CHEMICAL COMMUNICATION IN FISH

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Contents

Summary

Although the neural basis of olfactory function is highly conserved amongst all vertebrates, as is reliance upon semiochemicals to mediate everyday activities, fundamental aspects of olfactory function are poorly understood and only a few tetrapod semiochemicals have been clearly identified. Accordingly, recent information on the nature and function of fish semiochemicals presents abundant opportunities for understanding not only the basic function of the olfactory system but also the essential intra- and interspecific processes it mediates. From an evolutionary perspective, fish hormonal pheromones and injury-released chemicals inducing anti-predator responses offer numerous specific situations in which to study the evolution of chemical communication and determine if and how these semiochemicals are species-specific.

The management and conservation of fishes present many challenges, principally related to their aquatic existence. Control of maturation and spawning is a significant problem in fish culture and is an obvious area in which pheromones already could be applied to certain species. Perhaps even greater potential exists for the control of non-native, invasive fish species, for which few options other than toxicants are currently available. Aggregation (migratory) and/or sexual pheromones could be developed as lures in traps deployed for control and/or sampling; such techniques would not only be environmentally benign but also inexpensive and specific. To be effective, however, such techniques will require precise semiochemical identity and a comprehensive understanding of biological function. Repellents such as alarm cues might also be useful once their identities and specificities are known and the roles of learning in their actions are understood. Given the enormous utility of semiochemicals in insect pest management, the potential for similar applications of fish semiochemicals cannot be ignored.

1. Introduction

Living in a medium where visual information often is limited but where chemical information abounds, fish throughout their long history have had both cause and opportunity to evolve sensitive chemosensory systems enabling individuals to respond adaptively to conspecific and predator odors. Research throughout the past century provides many convincing demonstrations that such odors induce a remarkable array of apparently adaptive behavioral and physiological responses. We briefly review the three categories of response that are best understood: reproductive, antipredator, and

aggregatory. Our level of understanding differs greatly among these categories in terms of what is known about the chemical nature, production and mechanism of action of these odors, and the biological functions of the responses they induce. Reproductive responses are best understood, particularly in the goldfish (*Carassius auratus*) where there is considerable information on the production and release of odors (steroids, prostaglandins and their metabolites), the mechanisms through which they act, and the functions of responses they induce (Section 4.1). For antipredator responses (Section 5), there is considerable information on adaptive function in many species, although the nature of the odors and their mechanisms of action are virtually unknown. Although aggregation cues, of which migratory cues are a special example, are poorly understood, recent studies of sea lamprey (*Petromyzon marinus*) have identified a migratory cue and demonstrated biological response under natural conditions (Section 6.3.4). Because most major advances in understanding the responses of fish to conspecific and predator odors have occurred in the past two decades, we expect further significant progress in the near future.

2. Communication or Spying?

In discussions of intraspecific "chemical communication" of animals such as insects and mammals, it generally is implicit that chemical transfer of information is achieved by a pheromone, which performs a true communicative function by benefiting both the pheromone receiver and, through the receiver's response, the pheromone sender. Such pheromones typically are produced by structures specialized for synthesis and release and assumed to be the evolutionary consequence of a co-evolution of senders and receivers in which, at the very least, the receiver has selected for signaling specialization in the sender. Fish also provide examples of specialization for such pheromonal communication. In the black goby, *Gobius niger* (Section 4.5), the territorial and parental male attracts ovulated females to his nest. One component of male attractiveness is a steroid pheromone, etiocholanolone-glucuronide, a major product of a nonspermatogenic portion of the goby testis that appears specialized for the production of such conjugated steroids. In goldfish, however, the ovary appears unspecialized for production of the pheromonal steroids and prostaglandins that influence males, whereas changes in the rate of pheromone-containing urinary pulses indicate specialization in pheromone release (Section 4.1). In the context of predator–prey interactions, the epidermal alarm substance cells of ostariophysan fishes (Section 5.1.3) may be another example of a co-evolved communication system, although in most cases there is no clear evidence for such specialization. Such apparent lack of communicative specialization in reproductive and predator–prey functions is not a trivial issue, because it suggests that some interactions between sender and receiver could be fundamentally different from those in true communication.

From this perspective, we propose that, within the broad ecological context that includes antipredator and reproductive responses, three distinct states characterize the evolution of any chemical signal (Figure 1).
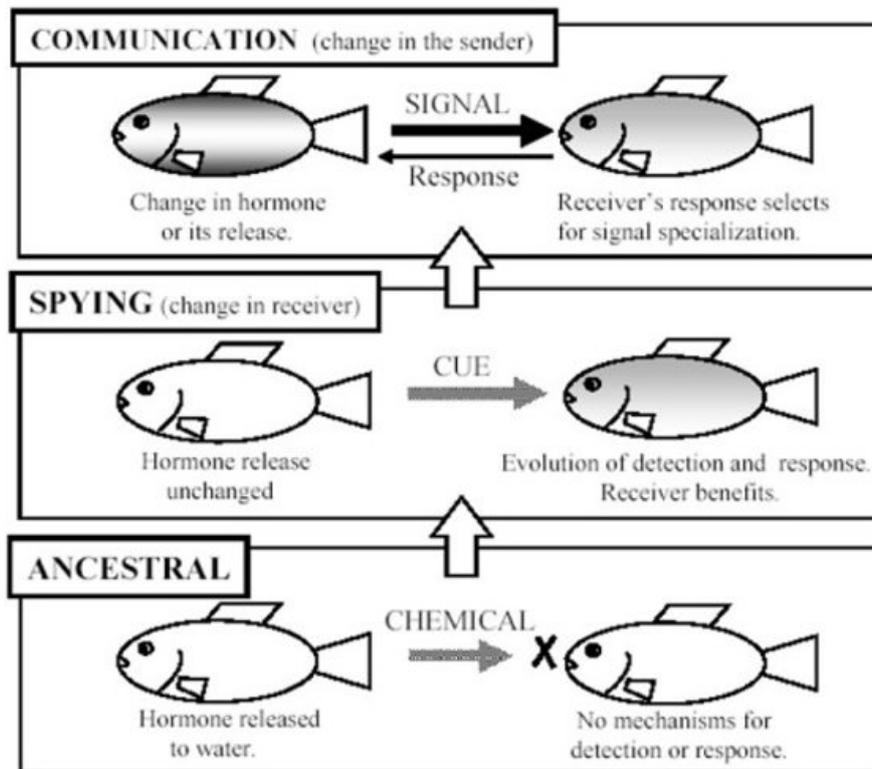
Figure 1. Proposed stages in the evolution of chemical signals in fish. Reprinted with permission from: Biochemistry and Molecular Biology of Fishes 1. 1991. PW Hochachka and TP Mommsen (eds.). Elsevier, Amsterdam; Advances in Chemical Signals in Vertebrates. 1999. RE Johnston, D Muller-Schwarze, and PW Sorensen (eds.). Kluwer Academic / Plenum Publishers, New York; Encyclopedia of Reproduction, Vol. 3. 1999. E Knobil and JD Neill (eds.). Academic Press, New York; Hormones, Brain, and Behavior". DW Pfaff (ed.) Academic Press, New York (in press).

First is the *ancestral* state, in which an individual releases a chemical(s) that other organisms are unable to detect. This state progresses to *spying* if receivers evolve the ability to detect and respond adaptively to the chemical(s), which we now would term a *cue*. Finally, spying progresses to *communication* if there is a mechanism for receivers to select for conspecific specialization in production and/or release of the chemical(s), which we now would term a *signal*. Ancestral and communicative states appear to be non-contentious. Because fish necessarily release numerous chemicals into the water medium bathing the chemosensory structures of all aquatic species, they are presently in the ancestral state with respect to all their released chemicals that do not currently function in spying or communication. And, as the example of the goby indicates, fish can evolve the true pheromonal communication so common in insects and mammals. The potentially controversial aspect of our proposal is whether chemical spying (on an unspecialized sender) can persist as a stable condition, or is simply a necessary but transitory stage in the evolution of chemical communication.

Some apparent examples of chemical spying in fish likely reflect our failure to detect subtle specialization in chemical production or release. In other cases, however, the nature of the interactions between senders and receivers make it unlikely that

pheromonal communication can evolve. In Pacific herring (*Clupea harengus pallasi*), for example, spawning is triggered by a chemical released in milt (sperm and seminal fluid), and can be induced even in monosex groups or single fish by small quantities of milt. In nature, synchronous spawning occurs in large, dense schools in which the sexes do not specifically coordinate their sexual activities, but independently deposit gametes on benthic substrates. Because a male is unlikely to fertilize the eggs of the females he stimulates to spawn, there appears to be no mechanism whereby the stimulatory quality of his milt could influence his individual reproductive success and thereby function in sexual selection leading to signal specialization. We therefore believe the spawning response to herring milt is an example of chemical spying on an unspecialized milt cue. At present, however, we know too little of fish semiochemicals to assess the relative importance of spying and communication among the myriad reports that fish respond to the odors of conspecifics and heterospecifics. Hopefully future research will directly address this issue, which has such important implications for understanding semiochemical function and evolution.

3. The Olfactory Sense in Fish

Fish possess three chemosensory systems: taste (cranial nerves VII, IX, X); solitary chemosensory cells of unclear function and embryological origin; olfaction (cranial nerve I). Semiochemicals appear to be detected exclusively by olfaction. Because this also is the situation in other vertebrates, and because olfactory anatomy has been highly conserved throughout vertebrate evolution, fish serve as valuable models of vertebrate olfactory function, particularly where a semiochemical has been identified.

As in other vertebrates, the olfactory system of fish contains three neuroanatomical components: olfactory epithelium, olfactory bulbs, and terminal fields within the brain. The olfactory epithelium contains three principal classes of intermingled olfactory receptor neurons - ciliated, microvillous, and crypt cells. This situation in fish differs from that in tetrapod vertebrates, many of which have two olfactory epithelia, the main olfactory epithelium, containing largely ciliated receptor cells, and the vomeronasal system, containing largely microvillous cells. The functional significance of the three classes of olfactory receptor neurons is unclear in vertebrates.

Most olfactory receptor neuron axons project from the olfactory epithelium *via* the olfactory nerves and terminate in the olfactory bulbs, although a few project directly to the brain. In the bulbs, olfactory receptor neurons synapse on mitral cells in bulbar glomeruli, dense aggregations of mitral and granule cell neuropil. From the glomeruli, mitral and other cells project centrally through the medial and lateral olfactory tracts to terminate in specific fields within the telencephalon and hypothalamus. Neurophysiological and behavioral studies show that food responses are mediated by the lateral olfactory tracts, whereas semiochemical responses are mediated by the medial tracts.

In addition to the unresolved functions of the different types of olfactory receptor neurons, major problems under investigation concern the receptor proteins presumed to bind odors and trigger olfactory receptor neuron response, and the coding of odors within the glomeruli of the olfactory bulbs. Probes based on G-protein-linked receptors

found in mammalian olfactory epithelia have been used to clone several classes of presumptive fish olfactory receptors, of which V2R and G-olf are the best characterized. The V2R class appears to be expressed in microvillous cells and in goldfish binds the amino acid L-arginine (a putative food odor). Ciliated cells also may mediate amino acids responses, leading some to suggest that the different olfactory receptor types may reflect some type of cellular specialization and not chemosensitivity *per se*. Although G-olf receptors have not been functionally expressed in fish, fish apparently possess about a hundred types (compared with over a thousand in mammals). Fish olfactory receptor neurons appear to be specialized for detecting particular odorants, as each expresses only one or a few G-olf receptor types.

How the complex neuronal interconnections in glomeruli process semiochemical information is not known, although each glomerulus likely processes information associated with specific olfactory receptor neurons. Preliminary data from goldfish and zebrafish (*Danio rerio*) suggest that semiochemical information is processed by relatively few mitral cells associated with specialized glomeruli.

4. Reproductive Responses to Pheromones

Pheromones of terrestrial animals including insects have been identified by analyses of the compounds produced in specialized pheromone-secreting glands. This approach was seldom applied to fish, however, because site(s) of pheromone synthesis were generally unknown. Thus, early work in the black goby (by Lorenzo Colombo's laboratory in Padua) and zebrafish (by Piet Van Oordt's laboratory in Utrecht) indicating that gonadal steroids can function as sex pheromones greatly facilitated fish research. The widespread ability of fish to detect water-borne hormones (steroids, prostaglandins and their metabolites) has since been demonstrated by underwater electro-olfactogram (EOG) recording, an extracellular technique that measures voltage changes from the surface of the olfactory epithelium in response to odor. EOG studies using synthetic steroids and prostaglandins can rapidly reveal whether fish detect specific compounds at the low (picomolar or nanomolar) concentrations expected of a hormonally-derived pheromone. If more than one compound is detected, EOG recording can then be used in cross-adaptation studies that assess the potential to discriminate detected compounds by determining if they act through separate olfactory receptor mechanisms. Together with studies of hormone release to the water, such EOG information has been essential to the design of physiologically meaningful behavioral and physiological bioassays.

Vertebrate gonadal steroids (androgens and estrogens) commonly generate internal (hormonal) sexual signals by modifying morphological and behavioral phenotype, processes that can require many days to become functional and that therefore transmit only indirect information about a signaler's past hormonal condition. In contrast, hormonal pheromones directly link the signaler's endocrine system to the sensory systems of conspecifics, potentially transmitting almost minute-by-minute information about current reproductive condition.

EOG studies that test fish with a large number of commercially available steroids and prostaglandins have shown that detection of these compounds is widespread among

freshwater fishes (Table 1) and also present in at least some marine and euryhaline species.

Orders	No. Species	No. Tested	Common Names	Example Genera	Evidence	
					PG	STER
ostariophysan orders						
Cypriniformes	2,662	> 80	cyprinids	*Carassius, Danio Cyrinus*	+	+
Characiformes	1,343	> 20	characins	*Astyanax*	+	+
Siluriformes	2,405	> 20	catfist	*Clarias, Synodontis*	+	+
Osmeriformes	236	1	smelts	*Plecoglossus*	+	0
Salmoniformes	66	9	salmon	*Salmo, Salvelinus Oncorynchus*	+	+
Cyprinodontoformes	807	1	rivulines	*Aplocheilus*	+	0
Perciformes	9,293	> 10	gobies	*Gobius*	0	+
			cichlids	*Haplochromus*	0	+

Table 1. Electro-olfactogram (EOG) evidence that fish detect hormones and hormone metabolites

Although there can be great differences among the compounds detected by distantly related species, the patterns of compounds detected within lower taxa (tribes, genera) can be remarkably similar. This is significant for two reasons. First, the fact that closely related species detect similar hormonal compounds indicates that, if their sex pheromones are species-specific, the specificity likely is achieved either by using different blends of a common hormonal mixture or by the addition of non-hormonal compounds. Second, similar patterns of detection by related fishes suggest that understanding the hormonal pheromones of even one key species could provide insight into the presumably homologous pheromones of close relatives: indeed, this has proven to be the case with goldfish and the closely related crucian carp (*Carassius carassius*) and common carp (*Cyprinus carpio*). Despite the evidence that hormonally-derived pheromones are widespread in fishes, there is no reason to expect that non-hormonal compounds also are not employed; indeed, bile acids appear to function as sex pheromones in sea lamprey (*Petromyzon marinus*), which we discuss below (Section 6.3.4).

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Biographical Sketches

Norm Stacey was born in Vancouver, British Columbia, Canada, where he received his Ph.D. (1977) from the University of British Columbia for studies of the role of prostaglandins in spawning behavior of female goldfish (*Nature* (1974) 247, 71–72; *Prostaglandins* (1976) 12, 1113–1126). After studying pheromonal control of spawning in Pacific herring as an NSERC PDF *(Canadian Journal of Fisheries and Aquatic Sciences* (1982) 39, 489–498), Norm moved to the University of Alberta at Edmonton, where he is now Professor in the Department of Biological Sciences. Initial research at Edmonton examined hormonal changes during ovulation and spawning of goldfish (*General and Comparative Endocrinology* (1979) 37, 246–249; and (1985) 57, 10–22) and native species (*General and Comparative Endocrinology* (1984) 56, 333–348 and 349–359). However, following the discovery with Peter Sorensen (doing a postdoctoral fellowship with Norm at the time) that female goldfish release a steroid pheromone (*Canadian Journal of Zoology* (1986) 64, 2412–2417), research has focused on the actions of this and other goldfish "hormonal pheromones" (*Nature* (1987) 325, 251–253; *Biology of Reproduction* (1988) 39, 1039–1050; *Journal of Experimental Zoology* (1996) 276, 287–295; *Journal of Experimental Biology* (1997) 200, 2833–2840). More recently, hormonal pheromone studies have expanded to other fish, such as gobies (*Journal of Chemical Ecology* (2001) 27, 443–470), catfish (*Fish Physiology and Biochemistry* (2003) 28, 275-276), cichlids (*Journal of Fish Biology* (2006) 68, 661-680), and crucian carp (*General and Comparative Endocrinology* (2006) in press), and also begun to explore potential pheromonal interactions among male goldfish (*Journal of Experimental Zoology* (2002) 293, 511-524).

Brian Wisenden took his early training in fisheries biology at the University of Guelph (B.Sc., 1985) and Lakehead University (M.Sc., 1988). He switched to behavioral ecology for his doctoral training at the University of Western Ontario (1993) in parental care (*Environmental Biology of Fishes* (1995) 43, 121-134; 145-151; *Animal Behaviour* (1995) 49, 623-639), variation in the mating system of convict cichlids in Costa Rican streams (*Behavioral Ecology* (1994) 5, 439-447; *Canadian Journal of Zoology* (1994) 72, 2177-2185) and alloparental care (*Behavioral Ecology and Sociobiology* (1992), 31, 263-269; *Ethology* (1994) 96, 203-212; *Reviews in Fish Biology and Fisheries* (1999) 9, 45-70. Since 1993, he has studied the role of chemical cues in mediating the context and timing of antipredator behavior in aquatic organisms in the field and in the lab. Early work on disturbance cues in darters (*Journal of Chemical Ecology* (1995) 21, 1469-1480) and active space of minnow alarm cues in the field (*Écoscience* (1995) 2, 116-122) led to a series of experiments on macroinvertebrates such as *Gammarus* amphipods (*Journal of Chemical Ecology* (1997) 23, 1163-1173; (2001) 27, 1249-1258; *Ethology* (1999) 105, 407-414;), and predator-recognition training experiments with *Enallagma* odonates (*Journal of Chemical Ecology* (1997) 23, 137-151; *Animal Behaviour* (1996) 52, 315-320) and planarian flatworms (*Animal Behaviour* (2001) 62, 761-766). Currently, Brian is working on predator-recognition training to enhance post-release survival of hatchery-reared walleye (*Canadian Journal of Fisheries and Aquatic Sciences* (2004) 62, 2144-2150). Brian was the first to document a metabolic cost to the production of ostariophysan club cells (*Journal of Fish Biology* (1997) 50, 799-808; (1998) 53, 841-846), the first to demonstrate hierarchical releaser stimuli for learned associations of predation risk with novel correlates of alarm cue release

(*Ethology* (2001) 107, 357-364, and the first to use underwater video to document alarm reactions of natural populations of free-swimming minnow populations (*Animal Behaviour* (2004) 67, 59-67; *Environmental Biology of Fishes* (2005) 72, 227-233). Brian currently serves as the receiving editor for North and South American and Pacific Region manuscript submissions for the journal *Behaviour*.

Peter Sorensen has had a life-long interest in olfactory function in fish, especially as it pertains to reproduction and migration. He was born in Billings, Montana, USA, but grew up on the east coast where he attended Bates College (Maine) before earning a Ph.D. in Oceanography at the University of Rhode Island (1984) for studies of the biological origins and chemical nature of the freshwater attractant for young migratory American eels (*Transactions of the American Fisheries Society* (1986) **115**, 256–268; *Environmental Biology of Fishes* (1986) **17**, 185–200). He then traveled to the University of Alberta where he was a postdoctoral fellow with Norm Stacey (1984–1988). In Alberta, Peter studied sex pheromones in the goldfish, laying the foundations of hormonal sex pheromone function (*Nature* (1987) **325**, 251–253; *Biology of Reproduction* (1988) **39**, 1039–1050; *Journal of Comparative Physiology A* (1990) **166**,:373–385). Peter was hired by the University of Minnesota (St Paul), Department of Fisheries and Wildlife, where he has been ever since, being promoted to full professor in 1997. At Minnesota, Peter's interests have broadened to include aggregatory attractants for migratory sea lamprey and their use in lamprey control (*Journal of General Physiology* (1995) **105**, 569–589; *Canadian Journal of Fisheries and Aquatic Sciences* (2001) **57**,:557–569; *Nature Chemical Biology* **6**: 324-328), alarm pheromones in ruffe and their possible use (*Journal of Great Lakes Research* (2000) **26**, 183–195), and migratory attractants in amphidromous Hawaiian gobies (*Environmental Biology of Fishes* 74: 31-42). Research on goldfish has centered on pheromonal mixtures (*Comparative Biochemistry and Physiology B* (2001) **129**, 645–651), and neural bases of pheromone perception (*Comparative Biochemistry and Physiology A* (1997) **180**, 39–52; *Current Opinions in Neurobiology* (1998) **8**, 458–467; *General and Comparative Endocrinology* 140: 164-175.