Chapter 1
Introduction to Pheromones and Related Chemical Cues in Fishes

Peter W. Sorensen

University of Minnesota, St. Paul, USA

1.1 CHEMICAL INFORMATION TRANSFER IN FISH

Information transfer between fishes, the largest and most diverse group of vertebrates, has long been both of practical importance and a source of wonder given the evolutionary, ecological, and economic importance of this group. Chemicals play an especially significant role in this process, presumably because they function well in vast dark spaces, can encode a great deal of information, are readily soluble, and are inherently "honest." This book specifically addresses how and why chemical information is transferred between fishes of the same species. First I define some basic terminology to promote clarity and then I introduce some other terms, types of chemical cues, and principals along with the chapters which discuss them. Information transfer between different species is not explicitly addressed except how it might occur as part of transfer within a species. This section introduces these terms and issues, and then where more information on them can be found in the book.

1.2 TERMINOLOGY

1.2.1 Overview

Because the terminology used to describe conspecific cues has been used in many ways since the term "pheromone" was first coined 50 years ago (Karlson and Luscher, 1959), I suggest and define some terms in this introductory section to provide clarity. Definitions were chosen for practical reasons and to be consistent with those used by researchers outside the world of fishes. Emphasis is placed on recent work by Tristram Wyatt (2003, 2010). Authors were asked to consider the terminology suggested herein, but not necessarily to use it if their opinions differed. Information transfer between members of different species (kariomones) is not directly addressed in this book.

1.2.2 Pheromones

Following Tristram Wyatt (2010), a "pheromone" may be defined as: "molecules that are evolved cues which elicit a specific reaction, for example a stereotyped behavior and/or development process in a conspecific." This definition is closely based on the original definition by Karlson and Luscher (1959). Key elements are that pheromones are "evolved cues" (stimuli whose production is in some

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way adaptive), "species-wide" (used by all members of the species), and that some type of innate recognition is implied. Nevertheless, responses to pheromones can be conditional on context, and/or internal state. Similarly, although pheromone composition (pheromones may be single compounds or mixtures) may vary slightly among individuals, this variation is expected to reflect physiological state (e.g., dominance) and not individual eccentricities or identity. In other words, I believe that the information contained in pheromones should be equally relevant to all individuals of the species (e.g. 'shared' by all members of that species). This type of rigidity appears to be associated with some type of specialized neural mechanisms. In contrast, organismal chemical cues that vary between individuals of the same species (either because of their chemical structures and/or because they are learned) should not considered to be pheromones but 'related conspecific cues.'

Identification of pheromones in fish is difficult and requires isolation of the released chemical(s) and proof that it/they elicit a specific adaptive response via some type of innate (neural) mechanism. This is not to say that learning cannot be involved but it should presumably be highly prescribed so that all members of the species recognize the same cues. Indeed, only a handful of fish pheromones meet these criteria these species include goldfish (*Carassius auratus*) hormonal sex pheromones, sea lamprey (*Petromyzon marinus*) migratory and sex pheromones, the Atlantic salmon (*Salmo salar*) sex pheromone, and perhaps the reproductive cues used by the African catfish (*Clarias gariepinus*). Nevertheless, there is a great deal of circumstantial evidence that pheromones are commonly produced and used by most, if not all, fishes. Their functions are diverse and include conspecific recognition, recognition of reproductive state, and the presence of injured conspecifics. These functions will be reviewed in Section 1.3; but first, a few terms that are commonly used to describe the pheromones in fish and other species are defined.

PRIMER PHEROMONE

A priming pheromone is a conspecific chemical cue that drives an adaptive developmental or otherwise wholly physiological response in an exposed conspecific. All members of a species in the same physiological state should typically be similarly affected. Examples include hormonal cues that drive endocrine changes in exposed conspecifics and alarm cues that change growth characteristics of exposed conspecifics.

RELEASER PHEROMONE

A releasing pheromone is a conspecific chemical cue that drives a rapid, adaptive, and innate behavioral response in a conspecific. All members of a species in the same physiological state should typically be similarly affected. Examples include hormonal metabolites that drive sexual arousal. Pheromones may have both releasing and priming effects.

PHEROMONE MIXTURE

Pheromones may comprise mixtures of chemical cues that may act on their own or synergistically. A "blend" is very specific type of mixture that requires that multiple components be present in very specific ratios for the mixture to have activity. Although commonly described in insects, no examples appear to exist in fish. By contrast, a "complex" is mixture of pheromonal components that can assume different functions depending on mixture composition. Ratios are not necessarily of primary importance but the overall composition is. Recent studies suggest that complexes in goldfish (see chapter 2) may include nonhormonal components that encode species identity and hormonal components that encode sexual condition.

1.2.3 Signature Mixtures

Fish, like all other vertebrates, release and learn to recognize conspecific chemicals for various purposes such as individual and kin recognition. Following Wyatt (2010), the term "signature mixture" is used for non-phermonal but related cues that can be defined as "variable chemical mixtures which are released by organisms and learned by other conspecifics to recognize individual or a member of some type of social group." The term "signature" implies some level of individuality; unlike pheromones, these cues are not anonymous and they are learned. The manner in which they are learned need not be prescribed. Further, their composition is typically complex and variable. In fishes, as in mammals, these cues appear to be commonly used to mediate recognition of individuals within social hierarchies or perhaps other aspect of special value such that they have been subject to recent stress. In mammals, these cues often appear to be genetically based on the major histocompatability complex (MHC) that codes genetic identity, but this possibility has not been fully resolved in fishes. A signature mixture is expected to be highly context dependent and may change with diet and other environmental factors. Recognition appears to require combinatorial responses of broad elements of the olfactory system. Signature mixtures may be found together with pheromones.

Identification of a signature mixture requires isolation of the released chemical(s) and proof that it elicits an adaptive response that is learned. Several examples have been described in fish. For example, Bryant and Atema (1987) show that diet influences production of odors associated with social hierarchy in the bullhead catfish, *Ictalurus nebulosus*, and that amino acids change in urine. Fish have also been show to readily learn to recognize the odors of conspecifics that have been attacked (Chivers and Smith, 1998). These functions will be reviewed in Section 1.3. Many ornamental odors such as those reviewed by Lynda Corkum and Karen Cogliati in Chapter 4 may fit this definition.

1.2.4 Other Definitions Relevant to this Book

A few other definitions associated with production and detection of conspecific chemical cues and signals are defined to promote clarity. Some of these definitions have also been the subject of considerable controversy which is not discussed here as they are defined largely for operational reasons.

Cues refer to any stimulus that elicits a sensory response in an animal's sensory system.

Signals are a prescribed set of cue(s) whose chemical identity has been influenced by evolutionary processes and may thus be considered to be specialized.

Communication may be defined as the exchange of adaptive information (e.g. signals) between two conspecifics.

The olfactory sense is the chemosensory component of the cranial nerve 1 (i.e., taste and common chemical sense are not included). It is also known as the sense of smell.

An odorant is a molecule that binds with olfactory receptor(s) and stimulates the olfactory sense.

An odor is an identifiable suite of odorant(s) that an animal's olfactory system can discriminate.

Fish are chordates with gills and fins that spend most or all of their live in water. (This book will address jawless, cartilaginous, and boney fishes.)

1.3 FUNCTIONS SERVED BY PHEROMONES AND RELATED CUES

1.3.1 Overview

Pheromones and related conspecific cues are known and defined by their biological function(s). Although these functions are diverse, they can be placed into five broad categories as outlined below. Some of these categories are not mutually exclusive, and presumably others may still await discovery.

1.3.2 Alarm Cues

As with other organisms, fish have evolved to recognize and respond to stimuli associated with the risk of predation, of which chemicals released by injured conspecifics are one (Chivers and Smith, 1998; Brown, 2003; Wisenden, Volbrecht, and Brown, 2004; Ferrari *et al*., 2010). Dozens of examples exist of fish-fleeing areas that contain extracts of damaged conspecific skin odor or reacting in other adaptive manners. In many instances, these responses seem to be species-specific, but this is not always the case. Also, there is evidence that fish can learn to respond to other species if they are damaged. These can be complex multicomponent cues, and there is even evidence that some can serve as primers. For example, the crucian carp, *C. carassius*, becomes more deep-bodied when exposed to damaged conspecific skin (Bronmark and Miner, 1992). Laboratory behavior studies suggest that hypoxanthine-3-N-oxide plays a role in the alarm response (Brown *et al.*, 2000), but this compound is yet to be measured in the water or shown to be detected by the fish nervous system. Quite possibly, multiple cue types are involved. Brian Wisenden reviews alarm responses in a critical manner while evaluating specific evidence of innate versus learned recognition in Chapter 6.

1.3.3 Nonreproductive Recognition and Aggregation

Conspecific recognition is important to fishes, and chemical cues appear to play a significant role in this process, especially amongst fishes that live in dark and/or deeper waters (Hemmings, 1966; Sisler and Sorensen, 2008). One important function is to promote shoaling and aggregation among nonreproductive individuals that seek to find each other to either avoid predation or locate food. Another function is to facilitate migratory orientation by adults or juveniles that seek habitat populated by conspecifics. Freshwater eels (*Anguilla* sp.), chars (*Salvelinus* sp.), galaxids (*Galaxias* sp.), and lampreys (*Petromyzontidae*) use conspecific body odors in this manner (Baker and Montgomery, 2001). It also appears that these conspecific cues may often be mixtures of nonhormonal body metabolites that function together with hormonal pheromones as part of pheromone complexes (Sorensen, Scott, and Kihslinger, 2000; Levesque *et al.*, 2011; Lim and Sorensen, 2011). Both bile acids (Selset and Døving, 1980) and L-amino acids (Saglio and Blanc, 1989) have been implicated in species recognition, but only for the sea lamprey have they been identified and then as sulfated bile sterols (Sorensen *et al.*, 2005). This topic is reviewed by Peter Sorensen and Cindy Baker in Chapter 2.

1.3.4 Individual and Kin Recognition

As is the case with mammals, the complex social systems used by some fish have favored the evolution of chemosensory mechanisms to determine relatedness of conspecifics (Olsén *et al.*, 1998). Functions of these “familial” odors include recognition of young and shoaling/schooling (Ward and Hart, 2003). In North American ictalurid catfish, at least some components of the odor used in individual recognition are L-amino acids (Bryant and Atema, 1987). Studies of salmonids suggest that kin odors are released in the urine and that a gene product associated with the major histocompatability complex (MHC) might be involved (Olsén, Grahn, and Lohm, 2002). The identity of individual, kin-specific odors is unknown although some speculate that peptide may be involved. This type of conspecific cue appears to represent a signature mixture and is reviewed by Ashley Ward in Chapter 5.

1.3.5 Ornamental Odors

Many species of fish are highly territorial and advertize their presence and identity using visual, acoustical, and chemical cues. Some fishes have specialized glands for the production of these cues (Bushmann, Burns, and Weitzman, 2002; Belanger, Corkum, and Zielinski, 2007), but the active components have not yet been identified. Both pheromones and signature mixtures can serve this function. Ornamental odors may assume communicatory roles. This topic is reviewed by Lynda Corkum and Karen Cogliati in Chapter 4.

1.3.6 Reproductive Stimulants

Arguably, the most important event in an organism’s life is finding a suitable mate and reproducing. Fish are no exception, and the challenges of life underwater appear to have favored the use of sexual signals including pheromones. A few of these have been identified, and the vast majority appears to be hormonal products and derivatives (“hormonal pheromones”) whose production presumably reflects inherent reproductive state and activity. Production, release, and response of select hormonal products have now been demonstrated in a few fishes: the goldfish, common carp (*Cyprinus carpio*), Atlantic salmon, and African catfish (Sorensen and Hoye, 2010). However, hundreds of species of fish from a broad variety of groups have now been shown to detect at least a few hormonal products with high sensitivity and specificity; therefore, the use of hormonal pheromones likely is widespread among fishes. Notable exceptions are a keto bile acid used by male sea lamprey (*P. marinus*; Li *et al*., 2002) and an unusual amino acid used by ovulated masu salmon (*Oncorhynchus masou*; Yambe *et al*., 2005). Hormonal pheromones have been especially well described among the minnows and carps where they function as changing mixtures in the contexts of other cues.

Several functions have been elucidated for hormonal sex pheromones. First, there is evidence that at least a few species of fish recognize the gender of maturing conspecifics. For instance, male goldfish release the androgen androstenedione by which females recognize males (Sorensen, Pinillos, and Scott, 2005). In addition, various fishes use priming sex pheromones derived from prespawning hormones to predict spawning and respond with hormonal surges of their own. The best understood of these is 17α,20β-dihydroxy-4-pregnen-3-one that is released along with other conjugates by ovulated female carps detected at picomolar concentrations (Dulka *et al*., 1987). Hormonal pheromones also mediate mate recognition and sexual encounters between sexually active conspecific fishes. The F prostaglandins that serve to mediate ovulation have an especially prominent role in this process (Sorensen *et al*., 1988; Stacey and Sorensen, 2009). Interesting questions about hormonal sex pheromones are how they might have come into use, how pheromone identity might relate to reproductive mode, how they might encode species identity, and whether they may influence hormonal function. It is possible that hormonal cues function as part of complexes. This topic is reviewed by Norm Stacey in Chapter 3 in which he addresses some new work exploring evolutionary questions in the African cichlids.

1.4 PHEROMONE IDENTITY, SYNTHESIS, AND RELEASE

The few fish pheromones that have been definitely identified (i.e., isolated and measured in the water and then shown to elicit sensory and biological responses) are relatively simple unspecialized structures. No signature cues, with the possible exception of the relatively simple L-amino acid mixtures employed by Ictalurid catfish (Bryant and Atema, 1987, see above) have been identified. The use of such simple structures in conspecific signaling presumably reflects the origins of these cues as bodily metabolites. To date, F prostaglandins, various C18, C19, and C21 sex steroids, an amino acid, and bile acids have been shown to have pheromonal function in various fishes. Many of these structures are conjugated with sugars or sulfates, perhaps because they increase solubility. These structures were reviewed by Sorensen and Hoye (2010); therefore, they are not reviewed in this book.

1.5 PHEROMONE DETECTION AND PHYSIOLOGICAL RESPONSIVENESS

1.5.1 Overview

Where studied, conspecific chemical cues in fishes have been found to be detected and discriminated by the olfactory system (cranial nerve 1). This also seems to be the case for all vertebrates and, presumably, reflects the inherent ability of this system to encode complex information and rapidly relay it to areas of the forebrain associated with social behaviors. Efforts to understand how social cues are processed in the fish olfactory system have focused on pheromones and the premise that they are discerned by specific components of the olfactory system. Nevertheless, a few studies suggest that this system also encodes signature information as it does in the mammals. Ongoing studies support this possibility, and they are reviewed herein. First, we address olfactory receptors (detection), then discrimination, and last responses (“higher” level function) and how these systems might be evolved.

1.5.2 Pheromone Receptors

The first step in the perception of a chemical cue involves binding of a ligand (odorant) to an olfactory receptor. There is every reason to believe that this is case with pheromones too, but it has yet to be directly demonstrated. Like other vertebrates, fish have many dozens of receptors of several types (Saraiva and Korsching, 2007). Pheromone receptors have unfortunately not been definitely isolated in fishes (although there is speculation (Bazáes, Olivares, and Schmachtenberg, 2013)); therefore, they are not reviewed.

1.5.3 Olfactory Discrimination of Pheromones

Following binding, electrical responses to odorants are transduced via the olfactory nerves whose activity creates neural maps of odor identity in the olfactory bulb. This is how a complex odor is discerned, and presumably pheromones have much simpler and more invariant maps than signature mixtures because only one receptor type is expressed in each olfactory receptor neuron. Various evidences, which include electrophysiological recordings, histological, and neural ablation, suggest that information on sex and alarm pheromones is conveyed by specific subclasses of olfactory neurons that project down the medial portions of the fish olfactory system (Hamdani and Døving, 2007). Although the crucian carp is perhaps the best understood model, there is compelling evidence that the olfactory systems of other fishes function in similar manners. Stine Lastein, El Hasan Hamdani, and Kjell Døving describe in Chapter 8 what we know about the key processes that underlie pheromone discrimination in fishes.

1.5.4 Pheromonal Signaling and Communication

Water-borne pheromones pass readily between conspecifics and present a myriad of opportunities to evolve and change with time. Thus, although many (most) pheromonal cues presumably evolved as unspecialized bodily metabolites whose detection instilled an advantage to the receiver, others with time have assumed secondary roles in which their production comes to impart an advantage to the donor. For example, male tilapia, *Oreochromis mossambicus*, maintain complex hierarchies and nests and have evolved urinary pheromones that convey their status to proximate conspecifics (Barata *et al*., 2007). This process involves various levels of physiological specialization that may involve specialization of cue production for its own sake and can be considered to be an example of true communication (Wisenden and Stacey, 2005; Stacey and Sorensen, 2009; Wyatt, 2010). Brian Wisenden examines how and why pheromonal cues may have come to be specialized in Chapter 7. New issues about definitions are also raised in the chapter.

1.6 PRACTICAL APPLICATIONS OF FISH PHEROMONES

1.6.1 Overview

Chemical cues, and pheromones in particular, play critical roles in the lives of many fishes. Laboratory and field studies consistently find that fish that experience olfactory damage will often fail to find key habitat or mate. Similarly, other studies show that addition of small quantities of pheromones to the water can exert powerful, adaptive effects. The potency of pheromones and the ease with which they can be added to the water make them excellent candidates for managing fish in aquacultural settings or in the wild (invasive fish in particular). A key component of applying pheromones is to understand their distributions and concentrations. These topics are addressed herein.

1.6.2 Effects of Pollution on the Perception of Conspecific Cues

The olfactory system appears to be exclusively responsible for detection and processing of conspecific chemical cues; yet because olfactory receptors are freely exposed to the water, they are extremely susceptible to environmental damage. In addition, drugs and other water-borne contaminants may specifically disrupt neural function in this sensitive system. Sublethal effects of poor-water quality on chemical information transfer in fishes have been documented (Jaennson *et al*., 2007). Håkan Olsén reviews this fascinating and important topic along with the effects of pollutants on the olfactory sense in chapter 10.

1.6.3 Application of Pheromones to the Management and Control of Wild Fisheries

Fish pheromones have been shown to exert powerful influences on fish behavior and physiological function at subpicomolar concentrations. They are also easy to apply and, at least in theory, most are environmentally safe because of the specificity of their actions. Management of wild fish is currently challenged by difficulties of censusing fish or in the case of invasive fish, removing them. Fishery agencies are presently examining pheromones for control of the exploding problem of invasive fishes and fishery conservation. The sea lamprey control program has made significant contributions in understanding the biology and application of pheromones to this invasive in the Laurentian Great Lakes. Peter Sorensen examines some of these possibilities in chapter 12.

1.6.4 Measuring and Interpreting Pheromones in the Water

To use pheromones effectively, one needs to know how they are found in natural waters so that levels can be maintained. Two techniques have been developed: radioimmunoassay (Scott and Ellis, 2007) and mass-spectrometry (Fine and Sorensen, 2005). Michael Stewart and Peter Sorensen explore the potential of these techniques and what they have shown in Chapter 9.

1.6.5 Applications of Pheromones in Marine Fish and Their Culture

Pheromones are powerful modulators of fish reproductive behavior and physiology in both fresh and salt water, yet little is known about the latter. Pheromones have also been identified in several species that have commercial importance, some of which will not reproduce without endocrine treatment. Unlike hormones, pheromones can be applied to fish without handling—saving time, money, and stress. Peter Hubbard in Chapter 11 addresses whether and how pheromones are used by marine fishes and how they might be used in aquaculture while focusing mainly on marine species.

1.7 SUMMARY

Chemical information transfer between fishes of the same species can take many forms and exert powerful effects. These effects can be either innate or learned, and all appear to be mediated by the olfactory system that makes them susceptible to damage and manipulation. The complexity of these scenarios requires the use of many terms whose precise meaning should not be overinterpreted because in most conditions they represent continua rather than absolutes.

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