recognize the smell of natural prey items? In a similar way, fishes may learn to recognize the characteristic odor of a predator when it is associated with alarm substance; they will then respond to the predator odor alone with similar behavioral responses (Kelley and Magurran, 2003).

Effects of anthropogenic activity

Unfortunately, any discussion of chemosensory-driven behavior in fishes cannot ignore the influence of anthropogenic activity on these processes. Human input can affect chemosensory systems in two ways: firstly, by sub-lethal damage to the chemosensory systems making them less sensitive to chemical cues and, secondly, by altering the bio-availability of the chemicals themselves. Pollutants, particularly heavy metals (such as copper) and agricultural pesticides, have been shown to reduce olfactory sensitivity at well below lethal concentrations (Tierney et al., 2010). This will, in turn, mean that fish are less able to detect potential prey items

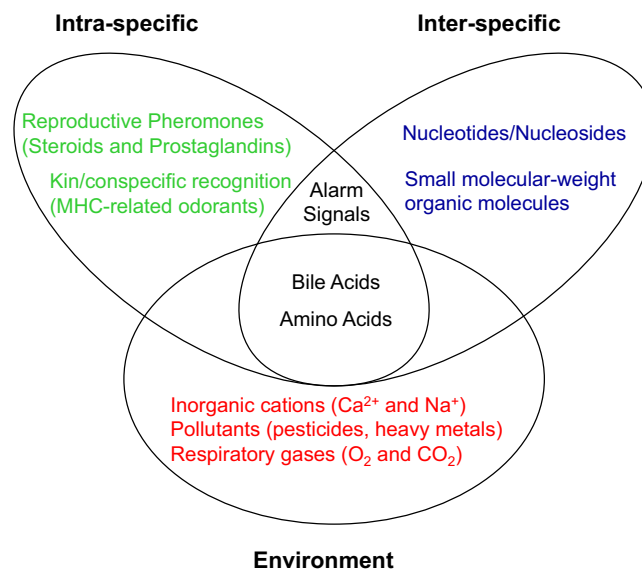


Fig. 6 Intra-specific behaviors are mediated by compounds released by conspecifics. In the case of reproductive pheromones, those identified to date have been mostly steroids and prostaglandins, but some fishes use bile acids or amino acids and their derivatives. Other social interactions, such as kin-recognition, mate-choice and parent-offspring interactions, may be mediated by MHC-related odorants but many remain to be identified. Less is known about the identification of chemicals involved in food-search or predator avoidance behaviors, but amino acids are well known to stimulate feeding behavior in many species, and some species have tastebuds that also respond to bile acids. Finally, some chemicals derived from the environment itself, such as respiratory gases (i.e., oxygen and carbon dioxide), and inorganic cations (e.g., calcium and sodium) are detected by fishes' chemosensory systems. These may be involved in homing and migration. Again, bile acids and amino acids—ubiquitous odorants and tastants for fishes—may also be involved in these behaviors. Anthropogenic activity—via pollution and ocean acidification—may interfere with all of these behaviors.

or nearby predators, thereby compromising survival. This is clearly a problem mainly of freshwater habitats and coastal waters close to dense human populations. However, as atmospheric CO₂ levels continue to rise, a proportion of this dissolves in the world's oceans, causing "ocean acidification" (a drop of seawater pH from about 8.2 to 7.8, or even lower). This acidification has been shown to alter chemosensory-driven behavior in fishes in different ways. For example, prey fishes were attracted to water conditioned by a predator when acidified with CO₂, rather than avoiding it at normal pH levels. On one hand, this may be due to changes in brain chemistry; the "GABA_A receptor theory" (Nilsson et al., 2012). On the other hand, it may be due to changes in protonation status of the odorants and/or the binding sites of their receptors, reducing the affinity of receptor-ligand binding and, consequently, olfactory sensitivity (Porteus et al., 2021). Clearly, these two mechanisms are not mutually exclusive. Either way, chemosensory systems are affected, and survival is threatened.

Conclusion

Chemosensory systems play important roles in many aspects of fish behavior (Fig. 6). Both olfactory and gustatory systems are involved in food-search and ingestion behaviors (the latter dominated by gustation), whereas the olfactory system is involved in intra-specific chemical communication, exemplified by reproductive behaviors and the alarm response. The olfactory system is also involved in migration and homing. Fishes are able to detect inorganic cations (Ca²⁺ and Na⁺) via the olfactory system, and CO₂ and O₂ via neuroepithelial cells in the gills. However, the behavioral consequences of these sensitivities are less well understood. The behavioral role of the common chemosensory system is also an open question. Fishes have well known olfactory and gustatory sensitivity to amino acids and bile acids, and the functional roles of these are likely multi-faceted. What little is known about the identity of pheromones and alarm cues suggests that many different compounds may be involved, and that there may be a degree of species-specificity. And, crucially, aquatic odors, be they pheromones or prey-related, are often complex mixtures, and it is only the full mixture that will elicit the full behavioral response. Thus, there is much left to learn.

Acknowledgments

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