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Review article

Pheromones in Aquatic Animals

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ABSTRACT
Pheromones, the semiochemicals are of great interest in animal husbandry and medical sciences due to their applications in food production, stock management and pest control activities. While several reviews on the subject are available, the present work is an attempt to summarise the advances in the area of aquatic animals, especially fishes.

Key words: Pheromones, Fish

INTRODUCTION

Pheromones a subclass of semiochemicals, used for communication within the species (intraspecific chemical signals), were originally defined as "substances secreted to the outside by an individual and received by a second individual of the same species in which they release a specific reaction, such as a definite behaviour (releaser pheromone) or developmental process (primer pheromone)" (Karlson and Lüscher 1959). Chemical communication occurs when both originator (signaller) and one or more receiver(s) possess specializations for chemical exchange of information, which can be used by them to locate food and mates, avoid predators and engage in social interactions (Corkum and Belanger 2007, Kashyap et al. 2024). It is well known that pheromones are released in response to stress, alarm, danger, and sexual cycles and are released by insects, reptiles, birds, and mammals. The pheromones in aquatic animals have been studied extensively in the last decade.

In aquatic animals, one member of the species (the sender) passively releases into the water a substance (usually a complex chemical mixture) that triggers a specific response from one or more members of the same species (the receivers). Receiver responses can either be a delayed, long-term change in the receivers' physiological state or an immediate behavioral response. Besides their body movements, fishes communicate (talk) with each other with the help of pheromones. Though, social control of maturation is a common phenomenon in fishes the associated mechanisms are yet to be identified. Pheromones in the goldfish (*Carrassius auratus*) have been extensively studied. Nowadays, research is being conducted on pheromones in fishes maintained in aquariums like zebra fishes, cichlids, gobies, poeciliids, sticklebacks, minnows, carp (koi) and on "sex steroids" in coral spawning. Peter W. Sorensen and Norm E. Stacey were the pioneer researchers on fish pheromones. The role of pheromones in various functions in aquatic animals is reviewed in this article.

Source of production

Significant anatomical differences characterizing mitral cells and ruffed cells were found in three teleost species. Zippel et al. (2000) recorded physiological responses from both types of relay neurons extracellularly and simultaneously in the plexiform layer using a single tungsten microelectrode. They found that during olfactory stimulation with important biological stimuli such as preovulatory, ovulatory, and alarm pheromones and certain amino acids, contrasting interactions between mitral cells and ruffed cells resulted during a drastic intensification of centrally transmitted information. The olfactory lamellae of teleosts contain two morphologically different types of olfactory receptor neurons (ORNs): ciliated ORNs (cORNs) and microvillous ORNs (mORNs). However, little is understood about the functional difference between two types of ORNs in fish olfaction. Sato and Suzuki (2001) isolated cORNs and mORNs from olfactory organs of the rainbow trout and concluded that cORNs are 'generalists' that respond to a wide variety of odourants, including pheromones, whereas mORNs are 'specialists', specific to amino acids. In the *Ostariophysi*, specialized epidermal cells (Alarm Substance Cells - ASCs) contain the alarm pheromone and these cells have no other known function (Pfeiffer 1963). Later it was demonstrated for the gobies *Brachygobius sabanus* and *Asteropteryx semipunctatus* (Smith et al. 1992, Smith and Lawrence 1992), also Perciformes and sculpin (*Scorpaeniformes*) (Smith 1992).

Chemistry

Though very few aquatic pheromones have been chemically identified, the main chemicals involved in fish pheromones cover a wide range of forms, including steroids such as androstenedione and polyamines as olfactory stimulants (Table 1). Aquatic animal pheromones are water-soluble and the diffusion rate is 10,000 times lower than in air (Chung-Davidson et al. 2011). Many fishes use steroid hormones as pheromones to initiate behavioral and physiological changes during spawning (Table 2). Fishes also produce pheromones in their gonads through the seminal fluid in males and ovulation in females and their rectal organs. Female fishes full of eggs release pheromones into the water to attract males. von Frisch (1941) termed one type of fish pheromone as "Schreckstoff" (fright stuff), which are injury released or chemical alarm pheromones released as an alarm signal to other fishes to flee. In fish and lobsters, pheromones may have evolved from molecules excreted in urine or leaking into the water across permeable membranes such as gills. The available details about the chemical nature of aquatic pheromones are presented in tabular form for better understanding (Table 3). Most pheromones are mixtures of multiple compounds and no mixture has been completely elucidated in fish (Li et al. 2018b).

Mode of action

All the vital activities of fish like alarm communication, individual identification, group cohesion, parent-offspring recognition, territorial markings, sex attraction, and synchronization of reproductive processes as well as migration are shaped by pheromones. Pheromones are specific in their action e.g. Alarm pheromones do not act as a sex pheromone. Only closely related species share similar pheromones. For example, a sex pheromone for carp might work on goldfish but it would not work on trout or bass or yellowbelly or cod or even any other distantly related species. The vomeronasal organs in their highly sensitive nostrils help the fishes to detect pheromones. The male olfactory system was also found to be extremely sensitive to Androstenedione, detecting it to near picomolar concentrations (Sorensen et al. 2005). Different scientists measured the level of pheromones in fish at which it acts (Table 4).

Table 1. Major types of pheromones in aquatic animals

Sr. No.	Types of pheromones	Releasing organ	Released through	References
1.	Alarm pheromone	Injured skin epithelial cells	—	von Frisch, 1941
2.	Sex pheromone (Reproductive pheromones)	Gonads		
		Ovaries	Ovulatory fluid	Applet and Sorensen 2007
			Urine	Yambe and Yamazaki 2001
		Testis	Semen (Milt)	Rice et al. 2002
			Urine	
		Rectal organs	Faeces	Miranda et al. 2005

Table 2. Chemical nature of the pheromones in aquatic animals

Sr. No.	Pheromone	Chemical nature	Remarks	References
1.	Steroids	Androstenidione	Initiate behavioural and physiological changes during spawning	Sorensen et al. 2005
		4-pregnen-17, 20_{β}-diol-3-one	Induces in males increase plasma LH and increases strippable milt	Wyatt 2003
2.	Prostaglandins	Prostaglandin $F_2\alpha$ 15-keto-$PGF_2\alpha$	Trigger courtship and increase LH and milt production in male	Wyatt 2003
3.	Non-hormonal pheromone	——	Teleost fish	Yambe et al. 2006
		Hypoxanthine - 3(N) –oxide	An important component of alarm pheromone	Smith 1979
		24-methyl-5á-cholestane-3α, 7α,12α,24,28-pentahydroxy 28-sulfate, an oxysterol sulfate,and 5α-cyprinol sulfate	Alarm substances in zebrafish	Li et al. 2024
		Phenylethylamine	Potential Density Stress Pheromone in Turbot (Scophthalmus maximus)	Li et al. 2023
		Etiocholanolone glucuronide	The male pheromone in Black Goby	Colombo et al. 1980
		3 keto-petromyzonol sulphate	Released by mature gills to attract spawning females to nest	Chung-Davidson et al. 2011
4.	Bile salts/acids		Aggregation Pheromone in sea lamprey	Sorensen et al. 2003

Table 3. Pheromones released in certain aquatic species

Sr. No.	Species	Chemical class	Chemical nature	References
1.	Goldfish	Steroid	4-pregnen-17, 20_{β}-diol-3-one	Wyatt 2003
		Prostaglandins	Prostaglandin $F_2\alpha$	Wyatt 2003
			15-keto-$PGF_2\alpha$	Wyatt 2003
2.	Brown Trout	F series prostaglandins	$PGF_1\alpha$	Moore et al. 2002
			$PGF_2\alpha$	Moore et al. 2002
3.	Chinese Black Sleeper	Progesterone	17 α progesterone	Hong et al. 2006
			17 α, 20 β - dihydroxy-4-pregnen-3-one	Hong et al. 2006
		Prostaglandins	PGE_2	Hong et al. 2006
			$PGF_2\alpha$	Hong et al. 2006
4.	Sea Lampreys (Larvae)	Pyrosulfate (Bile acids)	Pteromyzonamine disulfate	Sorensen et al. 2005
			Pteromyzosterol disulfate	
			Pteromyzonol sulphate	Vrieze and Sorensen 2001
			Allocholic acid	

Table 4. Concentration at which some pheromones act in aquatic species

Sr. No.	Hormone	Concentration at which they act	Species	References
1.	Androstenedione	50 ng/h to 1 µg/h	Male Goldfish	Sorensen et al. 2005
2.	Similar substance to L-kyneurenine	10^{-14} M (picomolar concentration)	Salmon	Yambe et al. 2006
3.	F series prostaglandins	10^{-11} M	Brown Trout	Moore et al. 2002
4.	15-keto-PGF$_2\alpha$(PGF metabolite)	10^{-8} M	Brown Trout	Moore et al. 2002
5.	Uridine diphosphate	10^{-5} M	Female Crab	Hardege et al. 2011

Effect of pheromones

Growth

The Redclaw crayfish has been cultured in ponds since 1990 and has evinced interest in fish culturists about the culture potential in areas where pond culture may not be feasible. It was found that factors that might cause the reduced growth in Red claw crayfish include inadequate diet, density effects, and pheromones (Rodriguez et al. 2002). It was suggested by Aday et al. (2003) that chemical cues are responsible for inhibiting the maturation of juvenile male bluegill (*Lepomis macrochirus*) in mesocosms when they interact with mature males. Power and Couturier (2006) found that mussels exposed to starfish scent grew slower and had a reduced clearance rate for food and mobility than those not exposed to starfish chemical cues.

Reproduction

Although it is established that many species of fish release hormonally derived sex pheromones in their urine, it is not known whether these cues are unspecialized metabolic by-products or specialized communicatory signals. Sex pheromones like steroids and prostaglandins have been identified in several fishes to find mating partners during their reproductive seasons and are broadly termed "hormonal pheromones" because they or their precursors act as hormones in these fishes. Stacey (2003) opined that reproductive hormones (steroid and prostaglandins) are used commonly by fish as an endogenous signal (between brain and reproductive tract) and as exogenous signal (pheromone) to synchronise gamete maturation and spawning between the same species. Chung-Davidson et al. (2011) found that the pheromone produced by mature female induce sperm maturation in the male.

Goldfish (*Carassius auratus*): The goldfish *Carassius auratus* is a good model system for the study of hormone-based sex pheromones in aquatic animals. Male goldfish are extraordinarily sensitive (with picomolar thresholds) to steroid [4-pregnen-17, 20$_\beta$-diol-3-one (17,20$_\beta$ -P)] and prostaglandin hormones and their metabolites released into the water by females which stimulates physiological responses in the male and reflect the blood concentrations of the hormones in the female indicating her biological state. When the female spawns the next morning, males respond to other hormone pheromones released by the female: blood prostaglandin F$_2\alpha$ (PGF$_2\alpha$) and 15-keto-PGF$_2\alpha$ (Wyatt 2003). During the preovulatory luteinizing hormone (LH) surge, females release a complex steroidal pheromone that induces in males a rapid increase of plasma LH, which in turn increases strippable milt (sperm and seminal fluid) before ovulation and spawning. Sexually receptive goldfish females increased the frequency with which they urinated releasing 15-keto-PGF$_2\alpha$ when placed with males but not with females (Applet and Sorensen 2007). Goldfish, like much other fish, control the discharge of urinary prostaglandin pheromones to advertise their condition and site, perhaps exemplifying an early step within the evolution of a chemical communication system. Moreover, isolation from conspecifics also appears to increase milt through a mechanism that is different from that which mediates the response to female pheromones (Stacey et al. 2001, Fraser and Stacey 2002). Species that employ amphimixis must synchronize gamete maturity with behaviour within and between genders. Reproductive hormones act both as an endogenous signal to synchronize sexual behaviour with gamete maturation and as an exogenous signal (pheromones) to synchronize spawning interactions between Teleost fish (Kobayashi et al. 2002). Ovulatory female goldfish release a spread of sex steroids into the water where they function as a pheromonal blend dominated by C_{21} steroids that stimulate male hormone release, sperm production, and behaviour. Sorensen et al. (2005) found that spermiated male goldfish release substantial quantities of androstenedione (AD; about 50 ng/h) together with smaller (10-20 ng/h) quantities of several other related C_{19} steroids but only very small quantities (<5 ng/h) of C_{21} steroids. Males released even greater quantities of AD (up to 1 micro g/h) while C_{21} steroid release rate changed little, on being sexually aroused by females or their pheromones.

Carp (*Carassius carassius*): The interactions of estrogenic (nonylphenol, dicofol, atrazine), androgenic (organotins, phthalates, fenarimol) and anti-androgenic compounds (vinclozolin, diuron, p,p’-DDE) with key enzymatic activities involved in both synthesis and metabolism of sex hormones were investigated by Thibaut and Porte (2004). Carp testicular microsomes incubated within the presence of androstenedione and different xenobiotics evidenced higher sensitivity of 5 alpha-reductase activity than 17 beta-hydroxysteroid dehydrogenase activity towards these chemicals with Dicofol, organotins, and phthalates being the most effective inhibitors. However, ovarian synthesis of maturation-inducing hormones (20 alpha - and 20 beta-hydroxysteroid dehydrogenase activities) was enhanced by nonylphenol, dicofol, fenarimol and p,p’-DDE. Similar studies by Olsen et al. (2006) on crucian carp (*Carassius carassius*), found that increases in male LH and milt occurred when untreated females ovulated spontaneously after addition to male pens which indicated that it was due to the release of preovulatory pheromonal steroid(s).

Salmon (*Oncorhynchus masou*) and trout (*Salmo trutta*): Yambe and Yamazaki (2001) demonstrated for the first time, under laboratory conditions, the species specificity of releaser pheromones (sex attractants) in the urine of ovulated salmonid females and suggested that the use of species-specific chemical signals may serve as one of the mechanisms of reproductive isolation in this species of fish. Yambe et al. (2003) reported that 17 alpha - methyltestosterone (MT) treated immature male masu salmon (*Oncorhynchus masou parr*) showed specific behavioral responses to the ovulated female urine. Further, Yambe et al. (2006) reported the identification of a “nonhormonal pheromone” in teleost fish. The urine of the reproductively mature female masu salmon (*Oncorhynchus masou*) which is ready to mate contains a male-attracting pheromone that is identical to L-kynurenine, which elicits male-specific behaviour at even picomolar concentrations (10^{-14} M). In vertebrates, L-Kynurenine is a major metabolite of L-tryptophan. It was however found that cypermethrin damages olfactory reception in brown trout (*Salmo trutta L.*) affecting their reproductive behaviour and lower blood plasma levels of 17,20 beta-Progesterone and 11-Keto Testosterone (Jaensson et al. 2007). F-series prostaglandins have a role as priming pheromones in male brown trout as demonstrated by Moore et al. (2002) that the olfactory epithelium of mature male brown trout (*Salmo trutta parr*) was acutely sensitive to F-series prostaglandins (PGFs) $PGF_1\alpha$ and $PGF_2\alpha$, with detection threshold concentrations of 10^{-11} M. The olfactory epithelium was also sensitive to the PGF metabolite 15-keto $PGF_2\alpha$ (threshold 10^{-8} M) but did not detect a further metabolite, 13,14,-dihydro-15-keto $PGF_2\alpha$.

Ovarian steroid glucuronide is employed as a sex pheromone by males of three sympatrically spawning species of Himalayan trout. Exposure of mature males of *Schizothorax richardsonii, Schizothorax plagiostomus* and *Schizothorax sinuatus* to the ovarian odours from ovulated conspecific and heterospecific females had a significant priming effect (increased milt volume, spermatocrit, and sperm motility) on conspecific males. However, no spawning act was observed by male *S. richardsonii* with heterospecific females, when conspecific females were present which might be a strategy to maintain the reproductive isolation in a spawning territory (Bhatt et al. 2004).

Chinese black sleeper (*Bostrichthys sinensis Lacepede*), round goby (*Neogobius melanostomus*) and tilapia (*Tilapia buttikoferi*): Ovarian, testicular, and seminal vesicle extracts of mature Chinese black sleeper (*Bostrichthys sinensis Lacepede*), synthetic steroids 17 alpha -progesterone (17 alpha -P), 17 alpha, 20 beta -dihydroxy-4-pregnen-3one (17 alpha, 20 beta -P), and prostaglandins PGE_2 and $PGF_2\alpha$ were used in an attempt to attract broodfish and to induce spawning. It was noted that the sex organs of *B. sinensis* contain 17 alpha-P, 17 alpha, 20 beta-P, PGE_2, and $PGF_2\alpha$ and that 17 alpha-P, 17 alpha, 20 beta-P, and PGE_2 may act as sex pheromones in this species, attracting both male and female conspecifics to spawning sites and inducing spawning. Among the compounds tested, PGE_2 was the most effective sex pheromone for induction of spawning in *B. sinensis* (Hong et al. 2006). The reproductive success of the round goby (*Neogobius melanostomus*), an invasive fish, could also be mediated by the utilisation of pheromones. Corkum et al. (2006) compared behavioural and electrophysiological responses of reproductive and non-reproductive female round gobies to conspecific males and found that reproductive male round gobies release a pheromone signal that attracts reproductive females. This finding may be useful to develop a control strategy by using natural pheromones to disrupt the reproductive behaviour of the invasive round goby and to curtail its effects on native species. Similarly, the ability of male tilapia to discriminate between females of differing reproductive status is mediated by odorants released into the water, probably via the urine and faeces, by pre-ovulatory females (Miranda et al. 2005).

Oysters (*Crassostrea virginica*) and mosquitofish (*Gambusia affinis):* Pheromones play a critical role in triggering spawning in oysters but none have been identified to date. Oyster sperm stimulates spawning in both male and female oysters but oyster eggs stimulate only male oysters to spawn but not females. Spawning activity associated with sperm may be membrane-bound. As a primarily step toward isolating and characterizing a spawning pheromone in sperm of the oyster *Crassostrea virginica*, Rice et al. (2002) presented evidence that the candidate oyster sperm pheromone is a heat and trypsin sensitive intrinsic membrane protein, whose synthetic or recombinant fragment could be used in the aquaculture industry to induce spawning in oysters. Male mosquitofish prefer female odors to male odors and plain water, indicating that female odors function as a sex attractant. Female western mosquitofish may produce sex pheromones and female pheromones during different stages of the reproductive cycle which stimulate different male sexual activities and help the males to discriminate parturient females from others based on pheromonal output (Park and Propper 2002). However, in the crayfish, *Austropotamobius pallipes*, males did not respond to chemical cues alone emitted by a female but required both chemical and visual stimuli (Acquistapace et al. 2002). Stacey (2003) opined that fish commonly use reproductive hormones (steroids and prostaglandins) both as endogenous signals between the reproductive tract and brain and as exogenous signals (hormonal pheromones) that synchronize gamete maturation and/or spawning interactions between and among conspecifics. This dual function makes it difficult to get a complete understanding of reproductive function in any fish without understanding both the endogenous and exogenous actions of its hormones and related released compounds. Information on goldfish and Atlantic salmon is now available. However, since hormonal pheromone studies have focused on oviparous gonochorists with relatively simple reproductive strategies, nothing is known about the potential hormonal pheromone functions of the numerous species with sequential hermaphroditism or alternative male strategies or the possible changes in pheromone function related to various transitions from oviparity to viviparity.

Aggregation

Pheromones are secreted or excreted chemical factors that trigger a social response in members of the same species. They can be either an attractant or repellant. In many fishes, including goldfish and common carp, conspecific odor promotes aggregation and shoaling. This response is apparently not based on immediate familial relationship, although this aspect has largely been ignored. Both bile acids and L-amino acids have been implicated in species-recognition, but little research has been directed to this question (Sorensen and Stacey 2004).

Pest control

Pheromone baited traps have proven highly effective for managing insect pests by selectively removing reproductively active adults before mating. Wagner et al. (2006) reported two pheromones produced by the sea lamprey, *Petromyzon marinus*, which may be useful for controlling pest populations in the Laurentian Great Lakes. Sea lamprey pheromone is the first vertebrate pheromone to be used in the field for pest control (Chung-Davidson 2011). Predation of mussels, *Mytilus* sp., by the common starfish, *Asterias vulgaris*, can be a serious problem on mussel farms because, in addition to direct predatory losses, starfish can affect the growth and behaviour of wild mussels. Corkum and Belanger (2007) reviewed the chemical signalling between mates or cues from nest sites or hosts by selected aquatic pest species and indicated how chemical information can be used to manage pests. The pests are vectors of disease (blood-sucking insects) or invasive species (crayfishes and fishes) that have exhibited detrimental effects on indigenous species. Pheromones released by females attract and stimulate males in some taxa (insects, crayfish, goldfish, and crucian carp), whereas pheromones released by males attract females in others (round goby, sea lamprey). Other chemicals (e.g., habitat odours or odours given off by developmental stages of conspecifics) can affect oviposition decisions of pest species. In areas of aquatic environments where other cues could also be limited (e.g., visual) freshwater organisms may rely solely on chemical signals or together with environmental cues for reproduction. If the chemical structure of odour attractants are identified and shown to lure conspecifics to traps, then odorants or their blends can be used to control the aquatic pests. By disrupting the reproductive behaviours of these species the application of pheromone traps may control the malarian vector (*Anopheles gambiae*) or invasive species such as signal crayfish (*Pacifastacus leniusculus*), sea lamprey (*Petromyzon marinus*), and the round goby (*Neogobius melanostomus*).

Alarm response

A wide diversity of aquatic organisms release chemical alarm cues when captured by a predator. The functional and evolutionary aspects of alarm pheromones in fish have been reviewed by Christopher (1994). von Frisch (1941) was the first to demonstrate the release of an alarm substance (Schreckstoff) on damage to the skin in European minnow (*Phoxinus phoxinus*) which initiates a fright reaction in other fishes. The detection of Alarm response in fish paved the way for further research in fish pheromones (Chung-Davidson, 2011). Alarm pheromones' were first demonstrated in *Ostariophysi* (Pfeiffer 1963) and two species of darters, *Etheostoma exile* and *E. nigrum* (Smith 1979). The possession of an alarm system does not give any benefit to the sender since the alarm substance does not deter predators and fish which are damaged in an encounter with a predator rarely survive and threatened but uninjured fish do not release alarm pheromone (von Frisch 1941, Smith 1979). The alarm pheromones are interspecific (provided an alarm pheromone system exists in both the species) (Mathis and Smith 1993) and intergeneric and are as sensitive as intraspecific responses (Smith 1982). This indicates that the alarm pheromones or the mechanism to detect them may be very similar among different species of fishes. Fish learn to associate predator chemical signatures with pheromone and with experience the predator stimulus alone produce appropriate anti-predation behaviour. When other prey fish detect alarm substances by olfaction, they perform stereotypical predator avoidance behaviours to decrease predation risk. Scott et al. (2003) found that on exposure of juvenile rain brow trout (*Oncorhynchus mykiss*) to waterborne Cadmium at environmentally realistic levels (2 micro g/litre), the normal behaviour and physiology of fish to alarm substance was disrupted thereby altering their predator avoidance strategies. For most animals, it is not known whether the specific chemicals that comprise the alarm cue are conserved as prey animals' age. In brook char (*Salvelinus fontinalis*) chemical(s) that act as the alarm cue for fish of different age/size classes may be identical and there may be other chemicals (s) that allow the test fish to distinguish between cues from fish of different ages/sizes, or the cues though not identical may be similar enough to be recognized (Mirza and Chivers 2002). Similarly, Rainbow trout elicit a stress response when exposed to stress-related alarm cues released from conspecifics, with plasma cortisol levels increasing at 12 hrs in fish exposed to water from a stressed fish and skin extract from a stressed fish. However, plasma glucose and hepatic hsp70 levels were not affected (Toa et al. 2004).

Olfactory response

The sense of olfaction in all the living things of world is unique and special (Padodara and Jacob, 2014).

Olfaction plays a major role in general animal awareness. Sommerville and Broom (1998), defined it as 'a state in which complex brain analysis is used to process stimuli or constructs based on memory'. Size of the nasal epithelium is a good indicator of the degree of an animal's sense of smell because the number of olfactory receptor cells per unit surface area is a constant. Olfaction when linked to memory allows the animal to recollect the sensory characteristics of the feed and also whether the metabolism of that feed is favourable to it. Thus animals exhibit 'nutritional wisdom' (Padodara and Jacob, 2014).

Fish have very sensitive noses and they are sensitive to both urine and faeces (Hubbard 2017). The behavioural and olfactory (electroolfactogram - EOG) responses observed with exposure to $PGF_2\alpha$ alpha and its metabolites suggest these compounds function as reproductive pheromones in brown trout and lake whitefish (Laberge and Hara 2003). However, Electroolfactogram (EOG) recordings from female Mozambique tilapia (*Oreochromis mossambicus*) suggested that chemical communication might be important in Mozambique tilapia, the exact chemical identity of the compounds involved, and their biological functions remain to be elucidated (Frade et al. 2002). Pheromone communication in tench (*Tinca tinca* L.), established that males have a high olfactory sensitivity to some typical teleost sex steroids (glucuronidated 17,20 beta-P) and prostaglandins which act as pheromones (Pinillos et al. 2002). In freshwater fish, reproductive pheromone release occurs through urine but since marine animals produce less urine, faeces was considered to be a possible route for pheromone release (Hubbard 2017). PGF2α itself does not directly induce male preference in cichlids. Rather, it plays a vital role that primes females to become attractive via an alternative male olfactory receptors (Li et al. 2023).

Uses of pheromones

Conservation of endangered species

Pheromones can be used for the conservation of endangered species like the European eel (*Anguilla anguilla*). Using their highly developed sense of smell (Huertas et al. 2008), sex pheromones could be used in hatchery operation protocols to induce reproduction, produce offspring and restore their population. Petromyric acid A (PMA) - a fatty acid derivative functions as a component of the sea lamprey migratory pheromone. Based on chemical, physiological, and behavioural evidence, Li et al. (2018a) suggested that PMA may be used for both control and conservation of sea lamprey populations.

To facilitate trapping

Helps in population control or to sterilize animal and re-release thus affecting the reproductive potential. Pheromone used along with other cues like light or sound (that attract the fishes) would be more successful (Sorensen and Stacey 2004).

Assess population

The concentration of species or gender-specific pheromone can be assessed in natural waters which could help to understand the population strength (or even presence/absence) of the aquatic animal. Fine and Sorensen (2004) using electrospray mass spectrophotometry tried to detect it in sea lamprey migratory pheromone.

Understand reproductive function

By expanding the pheromone (hormonal) research to non-traditional aquatic species will help to understand the varied nature of fish mating systems which will enhance our knowledge about fish reproductive function (Stacey 2003). PGE_2 revealed as functional novel molecule which activates black rockfish mating behaviour (Lyu et al. 2024).

CONCLUSIONS

In the aquatic medium, since visual information is limited the aquatic animals have to rely on their sense of olfaction especially to detect the pheromones released by the conspecifics. Pheromones affect the normal physiology and reproduction in all the aquatic species and are specific in their action and are detected in very minute (picomolar) concentrations. Alarm pheromones have been reported to be interspecific and intergeneric. Olfactory recordings have provided meagre proof that the patterns of hormone detection among closely related species are the selection for specificity. Moreover, the discovery of pheromones has increased the understanding of the fish reproductive function and also provides valuable model systems for future studies on the olfactory function and evolution of pheromones (Stacey et al. 2003).

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REFERENCES

Acquistapace, P., Aquiloni, L., Hazlett, B.A. and Gherardi, F. 2002. Multimodal communication in crayfish: sex recognition during mate search by male *Austropotamobius pallipes*. Canadian Journal of Zoology, 80(11), 2041-2045. https://doi.org/10.1139/z02-171

Aday, D.D., Wahl, D.H. and Philipp, D.P. 2003. A mechanism for social inhibition of sexual maturation in bluegill. Journal of Fish Biology, 62(2), 486-490. https://doi.org/10.1046/j.1095-8649.2003.00033.x

Appelt, C.W. and Sorensen, P.W. 2007. Female goldfish signal spawning readiness by altering when and where they release a urinary pheromone. Animal Behaviour, 74(5), 1329-1338. https://doi.org/10.1016/j.anbehav.2007.02.032

Bhatt, J.P., Purohit, M.K., Nautiyal, R. and Kandwal, J.S. 2004. Priming response in male *Schizothorax richardsonii* to the ovarian steroid glucuronides from conspecific and heterospecific females. Indian Journal of Animal Science, 74(11), 1169-1173. https://epubs.icar.org.in/index.php/IJAnS/article/view/39445

Christopher, B. 1994. Alarm Pheromones in Fish: Functional and Evolutionary Aspects. http://www.colostate.edu/Depts/Entomology/courses/en570/papers_1994/bosio. html)

Chung-Davidson, Y.S., Huertas, M. and Li, W. 2011. A review of research in fish pheromones. Pp 467-482. In: Breithaupt, T. and Thiel, M. (Eds.), Chemical Communication in Crustaceans. Springer Science, New York. https://doi.org/10.1007/978-0-387-77101-4_24

Colombo, L., Marconato, A., Belvedere, P.C. and Frisco, C. 1980. Endocrinology of teleost reproduction: a testicular steroid pheromone in the black goby, *Gobius jozo* L. Bulletin of Zoology, 47, 355-364. https://doi.org/10.1080/11250008009438692

Corkum, L.D. and Belanger, R.M. 2007. Use of chemical communication in the management of freshwater aquatic species that are vectors of human diseases or are invasive. General and Comparative Endocrinology, 153(1/3), 401-417. https://doi.org/10.1016/j.ygcen.2007.01.037

Corkum, L.D., Arbuckle, W.J., Belanger, A.J., Gammon, D.B., Li, W.M., Scott, A.P. and Zielinski, B. 2006. Evidence of a male sex pheromone in the round goby (*Neogobius melanostomus*). Biological Invasions, 8(1), 105-112. https:/ /doi.org/10.1007/s10530-005-0333-y

Fine, J. and Sorensen, P.W. 2004. Mass spectrometry demonstrates the presence of pteromyzonal sulfate in river water. In: Mason, R. and Muller-Schwarze, D. (Eds.), Advances in Chemical Signals in Vertebrates. Kluwer Academic/Plenum Publishers, New York.

Frade, P., Hubbard, P.C., Barata, E.N. and Canario, A.V.M. 2002. Olfactory sensitivity of the Mozambique tilapia to conspecific odours. Journal of Fish Biology, 61(5), 1239-1254. https://doi.org/10.1111/j.1095-8649.2002.tb02468.x

Fraser, E.J. and Stacey, N. 2002. Isolation increases milt production in goldfish. Journal of Experimental Zoology, 293(5), 511-524. https://doi.org/10.1002/jez.10120

Hardege, J.D., Bartels-Hardege, H.D., Fletcher, N., Terschak, J.A., Harley, M., Smith, M. A., Davidson, L., Hayden, D., Müller, C.T., Lorch, M., Welham, K., Walther, T. and Bublitz, R. 2011. Identification of a female sex pheromone in *Carcinus maenas*. Marine Ecology Progress Series, 436, 177-189. https://www.int-res.com/home/?eID=secured download&pdffile=%2Farticles%2Fmeps2011%2F436%2Fm436p177.pdf

Hong, W-S., Chen S-X., Zhang Q-Y. and Zheng W-Y. 2006. Sex organ extracts and artificial hormonal compounds as sex pheromones to attract broodfish and to induce spawning of Chinese black sleeper (*Bostrichthys sinensis Lacepede*). Aquaculture Research, 37(5), 529-534. https://doi.org/10.1111/j.1365-2109.2006.01462.x

Hubbard, P. 2017. Sole Pheromones: 'What we have here is a failure to communicate?' Atlas of Science. http://atlasofscience.org.

Huertas, M., Canário, A. and Hubbard, P. 2008. Chemical communication in the genus *Anguilla*: a minireview. Behaviour, 145(10), 1389-1407. https://doi.org/10.1163/15685390 8785765926

Jaensson, A., Scott, A.P., Moore, A., Kylin, H. and Olsen, K.H. 2007. Effects of a pyrethroid pesticide on endocrine responses to female odours and reproductive behaviour in male parr of brown trout (*Salmo trutta* L.). Aquatic Toxicology, 81(1), 1-9. https://doi.org/10.1016/j.aquatox.2006.10.011

Karlson, P. and Lüscher, M. 1959. 'Pheromones': a new term for a class of biologically active substances. Nature, 183(4653), 55-56. https://doi.org/10.1038/183055a0

Kashyap, N., Eswaran, S., Ramasre, J.R., Chandravanshi, S. and Kashyap, C. 2024. Harmonizing underwater: Exploring the influence of pheromones on fish communication and behaviour. Chronicle of Aquatic Science, 1(9), 67-72. https://chronicleofaquaticscience.in/public/temp/2073/44aa37bb6dcbb53753fea468108244f4.pdf

Kobayashi, M., Sorensen, P.W. and Stacey, N.E. 2002. Hormonal and pheromonal control of spawning behavior in the goldfish. Fish Physiology and Biochemistry, 26(1), 71-84. https://doi.org/10.1023/A:1023375931734

Laberge, F. and Hara, T.J. 2003. Behavioural and electrophysiological responses to F-prostaglandins, putative spawning pheromones, in three salmonid fishes. Journal of Fish Biology, 62(1), 206-221. https://doi.org/10.1046/j.1095-8649.2003.00020.x

Li, C.Y., Lawrence, K., Merlo-Coyne, J. and Juntti, S.A. 2023. Prostaglandin F2á drives female pheromone signaling in cichlids, revealing a basis for evolutionary divergence in olfactory signaling. Proceedings of the National Academy of Sciences, 120(1), e2214418120. https://doi.org/10.1073/

pnas.2214418120

Li, J., Wang, Y., Guo, T., Xu, S., Gao, G., Liu, F., Guo, X., Wu, Y., Zhao, H. and Li, J. 2023. Phenethylamine is a potential density stress pheromone in Turbot (*Scophthalmus maximus*). Fishes, 8(10), 506. https://doi.org/10.3390/fishes8100506

Li, K., Brant, C.O., Huertas, M., Hessler, E.J., Mezei, G., Scott, A.M., Hoye, T.R. and Li, W. 2018a. Fatty-acid derivative acts as a sea lamprey migratory pheromone. Proceedings of the National Academy of Sciences, 115(34), 8603-8608. https://doi.org/10.1073/pnas.1803169115

Li, K., Buchinger, T.J. and Li, W. 2018b. Discovery and characterisation of natural products that act as pheromones in fish. Natural Products Report, 35(6), 501-5013. https://doi.org/10.1039/C8NP00003D

Li, Y., Yan, Z., Lin, A., Yang, X., Li, X., Yin, X., Li, W. and Li, K. 2024. Epidermal oxysterols function as alarm substances in zebrafish. Iscience, 27(5), 1-16. https://doi.org/10.1101/2023.09.26.559639

Lyu, L., Yao, Y., Xie, S., Wang, X., Wen, H., Li, Y., Li, J., Zuo, C., Yan, S., Dong, J. and Qi, X. 2024. Mating behaviors in ovoviviparous black rockfish (*Sebastes schlegelii*): molecular function of prostaglandin E2 as both a hormone and pheromone. Marine Life Science & Technology, 6, 15-30. https://doi.org/10.1007/s42995-023-00214-w

Mathis, A. and Smith, R.J.F. 1993. Intraspecific and cross-superorder responses to chemical alarm signals by brook stickleback. Ecology, 74, 2395-2404. https://doi.org/10.2307/1939590

Miranda, A., Almeida, O.G., Hubbard, P.C., Barata, E.N. and Canario, A.V.M. 2005. Olfactory discrimination of female reproductive status by male tilapia (*Oreochromis mossambicus*). Journal of Experimental Biology, 208(11), 2037-2043. https://doi.org/10.1242/jeb.01584

Mirza, R.S. and Chivers, D.P. 2002. Brook char (*Salvelinus fontinalis*) can differentiate chemical alarm cues produced by different age/size classes of conspecifics. Journal of Chemical Ecology, 28(3), 555-564. https://doi.org/10.1023/A:1014544112763

Moore, A., Olsen, K.H., Lower, N. and Kindahl, H. 2002. The role of F-series prostaglandins as reproductive priming pheromones in the brown trout. Journal of Fish Biology, 60(3), 613-624. https://doi.org/10.1111/j.1095-8649.2002.tb01688.x

Olsen, K.H., Sawisky, G.R. and Stacey, N.E. 2006. Endocrine and milt responses of male crucian carp (*Carassius carassius* L.) to periovulatory females under field conditions. General and Comparative Endocrinology, 149(3), 294-302. https://doi.org/10.1016/j.ygcen.2006.06.011

Padodara, R.J. and Jacob, N. 2014. Olfactory sense in different animals. The Indian Journal of Veterinary Science, 2(1), 1-14.

Pandey, A.K. 2005. Recent advances in fish pheromone research with emphasis on their potential applications in fisheries. Journal of Applied Zoology Research, 16(2), 210-216. https://connectjournals.com/file_html_pdf/1299401H_A1.pdf

Park, D. and Propper, C.R. 2002. Pheromones from female mosquitofish at different stages of reproduction differentially affect male sexual activity. Copeia, 4, 1113-1117. https://www.jstor.org/stable/1448533

Pfeiffer, W. 1963. The fright reaction of North American fish. Canadian Journal of Zoology, 41, 69-77. https://doi.org/10.1139/z63-009

Pinillos, M.L., Guijarro, A.I., Delgado, M.J., Hubbard, P.C., Canario, A.V.M. and Scott, A.P. 2002. Production, release and olfactory detection of sex steroids by the tench (*Tinca tinca* L.). Fish Physiology and Biochemistry, 26(2), 197-210. https://doi.org/10.1023/A:102542192044

Power, J. and Couturier, C. 2006. Growth, feeding and motile behaviour in blue mussels (*Mytilus* sp.) in the presence of the starfish, *Asterias vulgaris*. Special Publication of Aquaculture Association of Canada, 12, 32-35.

Rice, P., Ray, S.M., Painter, S.D. and Nagle, G.T. 2002. An intrinsic membrane protein in oyster sperm stimulates spawning behaviors in *Crassostrea virginica*: implications for aquaculture. Journal of Shellfish Research, 21(2), 715-718.

Rodriguez Canto, A., Arredondo Figueroa, J.L., Ponce Palafox, J.T. and Rouse, D.B. 2002. Growth characteristics of the Australian redclaw crayfish, *Cherax quadricarinatus*, cultured in an indoor recirculating system. Journal of Applied Aquaculture, 12(3), 59-64. https://doi.org/10.1300/J028v12n03_06

Sato, K. and Suzuki, N. 2001. Whole-cell response characteristics of ciliated and microvillous olfactory receptor neurons to amino acids, pheromone candidates and urine in rainbow trout. Chemical Senses, 26(9), 1145-1156. https://doi.org/10.1093/chemse/26.9.1145

Scott, G.R., Sloman, K.A., Rouleau, C. and Wood, C.M. 2003. Cadmium disrupts behavioural and physiological responses to alarm substance in juvenile rainbow trout (*Oncorhynchus mykiss*). Journal of Experimental Biology, 206(11), 1779-1790. https://doi.org/10.1242/jeb.00353

Smith, R.J.F. 1979. Alarm reaction of Iowa and johnny darters (Etheostoma, Percidae, Pisces) to chemicals from injured conspecifics. Canadian Journal of Zoology, 57, 1278-1282. https://doi.org/10.1139/z79-164

Smith, R.J.F. 1982. Reaction of *Percina nigrofasciata, Ammocrypta beani*, and *Etheostoma swaini* (Percidae, Pisces) to conspecific and intergeneric skin extracts. Canadian Journal of Zoology, 60, 1067-1072. https://doi.org/10.1139/z82-14

Smith, R.J.F. 1992. Alarm signals in fishes. Reviews of Fish Biolology and Fisheries, 2, 33-63. https://doi.org/10.1007/BF00042916

Smith, R.J.F. and Lawrence, B.J. 1992. The response of a bumblebee goby, *Brachygobius sabanus*, to chemical stimuli from injured conspecifics. Environmental Biology of Fish, 34:103-108. https://doi.org/10.1007/BF00004789

Smith, R.J.F., Lawrence, B.J. and Smith, M.J. 1992. Cross-reaction to skin extract between gobies, *Asteropteryx semipunctatus* and *Brachygobius sabanus.* Journal of Chemical Ecology, 17, 2253-2259. https://doi.org/10.1007/BF00988005

Sommerville, B.A. and Broom, D.M. 1988. Olfactory awareness. Applied Behaviour Science 57, 269-286. https://doi.org/10.1016/S0168-1591(98)00102-6

Sorensen, P.W. and Stacey, N.E. 2004. Brief review of fish pheromones and discussion of their possible uses in the control of non-indigenous teleost fishes. New Zealand Journal of Marine Freshwater Research, 38(3), 399-417. https://doi.org/10.1080/00288330.2004.9517248

Sorensen, P.W., Pinillos, M and Scott, A.P. 2005. Sexually mature male goldfish release large quantities of androstenedione into the water where it functions as a pheromone. General and Comparative Endocrinology, 140(3), 164-175. https://doi.org/10.1016/j.ygcen.2004.11.006

Sorensen, P.W., Vrieze, L.A. and Fine, J.M. 2003. A multi component migratory pheromone in the sea lamprey. Fish Physiology and Biochemistry, 28(1), 253-257. https://doi.org/10.1023/B:FISH.0000030545.39156.2b

Stacey, N. 2003. Hormones, pheromones and reproductive behaviour. Fish Physiology and Biochemistry, 28(1/4), 229-235. https://doi.org/10.1023/B:FISH.0000030540.99732.2c

Stacey, N., Chojnacki, A., Narayanan, A., Cole, T. and Murphy, C. 2003. Hormonally derived sex pheromones in fish: exogenous cues and signals from gonad to brain. Canadian Journal of Physiology and Pharmacology, 81(4), 329-341.https://doi.org/10.1139/y03-024

Stacey, N., Fraser, E.J., Sorensen, P. and van der Kraak, G. 2001. Milt production in goldfish: regulation by multiple social stimuli. Comparative Biochemistry and Physiology C, Toxicology and Pharmacology, 130(4), 467-476. https://doi.org/10.1016/S1532-0456(01)00273-3

Thibaut, R and Porte, C. 2004. Effects of endocrine disrupters on sex steroid synthesis and metabolism pathways in fish. Journal of Steroid Biochemistry and Molecular Biology, 92(5), 485-494. https://doi.org/10.1016/j.jsbmb.2004.10.008

Toa, D.G., Afonso, L.O.B. and Iwama, G.K. 2004. Stress response of juvenile rainbow trout (*Oncorhynchus mykiss*) to chemical cues released from stressed conspecifics. Fish Physiology and Biochemistry, 30(2), 103-108. https://doi.org/10.1007/s10695-005-0266-5

von Frisch, K. 1941a. Uber einen Schreckstoff der Fischhaut und seine biologische Bedeutung. Zeitschrift für Vergleichende Physiologie, 29, 146-145. https://doi.org/10.1007/BF00304445

von Frisch, K. 1941b. Karl Escherich zum siebzigsten Geburtstage. Naturwissenschaften, 29(38), 561-563. https://doi.org/10.1007/BF01481763

Vrieze, L.A. and Sorensen, P.W. 2001. Laboratory assessment of the role of a larval pheromone and natural stream odour in spawning stream localisation by migratory sea lamprey. Canadian Journal of Fisheries and Aquatic Science, 58(12), 2374-2385. https://doi.org/10.1139/f01-17

Wagner, C.M., Jones, M.L., Twohey, M.B. and Sorensen, P.W. 2006. A field test verifies that pheromones can be useful for sea lamprey (*Petromyzon marinus*) control in the Great Lakes. Canadian Journal of Fisheries and Aquatic Science, 63(3), 475-479. https://doi.org/10.1139/f06-008

Wyatt, T.D. 2003. Animals in a chemical world. Pp. 1-22. In: Wyatt, T.D. (Ed.) Pheromones and Animal Behaviour. Cambridge University Press, U.K. https://doi.org/10.1017/CBO9780511615061

Yambe, H. and Yamazaki, F. 2001. Species-specific releaser effect of urine from ovulated female masu salmon (*Oncorhynchus masou*) and rainbow trout (*Oncorhynchus mykiss*). Journal of Fish Biology, 59(6), 1455-1464. https://doi.org/10.1111/j.1095-8649.2001.tb00211.x

Yambe, H., Kitamura, S., Kamio, M., Yamada, M., Matsunaga, S., Fusetani, N. and Yamazaki, F. 2006. L-kynurenine, an amino acid identified as a sex pheromone in the urine of ovulated female masu salmon. Proceedings of National Academy of Science, USA, 103(42), 15370-15374. https://doi.org/10.1073/pnas.0604340103

Yambe, H., Munakata, A., Kitamura, S., Aida, K. and Fusetani, N. 2003. Methyltestosterone induces male sensitivity to both primer and releaser pheromones in the urine of ovulated female masu salmon. Fish Physiology and Biochemistry, 28(1/4), 279-280. https://doi.org/10.1023/B:FISH.0000030554.18246.70

Zippel, H.P., Gloger, M., Luthje, L., Nasser, S. and Wilcke, S. 2000. Pheromone discrimination ability of olfactory bulb mitral and ruffed cells in the goldfish (*Carassius auratus*). Chemical Senses, 25(3), 339-349. https://doi.org/10.1093/chemse/25.3.339

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