

RECENT ADVANCES IN FISH PHEROMONE RESEARCH WITH EMPHASIS ON THEIR POTENTIAL APPLICATIONS IN AQUACULTURE AND FISHERY MANAGEMENT

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ABSTRACT – Most of vital activities of fish like alarm communication, sex attraction and synchronization of reproductive processes, individual identification, group cohesion, parent-offspring recognition, territorial markings and migration are shaped by pheromones. The involvement of chemical signals has been assessed mainly by the behavioural responses, chemical nature of these languages are being explored. Various aspects pertaining to fright reaction and alarm substances, sex pheromones and synchronization of reproductive processes, individual recognition and social structure as well as fish migration have been discussed. Problems associated with chemoreception under environmental pollution have been emphasized. Possibilities of utilizing pheromones in advancing maturation and breeding of cultivable species as well as in management of native fish and containment of the invasive/alien species are also highlighted.

Key words : Alarm pheromones, sex pheromones, individual recognition, migration, aquatic pollution.

INTRODUCTION

Recent studies have shown the wide distribution of chemical signals among all organisms ranging from protozoans to mammals (Scheuer, 1977; Croll, 1983; Dalozze *et al.*, 1983; Pandey, 1984, 1987, 2003; Duvall *et al.*, 1986; Burke, 1986; Doty and Muller-Schwarze, 1992; Watts *et al.*, 1993; Bushmann and Atema, 1996; Lonsdale *et al.*, 1998; Schneider and Moore, 2000; Jonston *et al.*, 1999; Slattery *et al.*, 1999, Johnston, 2003; Wyatt, 2003, 2009) including human beings (Wysocki and Preti, 2004, 2010). There are instances of chemical communication in yeast and aquatic plants especially for the attraction of gametes (Maier and Mueller, 1986; Mueller *et al.*, 1990; Kodama *et al.*, 1993; Boland, 1995). Pheromones (Greek: pherein- to carry or transfer; hormon- to excite or stimulate) are the substances which are secreted to outside by an individual and received by second individual of the same species, in which they release a specific reaction, for example, a definite behaviour (releaser pheromones) or developmental process (primer pheromones) (Karlson and Luscher, 1959). Unlike hormones, these substances are not secreted into the blood circulation but into the environment and produce effects involving a large degree of genetic programming and influenced little by experience (Pfeiffer, 1982; Sorensen *et al.*, 1998; Pandey, 2005). They are low molecular weight (80-300) volatile organic compounds in case of the terrestrial animals (Duvall *et al.*, 1986) whereas the semiochemicals of aquatic species appear to be larger in size (high molecular weight) and soluble in water (Liley, 1982; Hara, 1982;

Pandey, 1984, 2003; Sorensen, 1992; Lebedeva and Golovkina, 1994). Studies have demonstrated that odours emanating from an individual have encoded messages of its race, sex, age and biological status, however, it is rather difficult to predict which of the many chemicals released by the organism might have pheromonal effect (Sorensen and Stacey, 1999, 2004; Wyatt, 2003, 2009).

Though chemical senses are the most ancient of the sensory systems having evolved about 500 million years ago, studies regarding fish chemoreception have been delayed because they, unlike insects and mammals, live in the aquatic environment and the role of olfaction among this class of vertebrates was poorly understood (Hara, 1975). Teichmann (1962) demonstrated that fishes do have exquisitely sensitive organs of smell like dogs and even 3-4 molecules of the odorants were sufficient to evoke a behavioural response. Sorensen (1996) remarked that living in an aquatic environment, generally devoid of visual cues but rich in dissolved compounds, fish have evolved highly developed chemosensory and pheromonal signaling systems. Studies during the past four decades covering about more than one hundred species have proved that most of the vital activities of fish like alarm communication, sex attraction and synchronization of reproductive processes, individual identification, group cohesion, parent-offspring recognition, territorial markings and even migration are shaped by pheromones but our knowledge in this field is still fragmentary as we know their existence only by behavioral responses, chemical nature of these languages are now being explored

(Parzefall, 1973; Barnett, 1977; Solomon, 1977; Jolly, 1980; Liley, 1982; Colombo *et al.*, 1982; Smith, 1982a, 1992; Stacey, 1983, 2003; Stacey and Sorensen, 1991; van Weerd and Richter, 1991; Hara, 1992; Saglio, 1992; Sorensen and Scott, 1994; Sorensen, 1996; Pandey, 1998, 2005, 2009; Sorensen and Stacey, 2004; Hubbard and Scott, 2007; Burnard *et al.*, 2008). The mitral cells located in medial tracts of the olfactory pathway convey the pheromonal responses to the brain while the lateral olfactory bundlets are responsible for transducing the feeding stimuli in fishes (Doving and Selsø, 1980; Thommessen, 1982, 1983; Sorensen, 1996; Hansen *et al.*, 1998; Hamdani and Doving, 2006). An attempt has been made to discuss the recent advances in fish pheromones research and highlight the potential applications of such substances in aquaculture and fishery management.

Alarm Substances

Similar to the distress calls of birds and monkeys, alarm pheromones of fish communicate the presence of nearby danger to its conspecifics (Smith, 1986). Phylogenetically, such chemical alarm systems have been identified from the sea anemones to tadpoles of toads (Pfeiffer, 1962, 1963, 1974, 1982; Howe and Seikh, 1975; Smith, 1977, 1992; Chivers and Smith, 1994; Chivers *et al.*, 1999; Commons and Mathis, 1999; Brown and Godin, 1997, 1999; Brown and Brennan, 2000). von Frisch (1938) was the first who accidentally discovered fright reactions in the European minnows (*Phoxinus phoxinus*) when he introduced a mechanically injured (physically damaged) fish to the school of minnows, all members became

frightened, retreated and took refuge in a hidden place within 30-60 seconds. He showed that the skin contained alarm substance (substance d' alarme, Schreckstoff) which elicited fright reaction (reaction d' effroi, Schreckreaktion) among the minnows (von Frisch, 1941). Depending upon the species, alarm behaviour comprises rapid dashing, c-turns, hiding, immobility (freezing), cohesiveness or avoidance of the area (Pfeiffer, 1977, 1982; Malyukina *et al.*, 1977; Waldman, 1982; Smith, 1982a, 1992; Mathis *et al.*, 1995; Nordell, 1998; Brown *et al.*, 2000, 2003; Mirza *et al.*, 2001; Haney *et al.*, 2001; Wiesenden *et al.*, 2004; McCormick and Larson, 2007). *Puntius javanicus* exhibited c-turn behaviour and avoided the area when exposed to conspecific skin extract (Pandey and Chithar, unpublished). The chemically induced alarm reaction can be transmitted visually to other members of the school/ shoal (Pfeiffer, 1977; Smith, 1977, 1982a). There are reports that even the closely-related species also respond to alarm pheromones and experience also plays role in such perception (Smith, 1982b; Brown *et al.*, 1995; Chivers *et al.*, 1995; Wisenden *et al.*, 1995). There are instances that the predator northern pike (*Esox lucius*) consuming the preys (*Pimephales promelas* and *Culaea inconstans*) containing the ASCs in skin, releases the alarm pheromone in the faecal matter which are detected by the members of its own or closely-related species.

The distribution of alarm substance and fright reaction among different groups of fishes attracted wide attention (Pfeiffer, 1962, 1963, 1974, 1977, 1982; Gandolfi *et al.*,

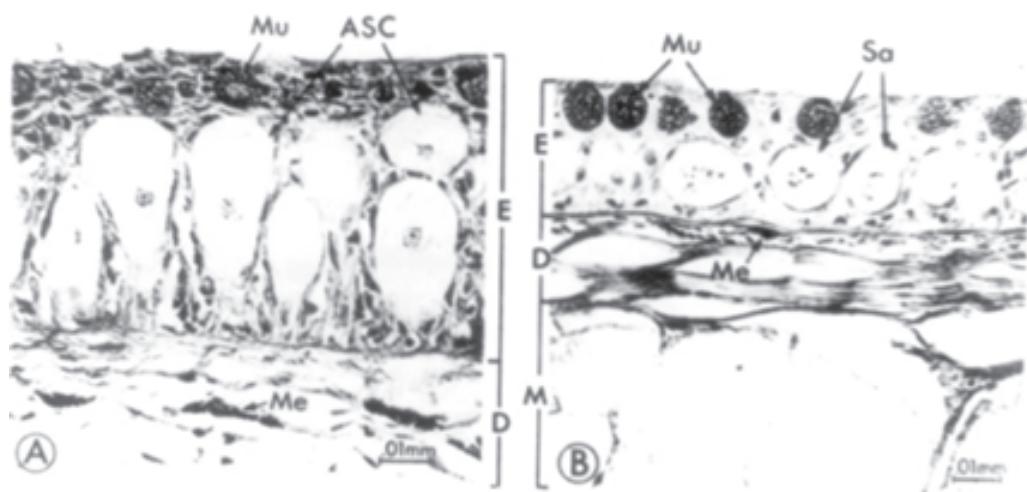


Fig. 1: The skin of two groups of fish that exhibit alarm response to skin extract. (a) The skin of an ostariophysan fish, the bluehead chub (*Nothonotus leptocephalus*) showing the alarm substance cells (ASC) in the epidermis. (B) The skin of the tessellated darter (*Etheostoma olmstedi*) exhibiting the sacciform cells (Sa) that may contain darter alarm pheromone. (ASC, alarm substance cells; D, dermis; E, epidermis, M, muscle; Me, melanophores; Mc, mucous cells; Sa, sacciform cells) (after Smith, 1986; Courtesy: R. Jan F. Smith and Plenum Press, New York).

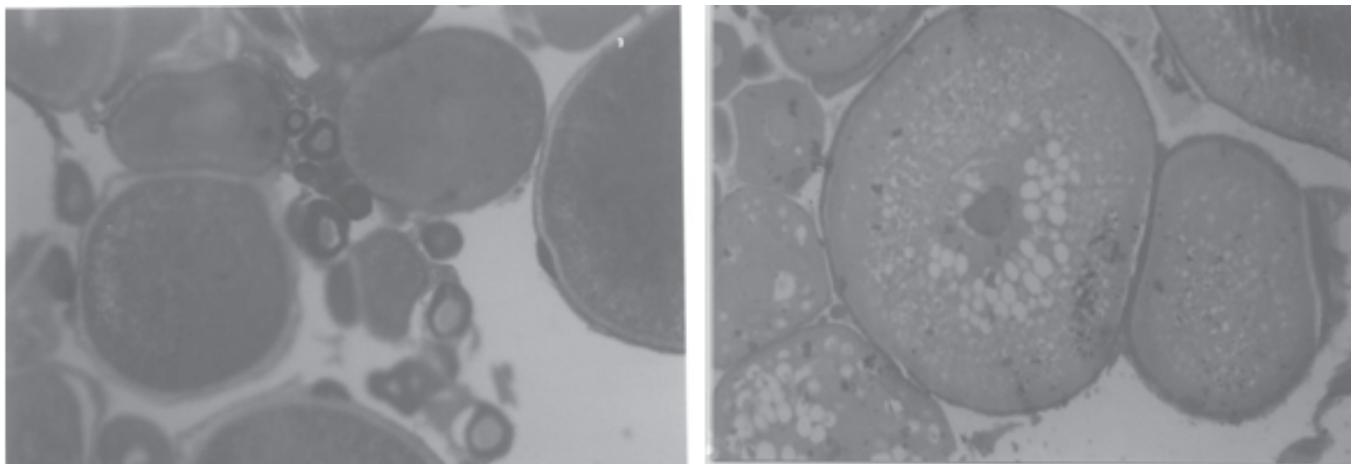


Fig. 2 : Ovary of *H. fossilis* - the site of sex signals and index to record the primer effects of male pheromone.

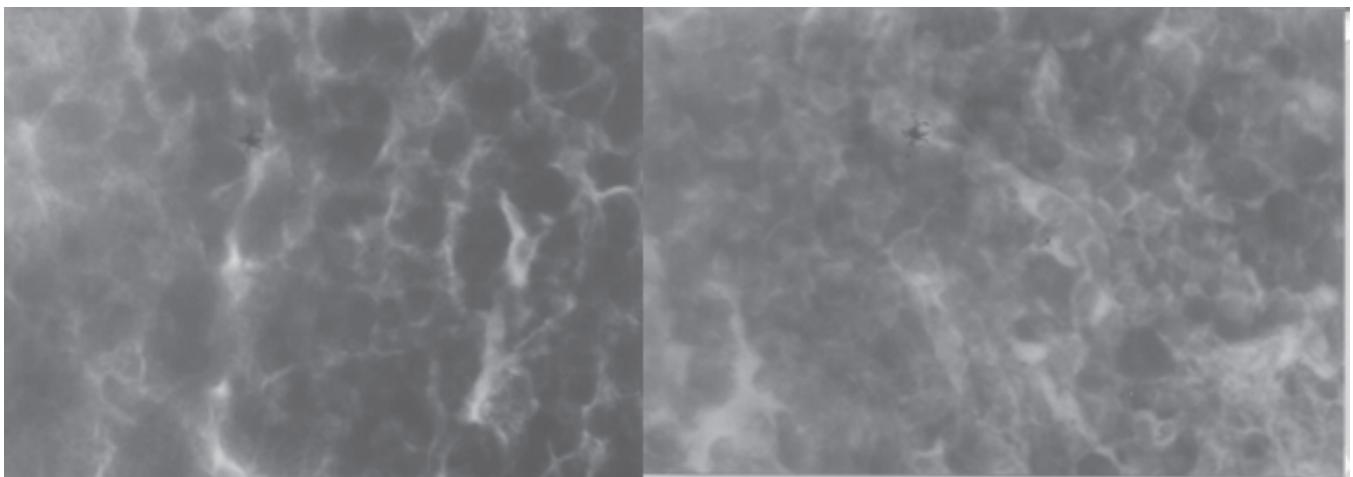


Fig. 3 : . Proximal pars distalis of *H. fossilis* showing gonadotrophs- a tool in primer sex pheromone studies.

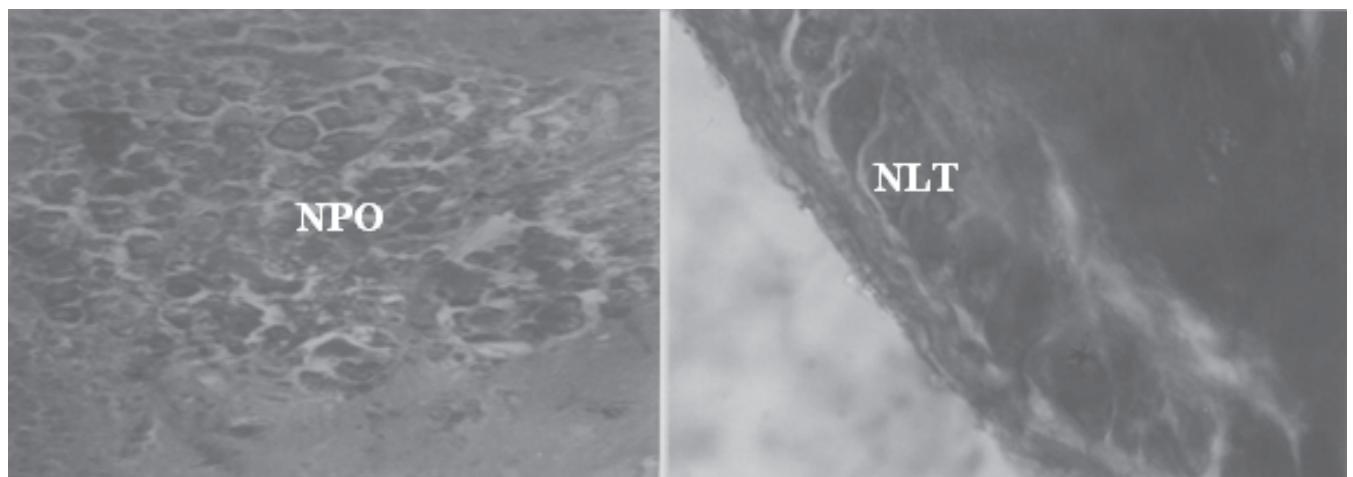


Fig. 4 : Hypothalamus of *H. fossilis* showing nucleus preopticus (NPO, left) and nucleus lateralis tuberis (NLT, right) - an importat link for neuroendocrine modulation of primer pheromones.

1969; Gandolfi, 1972; Thines and Legrain, 1973; Aoki and Kuroki, 1975; Carmichael, 1975; Smith, 1977, 1982a; Heczko, 1980; Ahsan and Prasad, 1982; Mathis *et al*, 1995; Nordell, 1997; Berejikian *et al*, 1999; Commens, 2000; Maniak *et al*, 2000; Mirza and Chivers, 2001; McCormick and Larson, 2007). It has been demonstrated that skin of ostariophysan, gonorhynchiform, perciform and other groups of fishes contains alarm pheromone in their large epidermal cells known as club cells (Kolbenzellen), alarm substance cells (ASCs) or sacciform (Sa) cells (Fig. 1). Though the club cells (presumably homologous to ASCs) have been identified in the primitive reedfish, *Erpetoichthys (Calamoichthys) calabaricus* (Polypteriformes) but the skin extract of this fish does not elicit fright reaction among conspecifics (Hugie and Smith, 1987). Ultrastructurally, alarm substance cells of *Ictalurus punctatus* contained fine homogenously dispersed fibrillar material, cytoplasmic granules concentrated peripherally, tubular type mitochondria with matrix granules (30-50 nm diameter), nucleus irregular with distinct nucleolus, and lysosomes and lipid inclusions in vicinity of the nucleus. Histochemically, proteins were demonstrated in ASCs of channel catfish but carbohydrates were not detected (Yoakim and Grizzle, 1982). These cells do not open directly to the surface of skin but release their contents only after a mechanical injury, presumably by a predator. Interestingly, alarm pheromones are also released into the environment along with the faecal matters of the predatory fishes following consumption of the prey (Brown *et al*, 1995). As per adaptive significance of alarm pheromone is concerned, it is assumed that alarm pheromone diffusing into the surrounding medium alerts and deters conspecifics from the hunting spots thus reducing hunting success of the predators (Smith, 1977; Chivers and Smith, 1998). Alternately, the alarm pheromone diffusing in the medium may function to attract additional predators that interfere with the predation act providing opportunity for the prey to escape (Mathis *et al*, 1995). The response to alarm pheromones appears to be innate and develops in late larval or early juvenile stages (Waldman, 1982). Further, possession of the alarm substance in fishes also reduces cannibalism of young. There exist ample evidences that the fish shows a strong fright reaction after eating its smaller conspecifics (Smith 1977). In a natural stream, the minnow (*Pimephales promelas*) avoided the traps marked with conspecific alarm pheromone (Mathis and Smith, 1992) Interestingly, males of certain ostariophysian fishes with abrasive spawning behaviour loose alarm substance cells during breeding season due to elevated levels of androgen (testosterone) but they still retain the

alarm reaction appropriate to their own species (Smith, 1973, 1976 a, b, 1978, 1979, 1982b; Pfeiffer *et al*, 1985a; Smith and Smith, 1986). Starvation/food deprivation appears to affect alarm reaction of *Ethyostoma exile* to skin extract of the conspecifics (Smith, 1981). Wisenden and Smith (1998) observed that presence of unfamiliar shoal-mate enhances the alarm substance cell counts whereas familiarity with the shoal-mate reduces proliferation of these cells among the ostariophysian fishes. Stabell and Lwin (1997) observed phenotypic changes like increase in body depth in crucian carp (*Carassius carassius*) exposed to the odour of northern pike fed on crucian carps. These phenotypic changes appear to be due to primer effect of the alarm pheromone.

Attempts have been made to identify chemical nature of the alarm pheromone of fish. Huttel (1941) suggested the minnow alarm substance to be purine- or pterin-like (double-ringed compounds usually associated with pigments), non-volatile and extremely water soluble. Histamine was also indicated to be alarm substance of certain cyprinids (Reed *et al*, 1972) while Pfeiffer and Lemke (1973) recorded the alarm substance of *Phoxinus phoxinus* to be pterine (isoxanthopterin). Needham (1974) suggested that pterine might be conjugated with a protein carrier to give species-specificity. However, Kasumyan and Lebedeva (1977, 1979) and Lebedeva and Golovkina (1994) showed that the alarm pheromone of the minnow (*Phoxinus phoxinus*) possesses molecular weight approximately 1100, behaves in alkaline medium (pH 8-9) as anion and breaks down when heated. They suggested it to be a carbohydrate compound containing amino groups or a peptide. Hypoxanthine-3-(N)-oxide has been reported to be an active component of the minnow (*Phoxinus phoxinus*) and black tetra (*Gymnophorus ternetzi*) alarm signaling system (Pfeiffer, 1978, 1982; Pfeiffer *et al*, 1985b). The central bundles in both tractus olfactorii of the medial olfactory tract of fish conduct the nervous excitation elicited by alarm substance to the higher centres in brain (Pfeiffer *et al*, 1984) resulting in elevation of plasma cortisol, glucose, potassium (K^+) and sodium (Na^+) levels while plasma calcium (Ca^{2+}) depicted an initial increase followed by decline to below normal level suggesting the alarm pheromone to serve as stressor to the recipient fish (Malyukina *et al*, 1982; Lebedeva and Golovkina, 1994, 1999).

Female Sex Pheromones

There exist reports on congregations of salmonid males around the cages/pens of the mature females during breeding seasons. Fishermen of Mississippi river usually catch large number of male channel catfish, *Ictalurus punctatus*, by placing ripe females in cages of flowing

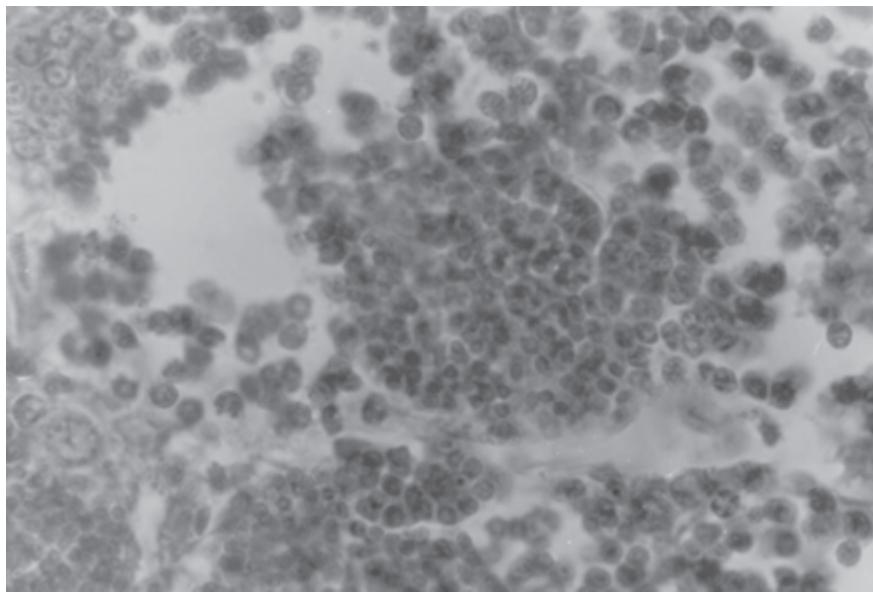
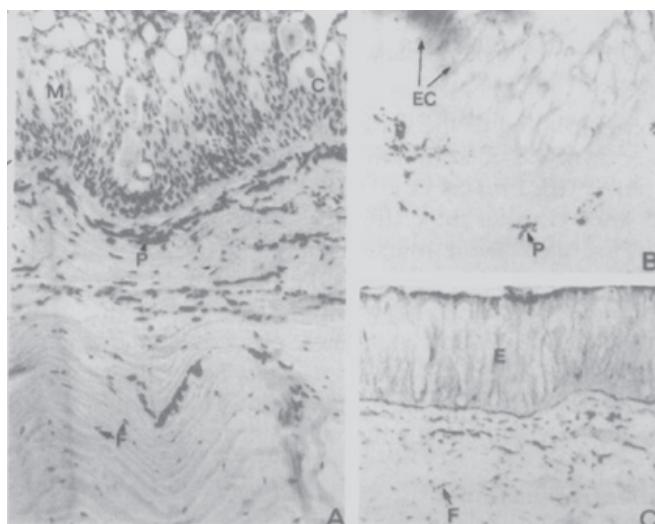


Fig. 5: Testis of *Tor putitora* - a source of male pheromones and tool for assessing primer effects of female sex pheromones.



Fig. 6 : *Heteropneustes fossilis* forming a tight school even during night.



river (Timms and Kleerekoper, 1972). Tavolga (1956) was the first who systematically studied the sexual behaviour of an estuarine goby, *Bothygobius soporator* and demonstrated that the spermated (matured) male discriminates between males and females, and also between non-gravid and gravid females on basis of the chemical cues released through their vent. Ovarian fluid was sufficient to evoke courtship behaviour in the males even in absence of females. Gravid female cichlid fish (*Haplochromis burtoni*) becomes attractive to the males during breeding season (Crapon de Caprom, 1974). Water from gravid females seems to increase the nesting and other activities among the males associated with reproduction in anabantids (Rossi, 1969) and cichlids (Crapon de Caprona, 1974). Partridge *et al* (1976) observed that the female goldfish releases a pheromone just after ovulation through vent which induced sexual behaviour among the males. Similar observations were also recorded in *Plecoglossus altivelis* (Honda, 1979), *Oncorhynchus mykiss* (Honda, 1980a), *Misgurnus anguilllicaudatus* (Honda 1980b), *Rhodurus ocellatus ocellatus* and *Acheilognathus laneolatus* (Honda, 1982a), *Oncorhynchus masau* and *Oncorhynchus rhodurus* (Honda,

1982b; Kitamura and Ogata, 1989; Yambe *et al*, 1999; Yambe and Yamazaki, 2000, 2001a), *Anguilla rostrata* (Sorensen and Winn, 1984) and *Oncorhynchus mykiss* (Yambe and Yamazaki, 2001b). A female sex pheromone appears to facilitate pair formation and copulation in the marine carcharhinid shark (Johnson, 1978). Also, mature female sea lamprey, *Petromyzon marinus*, releases a pheromone in the ovarian fluid that attracts male

Fig. 7 : Histological section of the skin of *Clarias gariepinus*. (A) General structure (Haemealum-eosin x 230).(B) 17 α -hydroxysteroid dehydrogenase with weak enzyme activity in the epithelial cells. X145. (C) Uridine-di-phospho-glucose dehydrogenase (UDPGD) enzyme activity is demonstrated in the epidermis and fibroblasts. X 145. (C, club cells; D, dermis; E, epidermis; Ec, epithelial cells; F, fibroblasts; M, mucous gland; P, pigment; SC, stratum compactum; SV, stratum vasculare) (after Ali *et al*, 1987; Courtesy: S.A. Ali and Academic Press, New York).

conspecifics (Teeter, 1980). A definite threshold of circulating androgen is essential to render the male differentially sensitive to the sex attractant released by gravid females (Yamazaki and Watanabe, 1979; Irvine and Sorensen, 1993; Cardwell *et al*, 1995; Yambe and Yamazaki, 2000, 2001b). Hamdani *et al* (2008) recorded seasonal variations in olfactory sensitivity of the epithelial crypt cells of crucian carp which coincided with the elevated circulating androgen level.

Mature females of goldfish (*Carassius auratus*-Kobayashi *et al*, 1986; Dulka *et al*, 1987; Defraipont and Sorensen, 1993; Stacey *et al*, 1994a; Sorensen *et al*, 1995; Zeng and Stacey, 1997; Zeng *et al*, 1997), yellowfin Baical sculpin (*Cottocomephorus grewingki*-Dmitrieva *et al*, 1988), Atlantic salmon (*Salmo salar*- Moore and Waring, 1996 a; Waring *et al*, 1996), rainbow trout (*Salmo gairdneri*= *Oncorhynchus mykiss*-Scott *et al*, 1994; Vermeirssen *et al*, 1997), Baikal cisco (*Coregonus automnalis migratorius*-Ostroumov and Dmitrieva, 1991), common carp (*Cyprinus carpio communis*-Billard *et al*, 1989; Sorensen *et al*, 1992; Stacey *et al*, 1994b) release primer pheromone in the urine which enhances plasma gonadotropin (GtH) and testosterone (T) levels within 15-30 minutes and milt (sperm and seminal fluid) volume as well as sperm motility among conspecific males after prolonged exposure (6 hours in case of goldfish (Zeng and Stacey, 1996 1997; Ostroumov *et al*, 1996; Stacey, 2003; Sorensen and Stacey, 2004). Males of grey mullet (*Mugil cephalus*) exposed to GnRH+domperidone-treated females registered higher levels of serum 11-ketotestosterone (11-KT) which may probably be due to the release of female sex pheromones (Aizen *et al*, 2005). Dulka *et al* (1992) observed a reduction in pituitary dopamine turnover ensuing enhanced gonadotropin secretion in the males goldfish exposed to the female sex pheromone. Interestingly, mature female *Oreochromis niloticus* becomes attractive to males after 17,20-dihydroxy-4-pregnen-3-one injection (De Souza *et al*, 1998). Though the exact chemical identity of the primer pheromones is not known but the maturation-inducing hormone, 17,20-dihydroxy-4-pregnen-3-one and its sulphate or glucuronide metabolites are the likely candidates because they induce electroolfactogram (EOG) recordings in the olfactory tract even at concentration from 10^{-9} - 10^{-13} mM. The primer pheromone released by the Atlantic salmon (*Salmo salar*) has been suggested to be F-type prostaglandin (Waring and Moore, 1997). Urine of the female evokes maximum response among the conspecific males pointing to the species-specificity of the pheromone (Kitamura and Ogata, 1989; Scott *et al*, 1994; Waring *et al*, 1996; Waring and Moore, 1997).

Mature females release chemical couplin (s) during ovulation which elicits attraction (locomotor behaviour), courtship and spawning in male conspecifics (Gandolfi, 1969; Theissen and Sturdivant 1977; Crow and Liley, 1979; Emanuel and Dodson, 1979; Liley, 1982; Pfeiffer, 1982; Pandey, 1984, 2005, 2009; Johanson, 1985; Yamazaki, 1990; Stacey and Sorensen, 1991; Sorensen, 1996; Sorensen *et al*, 1997; Leberge and Hara, 2003; Burnard *et al*, 2008; Bandypadhyay and Singh, 2009). Theissen and Sturdivant (1977) reported the role of thyroid hormone in releaee of sex attractant in female black molly, *Mollinesnsis latipinna*. Such releaser pheromones induce an immediate response (within 10-30 minutes) without altering the plasma concentration of gonadotrophin (Liley, 1982; Stacey, 1983; Sorensen and Scott, 1994; Yambe *et al*, 1999). Amouriq (1965) was the first to suggest female sex attractant (substance dynamoge'ne) of *Lebestes reticulatus* to be an oestrogen as hexestrol dipropionate elicited courtship behaviour among males. Okada *et al* (1978) demonstrated that the fraction (FP₁) on DEAE cellulose column that evoked male courtship behaviour in pond smelt, *Hypomesus olidus*, declined in activity after heat (80°C; 5 minutes) or trypsin (30°C; 60 minutes) treatments and presumed the substance in genital fluid was either a protein or a substance involving protein in its structure. Kawabata *et al* (1993) reported amino acids as inducer of sexual behaviour in male *Rhodurus occellatus occellatus*. L-Kynurenine (an amino acid) has been reported to serve as sex pheromone of *Oncorhynchus masau* (Yambe *et al*, 2006a) In *Pimephales promelas* (Cole and Smith, 1987), *Carassius auratus* (Sorensen *et al*, 1988), *Salvelinus alpinus* (Sveinsson and Hara, 1995), *Oncorhynchus rhodurus* (Kitamura and Ogata, 1989), *Misgurnus anguillicaudatus* (Kitamura and Ogata, 1990, 1993; Ogata *et al*, 1993, 1994; Kitamura *et al*, 1994) and *Astyanax mexicanus* (Cardwell and Stacey, 1995) the metabolites of prostaglandin F₂α (PGF₂α) like 15-keto-, 13,14-dihydro-15-keto-PG F₂α are suggested to function as releaser pheromones. Interestingly, Matsumura (1995) recorded tetrodotoxin as sex attractant pheromone to spermating males in the marine puffer fish (*Fugu niphobles*). Releaser pheromone found in the urine of mature female masu salmon appears to be one or more low molecular weight (less than 10,000) substance soluble in ether under basic condition (Yambe *et al*, 1999).

McKinnon and Liley (1987) and Cardwell *et al* (1992) have suggested the releaser pheromone(s) to function as reproductive isolating mechanism in sympatrically breeding gourami (*Trichogaster trichopterus* and *Trichogaster pectoralis*) and suckers (*Catostomus*

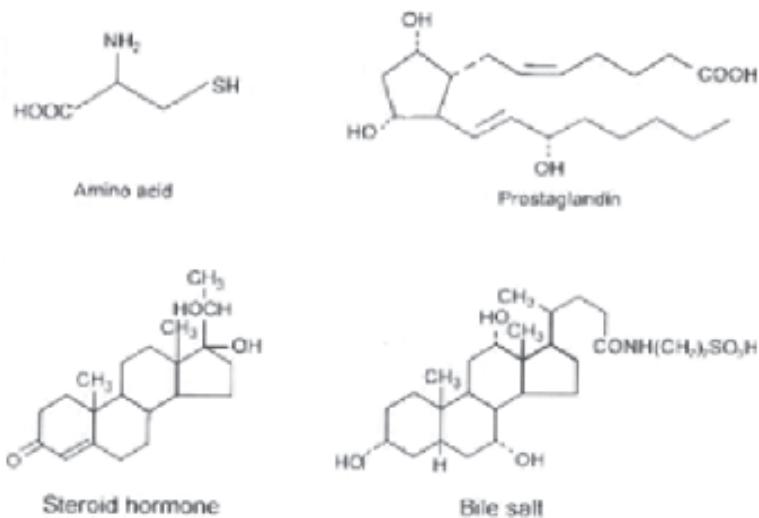


Fig. 8 : General chemical structures of four major aquatic odorants for fish (after Hara 1992; Courtesy: T.J. Hara and Chapman & Hall, London).

catastomus and *Catastomus commersoni*). As per definition, the pheromones should be species-specific but there are instances of closely-related species sharing to the sex pheromones (Rossi, 1969; Irvine and Sorensen, 1993; Essington and Sorensen, 1996; McLennan and Ryan, 2008) such as goldfish, *Carassius auratus*, crucian carp, *Carassius carassius* (Bjerselius and Olsen, 1993) and goldfish and common carp, *Cyprinus carpio* (Irvine and Sorensen, 1993). Hybridization/interbreeding among closely-related species including brook trout, *Salvelinus fontinalis* and brown trout, *Salmo trutta* is assumed to be due to sharing of the same pheromonal system of prostaglandin F and its derivatives (Essington and Sorensen, 1996). However, other signals like visual, auditory, tactile and electrical are also involved in spawning which may not be overlooked while discussing the process of hybridization/interbreeding in natural environment (Rossi, 1969; Irvine and Sorensen, 1993; Olsen *et al*, 2000; Burnard *et al*, 2008). Pheromone(s) are being implicated in mate choice of *Gasterosteus aculeatus* and *Xiphophorus birchmanni* (Milinski, 2003; Fisher and Rosenthal, 2006).

Male Sex Pheromones

During breeding season, males become attractive to the female conspecific. Sodefrin, a novel peptide pheromone secreted by the cloacal gland of newt, *Cynops pyrrhogaster* attracts sexually developed females (Kikuyama *et al*, 1998). The male tree frog, *Litoria splendida* releases sex-attracting pheromone, slendiphreneine, from paratoid and rostral gland that attracts females (Wabnitz *et al*, 1998). Male fish advertises its presence to the females by permeating the aquatic environment with male odours (Zielinski *et al*, 2003). In

some regions of France, male lampreys nearing sexual maturity are placed by the fishermen in the traps to attract females (Fontaine, 1976). The odouriferous secretion of the cutaneous anal gland (rich in mesorchial interstitial cells) of male *Blennius pavo* attracts the females during breeding season (Eggert, 1931). Laumen *et al* (1974) found that appendices of the 1st and 2nd anal fin spines of mature male *Blennius pavo* produce a pheromone which attracts conspecific females. Histological study revealed the presence of numerous invaginations in epidermis of the appendices and secretion of this pheromone is dependent on circulating gonadotropin levels. Burns and Weitzman (1996) suggested the gill gland of male swardtail characin, *Corynopoma riisei* as source of sex attractant pheromone. Sperm-duct gland of freshwater goby, *Padogobius martensi* appears to secrete sex attractant substance (Cinquetti and Rinaldi, 1987; Cinquetti, 1997). Jaski (1939) demonstrated that males of guppy, *Poecilia reticulata* secrete a “chemical couplin” which synchronizes the sexual receptivity among females. Water-borne substance (s) produced by the mature males that attract females to suitable spawning sites have also been described in rainbow trout, *Oncorhynchus mykiss* (Newcombe and Hartman, 1973), black goby, *Gobius joso* (Colombo *et al*, 1980), fathead minnow, *Pimephales promelas* (Cole and Smith, 1992), Arctic char, *Salvelinus alpinus* (Sveinsson and Hara, 1995) and round goby, *Neogobius melanostomus* (Murphy *et al*, 2001; Zielinski *et al*, 2003; Corkum *et al*, 2006; Marentette and Corkum, 2008). Male *Xiphophorus birchmanni* releases sex attractant pheromone in pulses in urine positioning upstream of females (Rosenthal *et al*, 2010). Colombo *et al* (1980) identified the male sexual pheromone of *Gobius joso* to be etiocholenolone glucuronide. Male sexual

pheromone of the round goby induces gill ventilation in females during breeding season appears to be derivatives of etiocholenolone (Murphy *et al*, 2001). Mature males of Arctic char become more odorous and release metabolites of prostaglandin F₂α to attract mature females and induce spawning behaviour (Sveinsson and Hara, 1995). Interestingly, male masu salmon (*Oncorhynchus masou*) parr avoid the proximity of sexually active males due to a pheromone released in the urine (Yambe *et al*, 2006b).

Teeter (1980) and Adams *et al* (1987) showed the presence of a pheromone in the urinogenital fluid of male sea lamprey, *Petromyzon marinus*, which elicited courtship behaviour in the females. Out of the nine steroid hormones (dehydroepiandrosterone, testosterone, dihydrotestosterone, progesterone, androstenedione, estrone, oestradiol, corticosterone and cortisol) tested, only testosterone evoked a preference response in spawning-run female sea lamprey. Testosterone or a closely related structural derivative was suggested as sex pheromone in the male cyclostome (Adams *et al*, 1987). However, recent studies have shown 7α,12α,24-trihydroxy-5α-cholan-2-one-24-sulphate (3 keto-petromyzonol sulphate, 3 keto-PZS), a bile acid derivative, as sex pheromone of spermating sea lamprey which induces search and preference behaviour in ovulating females signaling reproductive readiness as well as nest location. Mature ovulating females of *Petromyzon marinus* showed strong tendency to select traps with spermating males (Johnson *et al*, 2005, 2009; Wagner *et al*, 2006). This pheromone appears to be synthesized in hepatocytes and released in large amount via gill epithelia (Bjerselius *et al*, 1995a; Li and Sorensen, 1997; Li *et al*, 2002, 2003; Yun *et al*, 2002; Siefkes *et al*, 2003).

Seminal vesicles of male African catfish, *Clarias gariepinus*, secrete sex pheromone that attracts females during breeding season. Though 17 free and 8 glucuronide metabolites of sex hormones have been identified in the seminal vesicle fluid (SVF) but 5β-pregnene-3α, 17α-diol-20-one glucuronide and 5β-androstene-3α,17α-diol are more potent olfactory stimulants with threshold value 10⁻⁹mM (Schoonen, 1987; Resink, 1988). Wild breeding male *Clarias gariepinus* recorded 20-folds elevation in level of 5β-pregnene-3α,17 α-diol-20-one glucuronide in the seminal vesicle as compared to those maintained under captivity which may probably be the reason for lack of natural spawning in the catfish kept in ponds (van den Hurk and Resink, 1992).

Mature males of zebrafish, *Brachydanio rerio*, release a pheromone that induced ovulation among females (Chen and Martinich, 1975). Using gas

chromatography-mass spectrometry (GC-MS), van den Hurk *et al* (1987) observed the presence of glucuronides of 5α -androstane-3α,17β-diol and cholesterol in male-holding water and suggested that these compounds, probably originating from liver, may be functioning as ovulation-inducing pheromones in this species (van den Hurk and Resink, 1992).

In fishes, males appear to have the most profound effect on the neuroendocrine (hypothalamo-hypophysial-gonad) system the females (Fig. 2-5). Mosher (1954) reported that when a male is introduced into the group of females, it stimulated egg production and its continued presence led to regular oviposition cycles. In the angelfish (*Pterophyllum scalare*), blue gourami (*Trichogaster trichopterus*) and Indian catfish (*Heteropneustes fossilis*), paired females with males possessed ovaries filled with matured ova while ovaries of the grouped females (without males) contain almost no ova but numerous oocytes at various stages of development (Chien, 1973; Pollack *et al*, 1978; Pandey *et al*, 2000). Exposure to other female odours in *Brachydanio rerio* led to severe reproductive suppression because the females exposed to male odours produced 17% more viable eggs than did non-exposed females and 26% more viable eggs than did females exposed to female odour (Gerlach, 2006). There is evidence that the male pheromone(s) of African catfish, *Clarias gariepinus*, accelerates ovarian recrudescence and ovulation among the females probably by enhancing plasma gonadotropin (GtH) level (van Weerd, 1990; van den Hurk and Resink, 1992). Degani and Schreibman (1993) reported that the aquarium water in which mature male *Trichogaster trichopterus* built nests induced the release of immunoreactive gonadotropin (GtH) from hypophysis (pituitary) resulting in enhanced plasma 17β-estradiol (E₂), 17α,20β-dihydroxy-4-pregnene-3-one (17,20-P), 5β-pregnene-3,17α, 20β-triol and 11-ketotestosterone (11-KT) as well as vitellogenetic activities suggesting the primer effects of male pheromone on female blue gourami. Since unisexual groupings of the females (without males) disrupts (inhibits) the ovarian development (Pandey *et al*, 2000; Pandey, 2005), it offers opportunity to explore the female-female interacting primer pheromones in fishes.

Intrasexual Stimulants and School Formation

Though reports on the odouriferous secretions eliciting male-male and female-female stimulations are rare in vertebrates but the possibilities have been raised from time to time (Crapon de Crapona, 1976; Duvall *et al*, 1986). From the auxillary (underarm) sweat of human (both sexes), androstenol has been identified which arouses both the sexes (Kingsbury and Brooksbank, 1978;

Wysocki and Preti, 2010). Among fishes, male three-spined stickleback, *Gasterosteus aculeatus*, gets stimulated by smelling the odours of its own nest during breeding season. Losey (1969) demonstrated that males of *Hypsoblennius jenkinsi*, *H. robustus* and *H. genitilis* secrete a chemical during “high courting and mating periods” that releases the sexual appetitive behaviour and sexual receptivity among the males. A pheromone is found in the milt of male herring, *Clupea harengus pallasi* that triggers spawning behaviour (papilla extension) and release of milt in the males (Stacey and Hourston, 1982; Sherwood *et al*, 1991; Carolsfield *et al*, 1997a). This pheromone shows hydrophobic properties similar to those of polar steroids, prostaglandins, or other conjugate forms, and at least one form appears to contain a sulphate or glucuronide group (Sherwood *et al*, 1991). The role of male pheromone has been suggested in synchronization of spawning in the school of herrings. Further, Carolsfield *et al* (1997b) showed that elevated levels of plasma 3α , 17α -dihydroxy- 5β -pregnen-20-one and 17α -hydroxyprogesterone coincided with responsiveness to the spawning pheromone in these fish.

The possibility of involvement of pheromones in school formation and attraction of the mature conspecifics towards the spawning grounds was speculated by McFarland and Moss (1967). Presence of an aggregating pheromone has been implicated in schooling of the Japanese marine catfish, *Plotosus lineatus* (Hayashi *et al*, 1994). Bloom and Perlmutter (1977) have demonstrated the presence of male-male and female-female attractants in the zebrafish, *Brachydanio rerio*. Further, they suggested that the sexual aggregating pheromone system in the zebrafish may serve as reproductive isolating mechanism in the sympatrically breeding *Brachydanio rerio* and *Brachydanio albolineatus* (Bloom and Perlmutter, 1978). Teeter (1980) also hypothesized the involvement of pheromones in aggregating adult lampreys (*Petromyzon marinus*) prior to upstream movement or to keep them together in night during the migration. Algranti (1980) suggested the sexual-aggregating pheromones of zebrafish to be two in number-one attracting male conspecifics and other the females. Interestingly, this attraction was not affected by food or diet of the fish. Algranti and Perlmutter (1981) found that the attractants were contained in the cholesterol-ester fraction (R_f - 0.94) of the thin-layer chromatogram.

Individual Recognition

Some fishes display social organization with well-defined hierarchy. Since individual recognition being the cornerstone of the sociality, its members must be recognized from the individuals of other societies or

species (Ward *et al*, 2007). Individual recognition by scent is prominent in mammals (Wyatt, 2003; Thom and Hurst, 2004; Wysocki and Preti, 2010; Archunan, 2010). Todd *et al* (1967) demonstrated that the yellow bullheads (*Ictalurus natalis*), a nocturnal visually-deficient fish, recognizes individuals of its own group by means of pheromones secreted in the skin mucus. Methanol extract of the mucus was also attractive in the top smelt, *Atherinops affinis* (Rosenblatt and Losey, 1967). Individuals of *Salvelinus alpinus* (Hoglund and Astrand, 1973; Hoglund *et al*, 1975; Selset and Doving, 1980; Olsen, 1989, 1990), *Clupea herringus pallasi* (Dempsey, 1978), *Caecobarbus geertsi* (Berti and Thines, 1980), *Haplochromis burtani* (Crapon de Caprona, 1980), *Astyanax jordani* (Quinn, 1980), *Notropis lutrensis* (Asbury *et al*, 1981), *Oncorhynchus kisutch* (Quinn *et al*, 1983; Brannon *et al*, 1984; Quinn and Busack, 1985; Quinn and Tolson, 1986; Quinn and Hara, 1986), *Ictalurus nebulosus* (Carr and Carr, 1985), *Oncorhynchus nerka* (Groot *et al*, 1986), *Astyanax mexicanus* (Defraipont and Thines, 1986), *Phreatichthys andruzzii* (Berti *et al*, 1989; Berti and Zorn, 2001), *Carassius auratus* (Saglio, 1992), *Heteropneustes fossilis* (Pandey *et al*, 2000), *Danio rerio* (Mann *et al*, 2003), *Cyprinus carpio* and *Carassius auratus* (Sisler and Sorensen 2008) are attracted towards waters of the tank previously occupied by their conspecifics. Eels (*Anguilla anguilla*) are usually caught in the traps dripped with conspecific skin extracts (Saglio, 1982). Interestingly, a school of roach, *Rutilus rutilus*, does not disintegrate during night because members of the school maintain contact, presumably through chemical cues (Hemmings, 1966). Individuals of *H. fossilis* congregate and form tight schools during night keeping out the members of *Clarias batrachus* from their school which seems to be mediated by pheromone(s) (Fig. 6). Even broods and young are recognizable to their parents by the odours. McKaye and Barlow (1976) showed that parents of Midas cichlid fish, *Cichlasoma citrinellum*, recognize to their young by means of pheromone. Barnett (1981, 1982) demonstrated that fry of the Midas cichlid fish discriminates even between the mother and father on the basis of urine odour and remarked that the steroid titers in urine could provide information on sex and that of peptide chains in urine could indicate species. Doving *et al* (1980), Frisknes and Doving (1982), Stabell *et al* (1982), Olsen (1987) and Giaquinto and Hara (2008) suggested faecal matter, specifically the metabolites of bile salts, in individual recognition of the Arctic char (*Salvelinus alpinus*), Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*). Mature lake char (both the sexes) are attracted towards the reefs treated

with faeces of the juveniles of the same species. There exist reports that the diet also alters chemistry of the pheromones involved in individual recognition among fishes (Bryant and Atema, 1987). Interestingly, glucuronidation of sex hormones also takes place in the skin of the African catfish, *Clarias gariepinus* which may probably have certain implication in individual/sex recognition (Ali *et al*, 1987) (Fig. 7). Recently, Kime and Ebrahimi (1997) recorded synthesis of 17 α ,20 α -dihydroxy-4-pregnen-3-one, 17 α ,20 β -dihydroxy-4-pregnen-3-one, 11-ketotestosterone and other sex hormone conjugates in the gill of goldfish, common carp and trout suggesting gill epithelia to play a role in secretion of pheromones in these species.

During reproductive period, male of some species deposits a layer of mucus on spawning surface which may serve as chemical signals marking the breeding sites and may perhaps communicate status of the occupants (Smith and Murphy, 1974). There exist reports on the substrate marking behaviour in fishes and secretions of mucus, urophysis (caudal neurosecretory system) and urine have been implicated in the production/release of the territorial marking pheromones (Richard, 1974; Milligan, 1978; Atkin and Fink, 1979; Rubec, 1979; Stabell, 1987). Possibly, these marks bear the same biological significance as marking fluid (MF) of the mammals (Brahmachary, 1985; Brahmachary *et al*, 1991; Wyatt, 2009).

Beneficial conditioning of the water by conspecifics and inhibition/retardation of growth under over-crowded condition are assumed to be mediated through pheromones (Yu and Perlmutter, 1970; Francis *et al*, 1974; Solomon, 1977). Todd (1971) remarked that fighting and stress also alter the chemistry of the pheromones of yellow bullhead, *Ictalurus natalis* secreted in the mucus. Dominant male *Oreochromis mossambicus* exhibited increased urination frequency during aggressive behaviour suggesting the presence of a urinary "dominance" pheromone to modulate aggression in rivals (Almedida *et al*, 2005; Barata *et al*, 2007). There exists report that diets also modify the general odour of the catfish (Bryant and Atema, 1987). Chemical modulation of agonistic display has been observed in Siamese fighting fish, *Betta spendens* and the presence of an aggression-suppressing pheromone has been suggested in this species (Colyer and Jenkins 1976; Ingersoll *et al*, 1976). Carr and Carr (1986) observed that the aggression-suppressing pheromone of brown bullhead, *Ictalurus nebulosus* gets inactivated by heat and protease treatments and suggested a protein with molecular weight less than 10,000 as reasonable candidate for the water-borne pheromone.

Pheromones and Migration

How migratory fish locate their pathways from sea to freshwater and *vice versa* remains a mystery (Harden Jones, 1968; Quinn, 1985, 1990; Black and Dempson, 1986; Brannon and Quinn, 1990). Much work has been done on the homing of salmonids. Claussen Friss (1599-cited by Selset, 1980) remarked that these fishes migrate from the nursery areas to their parental river streams, out to sea and then back to their birth place to spawn (basis of the home-stream theory). Later, Buckland (1880) suggested that each stream has "unique bouquet of odours" and the fish has to "follow its nose" in the detection and discrimination of the natal stream. Though the role of metabolic products of a specific population (pheromones) as homing cues for the salmonids was proposed by Chidester (1924) and White (1934) but this hypothesis was totally eclipsed by the concept of "olfactory imprinting" propounded by Hasler and Wisby (1951) and Hasler *et al* (1978). According to this theory, the young "lock onto" the odours of aquatic vegetations, soil run-off, and other organic chemicals present in the parent stream in their brain and they "retain the olfactory memory" during the interim period of their homeward migration (Hasler and Cooper, 1976; Cooper *et al*, 1976; Hasler, 1983).

Nordeng (1971) realized the pheromone odour tracks to help guide homing of the Arctic char, *Salmo alpinus*. Solomon (1973) demonstrated that the migrating Atlantic salmon, *Salmo salar*, prefers the river in which young of its own populations were living. After exhaustive studies on *Salmo alpinus*, *Salmo trutta* and *Salmo salar*, Nordeng (1977) rejuvenated the pheromone hypothesis. He remarked that the homeward navigation is an inherent response to population-specific pheromone trails released from the descending smolts. The role of pheromones in upstream orientations has been confirmed in rainbow trout, *Oncorhynchus mykiss* and sea lamprey, *Petromyzon marinus*-an anadromous cyclostome (Teeter, 1980; Li and Sorensen, 1997). Miles (1968) demonstrated that elvers of the European eel, *Anguilla rostrata* are attracted towards the water of the streams inhabiting adults of the same species. Sorensen (1984) also corroborated this finding. Stabell (1992) remarked that the specific homing to a native site is under genetic influence and the possible genetic contamination of pheromones due to hatchery escapes or random stocking programmes might seriously interfere with the homing performance and population structure. He emphasized for introduction of the concept of chemical ecology in management practices of commercially important salmonid fisheries.

Our knowledge regarding the chemical nature of these

navigational cues is still fragmentary. Miles (1968) found the compound(s) involved with attraction of the elvers in *Anguilla rostrata* to be biodegradable, unaffected by autoclaving and non-volatile. Atema *et al* (1973) reported alwife, *Alosa pseudoharengus*, homing pheromones to be heat-stable, non-volatile, polar with molecular weight less than 1,000. Doving *et al* (1980) demonstrated the Arctic char, *Salmo alpinus*, migratory cue(s) are present in faecal matter of the smolts, likely to be derivatives of bile salts like taurolithocholate, taurolithocholic sulphate, sulphotaurolithocholate or taurochenodeoxycholate which convey the information to brain through medial portion of the olfactory tract (Thommenssen, 1982, 1983). By employing electrophysiological, biochemical and behavioural approaches, Zhang (1997) also confirmed the chemostimulatory roles of 9 out of 38 authentic bile acids in lake char, *Salvelinus namaycush* and remarked that the olfactory sensitivity and specificity of bile acids were affected by (i) position and orientation of hydroxyls, (ii) hydroxysulphation, (iii) side chain length and (iv) side chain substituents of the molecules. Petromyzonol sulphate (PS), petromyzonamine disulphate (PADS), petromyzosterol disulphate (PSDS) and 3-keto allocholic acid have been identified as migratory pheromone in *Petromyzon marinus* (Li and Sorensen, 1997; Yun *et al.*, 2002, 2003; Fine and Sorensen, 2008). The migratory pheromones of sea lamprey are being characterized for application in control and management of the invasive parasite under integrated pest management programme (IPM) (Li *et al*, 2007; Sorensen and Hoye, 2007; Wagner *et al*, 2006, 2009, 2011; Fine and Sorensen, 2008; Vrieze *et al.*, 2010, 2011).

Chemoreception and Water Pollution

Generally, four groups of chemicals like (i) amino acids, (ii) steroids, (iii) prostaglandins and (iv) bile acids (and their derivatives) (Fig. 8) have been found to be detected by the fish even at minute (10^{-7} - 10^{-13} mM) concentration and each group of chemicals have different receptors at the olfactory system (Hara, 1992). Hara (1982) has given a hypothetical model to show the mode of interaction of amino acids (which serve as feeding stimulants in fish) with olfactory receptor sites.

Bardach *et al* (1968) were the first to study effects of detergents on the chemical senses of the yellow bullhead, *Ictalurus natalis* and found that the concentration of 0.5 ppm (much lower value that inflict lethal damage) impaired the receptor functioning by causing erosion of the chemosensory organ. Bloom *et al* (1978) showed that sublethal (0.5 ppm) exposure to zinc affected the behaviour to the sexual aggregating pheromone (s) in the zebrafish, *Brachydanio rerio*. Linear alkylbenzene sulphate (LAS) significantly

depressed chemo-attraction of water conditioned by conspecifics to juvenile Arctic char, *Salvelinus alpinus* (Olsen and Hoglund, 1985). Laboratory studies have revealed that the freshwater spawning migration of salmons is being impaired by acidification of rivers (Hara, 1992; Leduc *et al*. 2009). Leduc *et al* (2004, 2008, 2009) found significant reduction in anti-predator response in juveniles of salmonids (*Oncorhynchus mykiss*, *Salvelinus fontinalis* and *Salmo salar*) under weakly acidic condition (pH 6.4) and abolished with further decrease of pH of the water under laboratory as well as field conditions. Electrophysiological recordings of the olfactory epithelium of the adult male *Salmo salar* to testosterone and urine of the ovulated females significantly reduced at pH 5.5-4.5 and abolished at pH 3.5 (Moore, 1994). Exposures of the sublethal concentrations of diazinone and carbofuran significantly reduced the ability of mature male Atlantic salmon parr to respond to priming pheromones of ovulated females (Moore and Waring 1996a; Waring and Moore, 1997).

Fisher *et al* (2006) reported impaired response of the matured female *Xiphophorus birchmanni* to the conspecific male chemical cues due (probably) to humic acid (HA) present ubiquitously in natural environment due to sewage effluent and agricultural runoff. They suggested the possible hybridization of *X. birchmanni* with *X. malinche* owing to the disruption of chemical communication.

Hara *et al* (1983) and Hara (1992) recorded the pernicious effects of an anionic detergent (sodium lauryl sulphate), pH, mercury (Hg), silver (Ag), cadmium (Cd), copper (Cu), nickel (Ni) and zinc (Zn). By calculating IC₅₀ value (concentration which inhibits electroolfactographic response by 50 %), they found Ag, Hg, Cu and Cd elicited the most depressive effects on chemoreception in salmonids. They also exposed whitefish, *Coregonus clupeaformis* and rainbow trout, *Oncorhynchus mykiss* to 2.4 mM copper sulphate (CuSO₄) solution for two weeks and noted a loss in the phospholipid stainable granules in the receptor neurones of olfactory mucosa, however, recovery in the granules were observed when the fishes were transferred to freshwater for 12 weeks (Hara, 1982). Phospholipids are involved in the electrophysiological (electroolfactogram, EOG) activities of the olfactory epithelium. There are reports that olfactory epithelial cytochrome P-450 and monooxygenase (mixed function oxidase (MFO) are activated by the pollutants (hydrocarbons and heavy metals) (Cangalon, 1983; Tierney *et al*, 2010). Since the present trends of rapid industrialization and increase in population have drastically changed the aquatic

environment, it is imperative to include studies pertaining to interactions of various pollutants with the pheromonal communication system in fishes. Barnett (1981) also remarked that the chemically polluted environment can interfere with the success of the parent care.

Conclusions

Earlier fishes were viewed as “leaky bags” that slowly release various chemicals which served as a “chemical picture” of the animal that others smell and identify as to sex, species, stress level and perhaps size and individuality (Atema, 1980). Urine, ovarian fluid, faeces and mucous are the likely vehicle for the release of pheromones in fishes (Liley, 19982; Colombo *et al.*, 1982; Yamazaki, 1990; Pandey, 2005, 2009; Yambe *et al.*, 2006a, b; Burnard *et al.*, 2008). From the foregoing discussion, it appears that fishes do employ releaser, primer and imprinter pheromones in their life (Pandey 1984, 2005, 2009; Ostroumov, 1997; Stacey, 2003; Sorensen and Stacey, 2004; Burnard *et al.* 2008). Though the chemical nature of pheromones and sites of their biosynthesis (except alarm substances) are not very clearly defined, there are growing evidences that these chemicals do have communicative roles and shape life among this Class of vertebrates (Stacey, 2003; Pandey, 2005; 2010; Burnard *et al.*, 2008)). Interestingly, GnRH has been identified as a potent olfactory stimulant in fish (Anderson and Doving, 1991) but its role in synchronization of the reproductive process is not known. Saralva and Korschning (2007) has identified a novel family of six olfactory receptor (*ora*, olfactory receptors related to class A) genes in teleost fishes (*Danio rerio*, *Gasterosteus aculeatus*, *Oryzias latipes*, *Tetradon nigroviridis* and *Takifugu rubripes*). Further studies on their expression in different Class of vertebrates will shed light on the evolution and conservation of these genes through phylogenetic evolution. Since these signals are species-specific and operate at molecular levels, they do have potentials for their applications in management and conservation of fisheries. In piscicultural operations, they may be used as selective stimulants to induce spawning at a time and place convenient to fishery managers (Liley, 1980). Since they are externally active, their delivery would eliminate the stress associated with the hormone or drug administration (Stacey *et al.*, 1991, 1992, 1994b; Zheng *et al.*, 1993, 1997). So far, only a small group of fishes have been studied mostly under controlled laboratory conditions. Such observations on fish pheromones may be extended under simulated natural environments for its better applications (van Weerd and Richter, 1991; Henderso *et al.*, 1997; Oslen *et al.*, 2006; Burnard *et al.*, 2008; Pandey, 2009; Johnson and Li, 2010).

There are growing evidence for potential utility of sex pheromones in the management/control of invasive species like sea lamprey, common carp and round goby under integrated pest management (IPM) (Zielinski *et al.*, 2003; Young *et al.*, 2003; Sorensen and Stacey, 2004; Corkum, 2004, Wagner *et al.*, 2006; Corkum and Belanger, 2007; Wagner *et al.*, 2009; Vrieze *et al.*, 2010, 2011). These chemical cues may also be employed as artificial baits, selective attractants/repellents, growth stimulators and inhibitors of aggression and cannibalism (Solomon, 1997; Wagner *et al.*, 2011). Furthermore, in not too distant future, we would be able to exploit these biogenic trace chemicals for propagating the migratory fishes in new rivers and streams.

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REFERENCES

- Adams M A, Teeter J H, Katz Y and Johnson P B (1987) Sex pheromones of the sea lamprey (*Petromyzon marinus*): steroid studies. *J. Chem. Ecol.* **13**, 387-395.
- Ahsan S N and Prasad M (1982) Occurrence of fright reaction in Indian fishes. *Biol. Bull. (India)* **4**, 41-47.
- Aizen J, Meiri I, Tzchori I, Levavi-Siaven B and Rosenfeld H (2005) Enhancing spawning in the grey mullet (*Mugil cephalus*) by removal of dopaminergic inhibition. *Gen. Comp. Endocrinol.* **142**, 212-221.
- Algranti F D (1980) Role of sex attractant pheromone (s) on spawning aggregation in the zebrafish, *Brachydanio rerio*: its isolation and partial purification. *Diss. Abstr. Intern.* **40B**, 108.
- Algranti F D and Perlmutter A (1981) Attraction of zebrafish, *Brachydanio rerio*, to isolated and partially purified chromatographic fractions. *Environ. Biol. Fishes* **6**, 31-38.
- Ali S A, Schoonen W G E J, Lambert G J D, van den Hurk R and van Oordt P G W J (1987) The skin of the male African catfish, *Clarias gariepinus*: a source of steroid glucuronides. *Gen. Comp. Endocrinol.* **66**, 415-424.
- Almeida, O G, Miranda A, Frade P, Hubbard P C, Barata E N and Canario A V M (2005) Urine as a social signal in the Mozambique tilapia (*Oreochromis mossambicus*). *Chem. Senses* **30**, 309-310.
- Amouriq L (1965) Origine de la substance dynamogène émise par *Lebistes reticulatus* female (Poisson: Poeciliidae: Cyprinodontiformes). *C. R. Acad. Sci. (Paris)* **260**, 2334-2335.
- Anderson O and Doving K B (1991) Gonadotropin releasing hormone (GnRH)- a novel olfactory stimulant in fish. *Neuroreport* **2**, 458-460.
- Aoki I and Kuroki T (1975) Alarm reaction of three Japanese cyprinid fishes, *Tribolodon hakonensis*, *Gnathopogon elongatus elongatus* and *Rhodeus ocellatus*. *Bull. Jpn. Soc. Sci. Fish.* **41**, 507-

513.

Archunan G (2010) Vertebrate pheromones and their biological importance. *J. Exp. Zool. India* **12**, 227-239.

Asbury K, Matthews W J and Hill L C (1981) Attraction of *Notropis lutrensis* (Cyprinidae) to water conditioned by the presence of conspecifics. *Southwest Nat.* **25**, 525-528.

Atema J (1980) Smelling and tasting underwater. *Oceanus* **23**, 2-18.

Atema J, Jacobson S, Todd J H and Baylan D (1973) The importance of chemicals in stimulating behaviour of marine organisms: effects of altered environmental chemistry on animal communication. In: *Bioassay Techniques and Environmental Chemistry* (ed: Glass G E), 177-197. Ann Arbor Scient. Pub., New York.

Atkins D L and Fink W L (1979) Morphology and histochemistry of the caudal gland of *Corynopoma riisei* Gill. *J. Fish Biol.* **14**, 465-469.

Baker C F (2003) Effect of adult pheromones on the avoidance of suspended sediments by migratory banded kokopu juveniles. *J. Fish Biol.* **62**, 386-394.

Bandyopadhyay M K and Singh S K (2009) Pheromone- a probable biostimulant for sympathetic spawning of the Indian major carps. In: *Recent Advances in Hormonal Physiology of Fish and Shellfish Reproduction* (eds: Singh B N and Pandey A K), 261-264. Narendra Publishing House, Delhi.

Barata E N, Hubbard P C, Almedia O G, Miranda A and Canario A V M (2007) Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). *B.M.C. Biol.* **5**, 54.

Bardach J E, Fujiya M and Holl A (1965) Detergents: effects on the chemical senses of the fish, *Ictalurus natalis* (LeSeur). *Science* **148**, 1605-1607.

Barnett C (1977) Aspects of chemical communication with special reference to fish. *Biosci. Commun.* **3**, 331-392.

Barnett C (1981) The role of urine in parent-offspring communication in a cichlid fish. *Z. Tierpsychol.* **52**, 173-182.

Barnett C (1982) The chemosensory response of young cichlid fish to parent and predators. *Anim. Behav.* **30**, 35-42.

Berejikian B A, Smith R J F, Tezak E P, Schroder S L and Knudsen C M (1999) Chemical alarm signals and complex hatchery rearing habits affect antipredator behaviour and survival of chinook salmon (*Oncorhynchus tshawytscha*) juveniles. *Can. J. Fish. Aquat. Sci.* **56**, 830-838.

Berti R and Thines G (1980) The influence of chemical signals on the topographic orientation of the cavefish, *Caecobarbus geertsii* (Pisces, Cyprinidae). *Experientia* **36**, 1384-1385.

Berti R and Zorn L (2001) Locomotory responses of the cave cyprinid, *Phreatichthys andruzzii* to chemical signals from conspecifics and related species: new findings. *Environ. Biol. Fishes* **62**, 107-114.

Berti R, Vezzosi R and Ercolini A (1989) Locomotory response of *Phreatichthys andruzzii* Vinciguerra (Pisces, Cyprinidae) to chemical signals of conspecifics and of closely-related species. *Experientia* **45**, 205-207.

Billard R, Bieniarz K, Popek W, Epler P and Sad A (1989) Observations on a possible pheromonal stimulation of milt production in carp (*Cyprinus carpio* L.). *Aquaculture* **77**, 387-392.

Bjerselius R, Sorensen P W and Li W (1995a) Spermated sea lamprey release a potent sex pheromone. In: *Proceedings of the Fifth International Symposium on Reproductive Physiology of Fish* (July 2-8, 1995) (eds: Goetz F W and Thomas P), 271. Texas A. & M. University, Austin.

Bjerselius R, Olsen K H and Zheng W (1995b) Behavioural and endocrinological responses of mature male goldfish to the sex pheromone, 17 α ,20 β -dihydroxy-4-pregnen-3-one in the water. *J. Exp. Biol.* **198**, 747-754.

Black G A and Dempson J B (1986) A test of the hypothesis of pheromone attraction in salmonid migration. *Environ. Biol. Fishes* **15**, 229-236.

Bloom H D and Perlmutter A (1977) A sexual aggregating pheromone system in zebrafish, *Brachydanio rerio* (Hamilton-Buchanan). *J. Exp. Zool.* **199**, 215-226.

Bloom H D and Perlmutter A (1978) Possible pheromone-mediated reproductive isolation in the two species of cyprinid fishes of the genus *Brachydanio*. *J. Fish Biol.* **13**, 47-50.

Bloom H D, Perlmutter A and Seeley R J (1978) Effect of sublethal concentration of zinc on an aggregating pheromone system in the zebrafish, *Brachydanio rerio* (Hamilton-Buchanan). *Environ. Pollut.* **17**, 127-131.

Boland W (1995) The chemistry of gamete attraction: chemical structures, biosynthesis, and (a) biotic degradation of algal pheromones. *Proc. Natl. Acad. Sci. (USA)* **92**, 37-43.

Brahmachary R L (1985) Ecology and chemistry of mammalian pheromones. *Endeavour (New Series)* **10**, 65-68.

Brahmachary R L, Dutta J and Poddar-Sarkar M (1991) The marking fluid of the tiger. *Mammalia (Paris)* **55**, 150-152.

Brannon E L and Quinn T P (1990) Field test of the pheromone hypothesis for homing by Pacific salmon. *J. Chem. Ecol.* **16**, 603-609.

Brannon E L, Whitman R P and Quinn T P (1984) Responses of returning coho salmon to home water and population specific odours. *Trans. Am. Fish. Soc.* **113**, 374-377.

Brown G E and Godin J -G J (1997) Anti-predator responses to conspecific and heterospecific skin extracts by three-spined sticklebacks: alarm pheromone revisited. *Behaviour* **134**, 1123-1134.

Brown G E and Godin J -G J (1999) Chemical alarm signals in wild Trinindadian guppies (*Poecilia reticulata*). *Can. J. Zool.* **77**, 562-570.

Brown G E and Brennan S (2000) Chemical alarm signals in juvenile green sunfish (*Lepomis cyanellus*, Centrachidae). *Copeia* **2000**, 1079-1082.

Brown G E, Chivers D P and Smith R J F (1995) Fathead minnows avoid conspecific and heterospecific alarm pheromones in the faeces of northern pike. *J. Fish Biol.* **47**, 387-393.

Brown G E, Adrian J C, Smyth E, Leet H and Brennan S (2000) Ostariophysan alarm pheromones: laboratory and field tests of the functional significance of nitrogen oxides. *J. Chem. Ecol.* **26**, 139-154.

Brown G E, Adrian J C and Shih M L (2001) Behavioural responses of fathead minnows to hypoxanthine-3-N-oxide at varying concentration. *J. Fish Biol.* **58**, 1465-1470.

Brown G E, Adrian J C, Naderi T, Harvey M C and Kelly J M (2003) Nitrogen oxides elicit antipredator responses in juvenile channel catfish, but not in convict cichlids of rainbow trout: conservation of the ostariophysan alarm pheromone. *J. Chem. Ecol.* **29**, 1781-1796.

Bryant B and Atema J (1987) Diet manipulation affects social behaviour of catfish: importance of body odours. *J. Chem. Ecol.* **13**, 1645-1662.

Buckland F (1880) *Natural History of British Fishes*. Unwin Pub., London.

Burke R D (1986) Pheromones and gregarious settlement of marine invertebrate larvae. *Bull. Marine Sci.* **39**, 323-331.

Burns, J R. and Weitzman S H (1996) Novel gill-derived gland in the male swordtail characin, *Corynopoma riisei* (Teleost: Characidae: Gladulocaudinae). *Copeia* **1996**, 627-633.

Bushmann P J and Atema J (1996) Nephropore rosette gland of the lobster, *Homarus americanus*: possible source of urine pheromone. *J. Crust. Biol.* **16**, 221-231.

Burnard D, Gozlan R E and Girffiths S W (2008) The role of pheromones in freshwater fishes. *J. Fish Biol.* **73**, 1-16.

Cancalon P (1983) Influence of a detergent on the catfish olfactory mucosa. *Tissue Cell* **15**, 245-258.

Cardwell J R and Stacey N E (1995) Olfactory hypersensitivity to sex pheromones in blind cavefish. In: *Proceedings of the Fifth International Symposium on Reproductive Physiology of Fish* (July 208, 1995) (eds: Goetz F W and Thomas), 272. Texas A. & M. University, Austin.

Cardwell J R, Dulka J G. and Stacey N E (1992) Acute olfactory sensitivity to prostaglandins but not to gonadal steroids in two sympatric species of *Catastomus* (Pisces: Cypriniformes). *Can. J. Zool.* **70**, 1897-1903.

Cardwell J R, Stacey N E, Tan E S P, McAdam D S O and Lang S L C (1995) Androgen increases olfactory receptor response to a vertebrate sex pheromone. *J. Comp. Physiol.* **176A**, 55-61.

Carmichael G J (1975) The fright reaction in North American teleost fishes of the Mississippi River basin. *M.Sc. Thesis*. St. Louis Univ., Missouri.

Carolsfield J M, Tester M, Kreiberg H and Sherwood N M (1997a) Pheromone-induced spawning in Pacific herring. 1. Behavioural characteristics. *Horm. Behav.* **31**, 256-268.

Carolsfield J M, Scott A P and Sherwood NM (1997b) Pheromone induced spawning in Pacific herring. 2. Plasma steroids distinctive to fish responsive to spawning. *Horm. Behav.* **31**, 269-276.

Carr M G and Carr J E (1985) Individual recognition in the juvenile brown bullhead (*Ictalurus nebulosus*). *Copeia* **1985**, 1060-1062.

Carr M G and Carr J E (1986) Characterization of an aggression-suppressing pheromone in the juvenile brown bullhead (*Ictalurus nebulosus*). *Copeia* **1986**, 540-545.

Chen L -C and Martinich R (1975) Pheromonal stimulation and metabolite inhibition of ovulation in the zebrafish, *Brachydanio rerio*. *Fish. Bull. (USA)* **73**, 889-894.

Chidester F E (1924) A critical examination of the evidence for physical and chemical influences on fish migration. *J. Exp. Biol.* **22**, 118-144.

Chien A K (1973) Reproductive behaviour of the angelfish, *Pterophyllum scalare* (Pisces: Cichlidae). II. Influence of male stimuli upon the spawning rate of females. *Anim. Behav.* **21**, 457-463.

Chivers D P and Smith R J F (1994) Intra- and interspecific avoidance of area marked with skin extract from brook sticklebacks (*Culaea inconstans*) in a natural habitat. *J. Chem. Ecol.* **20**, 1517-1524.

Chivers D P and Smith R J F (1998) Chemical alarm signaling in aquatic predatory-prey systems: a review and prospectus. *Ecoscience* **5**, 338-352.

Chivers D P, Wisenden B D and Smith R J F (1995) The role of experience in the response of fathead minnows (*Pimephales promelas*) to skin extract of Iowa darters (*Etheostoma exile*). *Behaviour* **132**, 665-674.

Chivers D P, Mathis A, Brown G E, Mirza R S and Wisenden B D (1999) Scratching the skin of predator-prey interactions in fishes: a tribute to R. Jan F. Smith (1940-1998). *Environ. Biol. Fishes* **56**, 343-350.

Cinquetti R (1997) Histochemical, enzyme histochemical and ultrastructural investigations on the sperm-duct glands of *Padogobius martensi* (Pisces: Gobiidae). *J. Fish Biol.* **50**, 978-991.

Cinquetti R and Rinaldi L (1987) Changes in the gonadal histology of *Padogobius martensi* (Pisces; Gobiidae) during reproductive cycle. *Boll. Zool.* **54**, 235-241.

Cole K S and Smith R J F (1987) Release of chemicals by prostaglandin-treated female fathead minnow, *Pimephales promelas*, that stimulates male courtship. *Horm. Behav.* **21**, 440-456.

Cole K S and Smith R J F (1992) Attraction of female fathead minnows, *Pimephales promelas*, to chemical stimuli from breeding males. *J. Chem. Ecol.* **18**, 1269-1284.

Colombo C, Marconato A, Belevedere A and Friso C (1980) Endocrinology of teleost reproduction: a testicular steroid pheromones in the black goby, *Gobius joso* L. *Boll. Zool.* **47**, 335-364.

Colombo C, Belevedere P C, Marconato A and Bentivegna F (1982) Pheromones in teleost fish. In: *Reproductive Physiology of Fish* (eds: Ritcher C J J and Goos H J Th), pp. 84-98. Cent. Docu. (PUDOC), Wageningen, The Netherlands.

Colyer S W and Jenkins C (1976) Pheromonal control of aggressive display in Siamese fighting fish (*Betta splendens*). *Percept. Motor Skills* **42**, 47-54.

Commens A M (2000) Response of three species of darters of the genus *Etheostoma* to chemical alarm signals from conspecifics and congeners. *M.Sc. Thesis*. South-West Missouri State University, Springfield, Missouri.

Commens A M, and Mathis A (1999) Alarm pheromones of rainbow darters: responses to skin extracts of conspecifics and congeners. *J. Fish Biol.* **55**, 1359-1362.

Cooper J C, Scholtz A T, Horrall R M, Hasler A D and Madison D M (1976) Experimental confirmation of the olfactory hypothesis with artificially-imprinted homing coho salmon (*Oncorhynchus kisutch*). *J. Fish. Res. Bd. Can.* **33**, 703-710.

Corkum L D (2004) Pheromone signalling in conservation. *Aquatic Conserv. Mar. Freshw. Ecosyst.* **14**, 327-331.

Corkum L D and Belanger R M (2007) Use of chemical communication in management of freshwater aquatic species that are vector of human diseases or are invasive. *Gen. Comp. Endocrinol.* **153**, 401-417.

Corkum L D, Arbuckle W J, Belanger A J, D B Gammon, Li W, A P Scott and B Zielinski (2006) Evidence of a male sex pheromone in the round goby (*Neogobius melanostomus*). *Biol. Invas.* **8**, 105-112.

Crapon de Caprona M D (1974) The effect of chemical stimuli from conspecifics on the behaviour of *Haplochromis burtoni* (Cichlidae: Pisces). *Experientia* **30**, 1394-1395.

Crapon de Caprona M D (1976) Chemical stimuli and reproduction in fish. *Experientia* **32**, 1098-1100.

Crapon de Caprona M D (1980) Olfactory communication in a cichlid fish, *Haplochromis burtoni*. *Z. Tierpsychol.* **52**, 113-134.

Croll R P (1983) Gastropod chemoreception. *Biol. Behav.* **58**, 293-319.

Crow R T and Liley N R (1979) A sexual pheromone in the guppy, *Poecilia reticulata* (Peters). *Can. J. Zool.* **57**, 184-188.

Daloze D, Braekman J C and Tursch B (1983) Chemical communication in the marine environment. In: *Marine Chemistry for Development* (ed: Kornprobst J M), 243-261. Environment Africa (Ser. Etude Rech.), Senegal.

Defraipont M and Thines G (1986) Response of the cavefish, *Astyanax mexicanus* (*Anopichthys antrobius*) to the odour of known or unknown conspecifics. *Experientia* **42**, 1053-1054.

Defraipont M and Sorensen P W (1993) Exposure to the pheromone 17 α ,20 β -dihydroxy-4-pregn-3-one enhances the behavioural spawning success, sperm production and sperm motility of male goldfish. *Anim. Behav.* **46**, 254-256.

Degani G and Schreibman M P (1993) Pheromone of male blue gourami and its effect on vitellogenesis, steroidogenesis and gonadotropin cells in pituitary of the female. *J. Fish Biol.* **43**, 475-485.

Dempsey C H (1978) Chemical stimuli as a factor in feeding and intraspecific behaviour of herring larvae. *J. Mar. Biol. Assoc. (UK)* **58**, 739-747.

De Souza S M G, Lucion A B and Wassermann G F (1998) Influence of 17 α ,20 β -dihydroxy-4-pregn-3-one injected into a post-ovulatory female on the reproductive behaviour of male Nile tilapia (*Oreochromis niloticus*). *Comp. Biochem. Physiol.* **119A**, 338-352.

Dmitrieva T M, Katsel P L, Baleyev R B, Ostroumov V A and Kozlov U P (1988) The isolation of the sexual pheromone of the male yellowfin Baikal sculpin (*Cottocomephorus grewingki*). *Biol. Nauk.* **1988**, 39-44.

Doving K B and Selset R (1980) Behaviour pattern of cod released by electrical stimulation of olfactory tract bundlets. *Science* **207**, 559-560.

Doving K B, Selset R and Thommesen G (1980) Olfactory sensitivity to bile acids in salmonid fish. *Acta Physiol. Scand.* **108**, 123-131.

Doty R and Muller-Schwarze D (1992) *Chemical Signals in Vertebrates*. Plenum Press, New York.

Dulka J G, Stacey N E, Sorensen P W and van der Kraak G J (1987) A sex steroid pheromone synchronizes male-female spawning readiness in the goldfish. *Nature* **325**, 251-253.

Dulka J G, Stacey B D, Stacey N E and Peter R E (1992) A reduction in pituitary dopamine turnover is associated with sex pheromone-induced gonadotropin secretion in male goldfish. *Gen. Comp. Endocrinol.* **86**, 496-505.

Duvall D, Muller-Schwarze D and Silverstein R M (1986) *Chemical Signals in Vertebrates. IV. Ecology, Evolution and Comparative Biology*. Plenum Press, New York.

Eggert B E (1931) Die Geschlechtsorgane der Gobiiformes. *Z. Wiss. Zool.* **193**, 249.

Emanuel M E and Dodson J J (1979) Modification of the rheotropic behaviour of male rainbow trout (*Salmo gairdneri*) by ovarian fluid. *J. Fish. Res. Bd. Can.* **36**, 63-68.

Essington T E and Sorensen P W (1996) Overlapping sensitivities of brook trout and brown trout to putative hormonal pheromones. *J. Fish Biol.* **48**, 1027-1029.

Fine J M and Sorensen P W (2008) Isolation and biological activity of the multi-component sea lamprey migratory pheromone. *J. Chem. Ecol.* **34**, 1259-1267.

Fisher H S and Rosenthal G G (2006) Female swardtail fish use chemical cues to select well-fed mates. *Anim. Behav.* **72**, 721-725.

Fisher H S, Wong B B M and Rosenthal G G (2006) Alteration of the chemical environment disrupts communication in a freshwater fish. *Proc. Royal Soc. London* **273**, 1187-1193.

Frisknes B and Doving K B (1982) Olfactory sensitivity to group-specific substances in Atlantic salmon (*Salmo salar* L.). *J. Chem. Ecol.* **8**, 1083-1092.

Fontaine M (1976) Hormones and control of reproduction in aquaculture. *J. Fish. Res. Bd. Can.* **33**, 922-929.

Fransis A A, Smith F and Pfuderer P (1974) A heart-rate bioassay for crowding factors in goldfish. *Progr. Fish-Cult.* **36**, 196-200.

Gandolfi G (1969) A chemical sex attractant in the guppy, *Poecilia reticulata* (Pisces : Poeciliidae). *Monit. Zool. Ital.* **3**, 89-98.

Gandolfi G (1972) Selection for high and low reactivity to alarm substances in the zebrafish, *Brachydanio rerio* (Osteichthys: Cyprinidae). *Atti. Soc. Ital. Sci. Nt. Mus.* **113**, 28-36.

Gandolfi G, Mainardi D and Rossi A C (1960) The fright reaction in zebrafish, *Brachydanio rerio*. *Atti. Soc. Ital. Sci. Nt. Mus.* **107**, 74-88.

Gerlach G (2006) Pheromonal regulation of reproductive success in female zebrafish: female suppression and male enhancement. *Anim. Behav.* **72**, 1119-1124.

Giaquinto P C and Hara T J (2008) Discrimination of bile acids by the rainbow trout olfactory system: evidence as potential pheromone. *Biol. Res.* **41**, 33-42.

Groot C, Quinn T P and Hara T J (1986) Responses of migratory sockeye salmon (*Oncorhynchus nerka*) to population-specific odours. *Can. J. Zool.* **64**, 926-937.

Hamdani E H and Doving K B (2006) Specific projection of the sensory crypt cells in the olfactory system in crucian carp. *Chem. Senses* **31**, 63-67.

Hamdani E H, Stine L, G Finn and Doving K B (2008) Seasonal variations in olfactory sensory neurons: fish sensitivity to sex pheromones explained. *Chem. Senses* **33**, 119-123.

Haney D C, Vokoun J C and Nolte D B (2001) Alarm pheromone recognition in a Missouri darter assemblage. *J. Fish Biol.* **59**, 810-817.

Hansen L R, Sorensen P and Cohen Y (1998) Sex pheromones and amino acids evoke distinctly different patterns of electrical activity in the goldfish olfactory bulb. In: *Proceedings of the International Symposium on Olfaction and Taste* (ed: Murphy C), 521-524. N. Y. Academy of Sciences, New York.

Hara T J (1975) Olfaction in fish. *Progr. Neurobiol.* **5**, 271-335.

Hara T J (1982) *Chemoreception in Fishes*. Elsevier Scientific Pub. Co., Amsterdam.

Hara T J (1992) *Fish Chemoreception*. Chapman & Hall, London.

Hara T J, Brown S B and Evans R E (1983) Pollutants and chemoreception in aquatic organisms. In: *Aquatic Toxicology* (ed: Nriagu J O), 248-306. John Wiley & Sons, New York.

Harden Jones F R (1968) *Fish Migration*. Edward Arnold Pub., London.

Hasler A D (1983) Synthetic chemicals and pheromones in homing salmon. In: *Control Processes in Fish Physiology* (eds: Rankin J C, Pitcher T J and Duggan R T), 103-116. Croom-Helm, London.

Hasler A D and Wisby W J (1951) Discrimination of stream odours by fishes and its relation to parent stream behaviour. *Am. Nat.* **85**, 223-238.

Hasler A D and Cooper J C (1976) Chemical cues for homing salmon. *Experientia* **32**, 1091-1093.

Hasler A D, Scholz, A T and Horall R M (1978) Olfactory imprinting and homing in salmon. *Am. Sci.* **66**, 347-355.

Hayashi N, Nakamura S, Yoshikawa H, Abe T and Kobayashi H (1994) A role of olfaction in schooling of Japanese sea catfish, *Plotosus lineatus*. *Jpn. J. Ichthyol.* **41**, 7-13.

Heczko E (1980) The effect of schreckstoff on the behaviour of the common shiner (*Notropis conatus*, Cyprinidae). *M.Sc. Thesis*. University of Western Ontario, London.

Hemmings C C (1966) Olfaction and vision in fish schooling. *J. Exp. Biol.* **45**, 449-464.

Henderson P A, Irwing P W and Magurran A E (1997) Fish pheromones and evolutionary enigmas: a reply to Smith. *Proc. R. Soc. London* **264B**, 451-453.

Hoglund L B and Astrand M (1973) Preference among juvenile char (*Salvelinus alpinus* L.) to intraspecific odours and water current studied with the fluvarium technique. *Inst. Freshwater Res., Drottningholm Rep.* **53**, 21-30.

Hoglund L B, Bohman A and Nilsson N A (1975) Possible odour responses of juvenile Arctic char (*Salvelinus alpinus* L.) to three other species of subarctic. *Inst. Freshwater Res., Drottningholm Rep.* **54**, 21-35.

Honda H (1979) Female sex pheromone of the ayu, *Plecoglossus altivelis*, involved in courtship behaviour. *Bull. Jpn. Soc. Sci. Fish.* **45**, 1375-1380.

Honda H (1980a) Female sex pheromone of rainbow trout, *Salmo gairdneri*, involved in courtship behaviour. *Bull. Jpn. Soc. Sci. Fish.* **46**, 1109-1112.

Honda H (1980b) Female sex pheromone of the loach, *Misgurnus anguillicaudatus*, involved in courtship behaviour. *Bull. Jpn. Soc. Sci. Fish.* **46**, 1223-1225.

Honda H (1982a) On the female sex pheromones and courtship behaviour in the bitterlings, *Rhodurus ocellatus ocellatus* and *Acheilognathus lanceolatus*. *Bull. Jpn. Soc. Sci. Fish.* **48**, 43-46.

Honda H (1982b) On the female sex pheromones and courtship behaviour in the salmonids *Oncorhynchus masau* and *O. rhodurus*. *Bull. Jpn. Soc. Sci. Fish.* **48**, 47-50.

Howe N R and Seikh Y M (1975) Anthopleurine : a sea anemone alarm pheromone. *Science* **189**, 386-388.

Hubbard P and Scott A P (2007) Pheromone and other chemical communication. *Gen. Comp. Endocrinol.* **153**, 390-391.

Hugie D M and Smith R J F (1987) Epidermal club cells are not linked with an alarm response in reedfish, *Erpetoichthys calamoichthys* (*Calamoichthys calabaricus*). *Can. J. Zool.* **65**, 2057-2061.

Huttel R (1941) Die chemische Untersuchung des Schreckstoffes aus Elritzenhaut. *Natur-ewissenschaften* **39**, 333-334.

Ingersoll D W, Bronstein R M and Bonventre J (1976) Chemical modulation of agonistic display in *Betta splendens*. *J. Comp. Physiol. Psychol.* **90**, 198-202.

Irvine I A S and Sorensen P W (1993) Acute olfactory sensitivity of wild common carp, *Cyprinus carpio*, to goldfish hormonal sex pheromones is influenced by gonadal maturity. *Can. J. Zool.* **71**, 2199-2210.

Jaski C J (1939) Ein oestrus-zyklus bei *Lebistes reticulatus* (Peters). *Proc. Koninkl. Ned. Akad. Wetenschap.* **42**, 201-212.

Johanson P H (1985) Female pheromone and the behaviour of male guppies (*Poecilia reticulata*) in a temperature gradient. *Can. J. Zool.* **63**, 1211-1213.

Johnson R H (1978) Copulation and possible olfaction-mediated pair formation in two species of carcharhinid sharks. *Copeia* **1978**, 539-542.

Johnson N S, Yun S -S, Thompson H T, Brant C O and Li W (2009) A synthesized pheromone induces upstream movement in female sea lamprey and summons them into traps. *Proc. Natl. Acad. Sci. (USA)* **106**, 1021-1026.

Johnson N S and Li W (2010) Understanding behavioural responses of fish to pheromones in natural water environment. *J. Comp. Physiol.* **196A**, 196-701.

Johnson N S, Siefkes M J and Li W (2005) Capture of ovulating female sea lampreys in traps baited with spermating male sea lampreys. *N. Am. J. Fish. Manage.* **25**, 67-72.

Johnston R E (2003) Chemical communication in rodents: from pheromones to individual recognition. *J. Mammal.* **84**, 1141-1162.

Johnston R E, Muller-Schwarze D and Sorensen P W (1992) *Advances in Chemical Signals in Vertebrates*. Plenum Press, New York. .

Jolly D W (1980) Pheromones in fish communication. *Appl. Anim. Ethol.* **6**, 90-98.

Karlson, P. and Luscher M (1959) "Pheromones": a new term for a class of biologically active substances. *Nature* **183**, 55-56.

Kasumyan A O and Lebedeva N E (1977) On the chemical nature of the alarm substance from skin of the European minnow (*Phoxinus phoxinus*). *Biol. Nauk.* **1**, 37-41.

Kasumyan A O and Lebedeva N E (1979) New data on the nature of the alarm pheromone in cyprinids. *J. Ichthyol.* **19**, 109-114.

Kasumyan A O and Pashchenko N I (1982) The role of olfaction in defensive reaction of the grass carp, *Ctenopharyngodon idella* (Val.) (Cyprinidae) to alarm pheromone. *Vopr Ikhtiol.* **22**, 303-307.

Kawabata K (1993) Induction of sexual behaviour in male fish (*Rhodeus ocellatus ocellatus*) by amino acids. *Amino Acids* **5**, 323-327.

Kikuyama S, Toyoda F, Iwata T, Umezawa K, Takahashi N, Matsukawa H and Miura S (1998) Sodefrin, a novel peptide pheromone in the newt cloacal gland. *Ann. N.Y. Acad. Sci.* **839**, 60-65.

Kime D E and Ebrahimi M (1997) Synthesis of 17 α ,20 α β - and 17 α , 20 β -dihydroxy-4-pregn-3-one, 11 ketotestosterone and their conjugates by gill of teleost fish. *Fish Physiol. Biochem.* **17**, 117-121.

Kingsbury A E and Brooksbank B W L (1978) Metabolism in man of (3 H)-5-16-androsten-3-ol and (3 H)-5-16-androsten-3-one. *Horm. Res.* **9**, 254-270.

Kitamura S and Ogata H (1989) Olfactory responses of male Amago salmon, *Oncorhynchus rhodurus*, to the urinogenital fluid of

ovulated female. *Comp. Biochem. Physiol.* **94A**, 713-716.

Kitamura S and Ogata H (1990) Olfactory responses of male loach, *Misgurnus anguillicaudatus*, to F-type prostaglandins. In: *Proceedings of the 24th Japanese Symposium on Taste and Smell*. 166.

Kitamura S and Ogata H (1993) Olfactory responses of male loach, *Misgurnus anguillicaudatus*, to holding water of ovulated female. *Bull. Natl. Inst. Aquacult.* **22**, 37-42.

Kitamura S, Ogata H and Takashima F (1994) Olfactory responses of several species of teleosts to F-prostaglandins. *Comp. Biochem. Physiol.* **107A**, 463-467.

Kobayashi M, Aida K. and Hanyu I (1986) Pheromone from ovulatory female goldfish induces gonadotropin surge in males. *Gen. Comp. Endocrinol.* **63**, 451-455.

Kodama K, Matsui K, Hatanaka A and Kajiwara T (1993) Sex-attractants secreted from female gametes of Japanese brown algae of the genus *Scytoniphon*. *Phytochemistry* **32**, 817-819.

Laberge F and Hara T J (2003) Behavioural and electrophysiological responses to F-prostaglandins, putative spawning pheromones, in three salmonid fishes. *J. Fish Biol.* **62**, 206-221.

Laumen J, Pern W and Blun V (1974) Investigations on the functions and hormonal regulation of anal appendices in *Blennius pavo* (Risso). *J. Exp. Zool.* **190**, 47-50.

Lebedeva N Y and Golovkina T V (1994) Pheromone of the trout stress inducer. *Biophysics* **39**, 527-530.

Lebedeva N Y, Tomkevich M S, Golovkina N A, Vosyliene M Z and Golovkina T A (1999) On hormesis of alarm pheromone of cyprinids. *Pheromones* **6**, 65-68.

Leduc A H C, Kelly J M and Brown G E (2004) Detection of conspecific alarm cues by juvenile salmonids under natural and weakly acidic conditions: laboratory and field tests. *Oecologia* **139**, 318-324.

Leduc A H C, Lamaze F C, McGraw L and Brown G E (2008) Response to chemical alarm cues under weakly acidic conditions: a gradual loss of anti-predator behaviour in juvenile rainbow trout. *Water Air Soil Pollut.* **180**, 179-187.

Leduc A H C, Roh E and Brown G E (2009) Effects of acid rainfall on juvenile Atlantic salmon (*Salmo salar*) anti-predator behavior: loss of chemical alarm function and potential survival consequences during predation. *Mar. Freshw. Res.* **60**, 1223-1230.

Li W and Sorensen P W (1997) Highly independent olfactory receptor sites for naturally occurring bile acids in the sea lamprey, *Petromyzon marinus* to pheromonal bile acids. *J. Comp. Physiol.* **180A**, 429-438.

Li W, Scott A P, Siefkes M J, Yan H G, Liu Q, Yun S -S and Gage D A (2002) Bile acids secreted by male sea lamprey that act as pheromone. *Science* **296**, 138-141.

Li W, Scott A P, Siefkes M J, Yun S -S and Zielinski B (2003) A male pheromone in the sea lamprey (*Petromyzon marinus*): an overview. *Fish Physiol. Biochem.* **28**, 259-262.

Li W, Twohey M B, Jones M L and Wagner C M (2007) Research to guide use of pheromones to control sea lamprey. *J. Great Lake Res.* **33**, 70-86.

Liley N R (1980) Patterns of hormonal control in the reproductive behaviour in fish and their relevance in fish management and culture. In: *Fish Behaviour and its Use in the Capture and Culture of Fishes* (eds: Bardach J E, Mugnuson J J, May R and Reinhart J M), 210-246. ICLARM, Manila.

Liley N R (1982) Chemical communication in fish. *Can. J. Fish. Aquat. Sci.* **39**, 22-35.

Lonsdale D J, Frey M A and Snell T W (1998) The role of chemical signals in copepod reproduction. *J. Mar. Sys.* **15**, 1-12.

Losey G S Jr (1969) Sexual pheromone in some fishes of the genus, *Hypsoblennius* Gill. *Science* **163**, 181-183.

Maier I and Mueller D G (1986) Sexual pheromones in algae. *Biol. Bull. Mar. Biol. Lab. Woods Hole* **170**, 145-172.

Malyukina G A, Kasumyan A O, Marusov E A and Pashchinko N I (1977) The alarm pheromone and its significance. *Zh. Obshch. Biol.* **38**, 123-132.

Malyukina G A, Martemyanov V V I and Flerova G I (1982) Alarm pheromone as a stress factor for fish. *J. Ichthyol.* **22**, 147-150.

Maniak P J, Lossing R and Sorensen P W (2000) Injured Euresian ruffe, *Gymnocephalus cernuus*, release an alarm pheromone that could be used to control their dispersal. *J. Great Lake Res.* **26**, 183-195.

Mann K D, Turnell E R, Atema J and Gerlach G (2003) Kin recognition in juvenile zebrafish (*Danio rerio*) based on olfactory cues. *Biol. Bull. (USA)* **205**, 224-225.

Marentette J R and Corkum L D (2008) Does the reproductive status of the male round gobies (*Neogobius melanostomus*) influence their response to conspecific odours? *Environ. Biol. Fishes* **81**, 447-455.

Mathis A P and Smith R J F (1992) Aviodance of area marked with a chemical alarm substance by fathead minnows (*Pimephales promelas*) in a natural habitat. *Can. J. Zool.* **70**, 1473-1476..

Mathis A, Chivers D P and Smith R J F (1995) Chemical alarm signals: predator deterrents or predator attractants? *Am. Nat.* **145**, 994-1005.

Matsumura K (1995) Tetradotoxin as a pheromone. *Nature* **378**, 563-564.

McCormick M I and Larson J K (2007) Field verification of the use of chemical alarm cues in a coral reef fish. *Coral Reefs* **26**, 571-576.

McFarland W N and Moss S A (1967) Internal behaviour of fish in schools. *Science* **156**, 260-262.

McKaye K R and Barlow G W (1976) Chemical recognition of young by the Midas cichlid, *Cichlasoma citrinellum*. *Copeia* **1976**, 276-282.

McKinnon J S and Liley N R (1987) Asymmetric species-specificity in responses to female sexual pheromone by males of two species of *Trichogaster* (Pisces: Belontiidae). *Can. J. Zool.* **65**, 1129-1134.

McLennan D A and Ryan M J (2008) Female swardtails, *Xiphophorus continens*, prefer the scent of heterospecific males. *Anim. Behav.* **75**, 1731-1737.

Miles S G (1968) Rheotaxis of elevers of the American eel (*Anguilla rostrata*) in the laboratory to water from different streams in Nova Scotia. *J. Fish. Res. Bd. Can.* **25**, 1591-1602.

Milinski M (2003) The function of mate choice in sticklebacks: optimizing MHC genetics. *J. Fish Biol.* **63A**, 1-16.

Milligan T A (1978) The fine structure of the caudal neurosecretory system and its role as a producer of territorial marking pheromones in the brown bullhead catfish, *Ictalurus nebulosus*.

Diss. Abstr. Intern. **39B**, 2612.

Mirza R S and Chivers D P (2001) Are chemical alarm cues conserved within salmonid fishes? *J. Chem. Ecol.* **27**, 1641-1655.

Mirza R S, Scott J J and Chivers D P (2001) Differential responses of male and female red swardtails to chemical alarm cues. *J. Fish Biol.* **59**, 716-728.

Moore A (1994) An electrophysiological study on the effects of pH on olfaction in mature male Atlantic salmon (*Salmo salar*) parr. *J. Fish Biol.* **45**, 493-502.

Moore A and Waring C P (1996a) Electrophysiological and endocrinological evidence that F-series prostaglandins function as priming pheromones in mature male Atlantic salmon (*Salmo salar*) parr. *J. Exp. Biol.* **199**, 2307-2316.

Moore A and Waring C P (1996b) Sublethal effects of the pesticide diazinon on olfactory function in mature male Atlantic salmon parr. *J. Fish Biol.* **48**, 1027-1029.

Mosher C (1954) Observations on the spawning behaviour and the early larval development of the sargassum fish, *Histrio histrio*. *Zoologica* **39**, 141-156.

Mueller D G, Kawai H, Stache B, Foelster E. and Boland W (1990) Sexual pheromones and gamete chemotaxis in *Analipus japonicus* (Phaeophyceae). *Experientia* **46**, 534-536.

Murphy C A, Stacey N.E. and Corkum L.D. (2001) Putative steroidal pheromones in the round goby, *Neogobius melanostomus*: olfactory and behavioural responses. *J. Chem. Ecol.* **27**, 443-470.

Needham A E (1974) *The Significance of Zoothymes: Zoophysiology and Ecology*. Springer-Verlag, New York.

Newcombe C and Hartman G (1973) Some chemical signals in the spawning behavior of rainbow trout (*Salmo gairdneri*). *J. Fish Res. Bd. Can.* **30**, 995-997.

Nordell S E (1998) The response of female guppies, *Poecilia reticulata*, to chemical stimuli from injured conspecifics. *Environ. Biol. Fishes* **51**, 331-338.

Nordeng H (1971) Is the local migration of anadromous fishes determined by pheromones? *Nature* **233**, 411-413.

Nordeng H (1977) A pheromone hypothesis for homeward migration in anadromous salmonids. *Oikos* **28**, 155-159.

Ogata H, Kitamura S and Takashima F (1993) F-prostaglandins in the holding water of female loach. *Nippon Suisan Gakkaishi* **59**, 1259.

Ogata H, Kitamura S and Takashima F (1994) Release of 13,14-dihydro-15-keto-prostaglandin F₂α, a sex pheromone, to water by cobitid loach following ovulatory stimulation. *Fish. Sci.* **60**, 143-148.

Okada H, Sakai D K and Sugiwaka K (1978) Chemical stimulus on the reproductive behaviour of the pond smelt. *Sci. Rep. Hokkaido Fish Hatch.* **33**, 89-99.

Olsen K H (1987) Chemoattraction of juvenile Arctic char (*Salvelinus alpinus* L.) to water scented by conspecific intestinal content and urine. *Comp. Biochem. Physiol.* **87A**, 641-643.

Olsen K H (1989) Sibling recognition in juvenile Arctic char, *Salvelinus alpinus* (L.). *J. Fish Biol.* **34**, 571-581.

Olsen K H ((1990) Further studies concerning chemoattraction among fry of Arctic char, *Salvelinus alpinus* (L.) to water conditioned by conspecifics. *J. Chem. Ecol.* **16**, 2081-2090.

Olsen K H and Huglund L B (1985) Reduction by a surfactant of the olfactory-mediated attraction between juveniles of Arctic char, *Salvelinus alpinus* (L.). *Aquat. Toxicol.* **6**, 57-69.

Olsen K H, Bjerselius R, Peterson E, Jarvi T, Mayer I and Hendenskog M (2000) Lack of species-specific primer effects of odours from female Atlantic salmon, *Salmo salar* and brown trout, *Salmo trutta*. *Oikos* **88**, 213-220.

Olsen K H, Swaisky G R and Stacey N E (2006) Endocrine and milt responses of male crucian carp (*Carassius carassius* L.) to periovulatory females under field conditions. *Gen. Comp. Endocrinol.* **149**, 294-302.

Ostromov V A (1997) The role of chemical signals in regulation of fish maturation and reproductive behaviour. *J. Ichthyol.* **37**, 103-109.

Ostromov V A and Dmitreva T M (1991) Effect of sex pheromones on gonad maturation and behaviour of the Baikal cisco, *Coregonus autumnalis migratorius*. *Vopr. Ichtyol.* **30**, 497-501.

Ostromov V A, Dulka J G and Stacey N E (1996) The preovulatory behavioural pheromone of the goldfish (*Carassius auratus*). *J. Ichthyol.* **36**, 482-485.

Pandey A K (1984) Chemical signals in fishes: theory and application. *Acta Hydrochim. Hydrobiol.* **12**, 463-478.

Pandey A K (1987) A bibliography on the chemical communication in fishes. *Intl. J. Acad. Ichthyol.* **8**, 17-26.

Pandey A K (1998) Chemical communication in fishes: an overview. *Fishing Chimes* **18**, 15-20.

Pandey, A.K. (2003) Current status and potential applications of fish pheromones in aquaculture and fishery management. In: *Aquaculture Medicine* (eds: Bright Singh I S, Pai S S, Philip R and Mohandas A), 271-292. School of Environmental Sciences, Cochin University of Science & Technology, Cochin.

Pandey A K (2005) Recent advances in fish pheromone research with emphasis on their potential applications in fisheries. *J. Appl. Zool. Res.* **16**, 210-216.

Pandey A K (2009) Fish pheromones and their potential applications in breeding, aquaculture and fishery management. In: In: *Recent Advances in Hormonal Physiology of Fish and Shellfish Reproduction* (eds: Singh B N and Pandey A K), 69-98. Narendra Publishing House, Delhi.

Pandey A K, Mitra A and Sarkar B (2000) An instance of chemical communication in the Indian catfish, *Heteropneustes fossilis* (Bloch). In: *Fifth Indian Fisheries Forum* (January 17-20, 2000), 83. Central Institute of Freshwater Aquaculture, Bhubaneswar.

Partridge B L, Liley N R and Stacey N E (1976) Role of pheromones in sexual behaviour of the goldfish. *Anim. Behav.* **24**, 291-299.

Parzefall J (1973) Attraction and sexual cycles of Poeciliids. In: *Genetics and Mutagenesis of Fishes* (ed: Schroeder H), 177-183. Springer-Verlag, Berlin.

Pfeiffer W (1962) The fright reaction of fish. *Biol. Rev.* **37**, 495-511.

Pfeiffer W (1963) Alarm substance. *Experientia* **19**, 113-123.

Pfeiffer, W. (1974). Pheromones in fish and Amphibia. In: *Pheromones* (ed: Birch M C), 269-296. Elsevier/ North -Holland, Amsterdam, The Netherlands.

Pfeiffer W (1977) The distribution of fright reaction and alarm substance cells in fishes. *Copeia* **1977**, 653-665.

Pfeiffer W (1978) Heterocyclic compounds as releasers of fright reaction in giant danio, *Danio malabaricus* (Jerdon) (Cypinidae, Ostariophysi, Pisces). *J. Chem. Ecol.* **4**, 665-673.

Pfeiffer W (1982) Chemical signals in communication. In: *Chemoreception in Fishes* (ed: Hara T J), 307-336. Elsevier Sci. Pub.Co., Amsterdam.

Pfeiffer W and Lemke J (1973) Untersuchungen zur Isolierung und Identifizierung des Schreckstoffes aus der Haut der Elritze, *Phoxinus phoxinus* (L.) (Cyprinidae, Ostariophysi, Pisces). *J. Comp. Physiol.* **82**, 407-410.

Pfeiffer W, Mangold-Wernado U and Neusteurer P (1984) Identification of nerve bundle in the tractus olfactorius of the tench, *Tinca tinca* L., which conduct the nervous excitation elicited by alarm substance. *Experientia* **40**, 219-220.

Pfeiffer, W, Walz U, Wolf and Mangold-Wernadu U (1985a). Effects of steroid hormones and other substances on alarm substance cells in the epidermis of the European minnow, *Phoxinus phoxinus* and other ostariophysi (Pisces). *J. Fish Biol.* **27**, 553-570

Pfeiffer W, Riegelbauer G, Meier G and Scheibler B (1985b) Effects of hypothanthine-3(N)-oxide and hypothanthine-1(N)-oxide on central nervous excitation of the black tetra, *Gymnocorymbus ternetzi* (Characidae, Ostariophysi, Pisces) indicated by dorsal light response. *J. Chem. Ecol.* **11**, 507-524.

Pollack E I, Becker L R and Haynes K (1978) Sensory control of mating in the blue gourami, *Trichogaster trichopterus* (Pisces: Anabantidae). *Behav. Biol.* **22**, 2-105.

Quinn T P (1980) Locomotor responses of juvenile blind cavefish, *Astyanax jordani*, to odours of conspecifics. *Behav. Neural Biol.* **29**, 123-127.

Quinn T P (1985) Salmon homing: is the puzzle complete? *Environ. Biol. Fishes* **12**, 315-317.

Quinn T P (1990) Current controversies in the study of salmon homing. *Ethol. Ecol. Evol.* **2**, 49-63.

Quinn T P and Busack C A (1985) Chemosensory recognition of siblings in juvenile coho salmon (*Oncorhynchus kisutch*). *Anim. Behav.* **33**, 51-56.

Quinn T P and Tolson G M (1986) Evidence of chemically mediated population recognition in coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* **64**, 84-87.

Quinn T P and Hara T J (1986). Sibling recognition and olfactory sensitivity in juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* **64**, 921-925.

Quinn T P, Brannon E L and Whitman R P (1983) Pheromones and the water source preferences of adult coho salmon, *Oncorhynchus kisutch* Walbaum. *J. Fish Biol.* **22**, 677-684.

Reed J R, Wieland W and Kimbrough T D (1972) A study of the biochemistry of alarm substances in fish. *Proceedings of 26th Annual Conference of the Southeastern Association of Game and Fish Commissioners*. 608-610.

Resink J W (1988) Steroid glucuronides as pheromones in the reproduction of the African catfish, *Clarias gariepinus*. *Ph.D. Thesis*, University of Utrecht, Utrecht, The Netherlands.

Richards I S (1974) Caudal neurosecretory system: possible role in pheromone production. *J. Exp. Zool.* **187**, 405-408.

Rosenblatt R N and Losey G S Jr (1967) Alarm reaction in the top smelt, *Atherinops affinis*. Re-examination. *Science* **158**, 671-672.

Rosenthal G G, Fitzsimmons J N, Woods K U, Gerlach G and Fisher H S (2011) Tactical release of a sexually-selected pheromone in a swordtail fish. *PLoS ONE* **6** (2), e16994.

Rossi A C (1969) Chemical signals and nest-building in two species of *Colisa* (Pisces: Anabantidae). *Monit. Zool. Ital.* **3**, 225-237.

Rubec P J (1979) Effect of pheromones on behaviour of ictaluriid catfish. *Ph. D. Thesis*. Texas A. & M. University, Austin.

Saglio P (1982) Use of intraspecific biological extracts to trap eels (*Anguilla anguilla* L.) in the field. Demonstration of the pheromonal attractivity of the skin mucus. *Acta Oecol. Applic.* **3**, 223-231.

Saglio P (1992) La communication chimique chez les Poissons. *La Recher.* **248**, 1282-1293.

Saralva L R and Korschning S I (2007) A novel olfactory receptor gene family in teleost fish. *Genome Res.* **17**, 1448-1457.

Scheuer P J (1977) Chemical communication in marine invertebrates. *Bioscience* **27**, 664-668.

Schneider R A Z and Moore P A (2000) Urine as a source of conspecific disturbance signals in the crayfish, *Procambarus clarkii*. *J. Exp. Biol.* **203**, 765-771.

Schoonen W G E J (1987) Analysis of steroid synthesis in the reproductive organs of the African catfish, *Clarias gariepinus*: a basis for the study of sex pheromones. *Ph.D. Thesis*. University of Utrecht, Utrecht, The Netherlands.

Scott A P, Liley N R and Vermeirissen E L M (1994) Urine of reproductively mature female rainbow trout, *Oncorhynchus mykiss* (Walbaum), contains a priming pheromone which enhances plasma levels of sex steroids and gonadotrophin II in males. *J. Fish Biol.* **44**, 131-147.

Selset R (1980) Chemical methods for fractionation of odorants produced by char smolts and tentative suggestions for pheromone origins. *Acta Physiol. Scand.* **108**, 97-103.

Selset R and Doving K B (1980) Behaviour of mature anadromous char (*Salmo alpinus*) towards odorants produced by smolts of their own population. *Acta Physiol. Scand.* **108**, 113-122.

Sherwood N M, Kyle A L, Kreiberg H, Warby C M, Magnus T H, Carolsfield J and Price W S (1991) Partial characterization of a spawning pheromone in the herring, *Clupea herengus pallasi*. *Can. J. Zool.* **69**, 91-97.

Siefkes M J, Scott A P, Zielinski B, Yun S-S and Li W (2003) Male sea lampreys, *Petromyzon marinus* L., excrete a sex pheromone from gill epithelia. *Biol. Reprod.* **69**, 125-132.

Sisler S P and Sorensen P W (2008) Common carp and goldfish discern conspecific identity using chemical cues. *Behaviour* **145**, 1409-1425.

Slattery M, Hines G A, Starmer J and Paul V J (1999) Chemical signals in gametogenesis, spawning, and larval settlement, and defense of the soft coral, *Sinularia polydactyla*. *Coral-Reefs* **18**, 75-84.

Smith J D and Smith R J F (1986) The effect of hormone treatment on alarm substance cell counts in the pearl dace, *Semotilus marginatus*. *Can. J. Zool.* **64**, 291-295.

Smith R J F (1973) Testosterone eliminates alarm substance cells in fathead minnows. *Can. J. Zool.* **51**, 875-876.

Smith R J F (1976a) Seasonal loss of alarm substance cells in North American cyprinoid fishes and its relation to abrasive spawning behaviour. *Can. J. Zool.* **54**, 1172-1182.

Smith R J F (1976b) Male fathead minnows (*Pimephales promelas* Rafinesque) retain their fright reaction to alarm substance during breeding season. *Can. J. Zool.* **54**, 2230-2231.

Smith R J F (1977) Chemical communication as adaptation. In: *Chemical Signals in Vertebrates* (eds: Muller-Schwarze D and Mozell M M), 303-320. Plenum Press, New York.

Smith R J F (1978) Seasonal changes in the histology of the gonads and dorsal skin of the male fathead minnow, *Pimephales promelas*. *Can. J. Zool.* **56**, 2103-2109.

Smith R J F (1979) Alarm reaction of Iowa and Johnny darters (*Etheostoma exile*) to chemicals from injured conspecifics. *Can. J. Zool.* **57**, 1278-1282.

Smith R J F (1981) Effect of food deprivation on the reaction of Iowa darters (*Etheostoma exile*) to skin extract. *Can. J. Zool.* **59**, 558-560.

Smith R J F (1982a) The adaptive significance of alarm substance-fright reaction system in fish. In: *Chemoreception in Fishes* (ed: Hara T J), 327-347. Elsevier/North-Holland, Amsterdam.

Smith R J F (1982b) Reaction of *Percina nigrofasciata*, *Ammocrypta beani* and *Etheostoma swaini* (Percidae, Pisces) to conspecific and intergeneric skin extracts. *Can. J. Zool.* **60**, 1067-1072.

Smith R J F (1986) The evolution of chemical alarm signals in fishes. In: *Chemical Signals in Vertebrates. IV. Ecology, Evolution and Comparative Biology* (eds: Duvall D, Muller-Schwarze D and Silverstein R M), 99-115. Plenum Press, New York.

Smith R J F (1992) Alarm signals of fishes. *Rev. Fish Biol. Fish.* **2**, 33-63.

Smith R J F and Murphy B D (1974) Functional morphology of the dorsal pad in fathead minnows (*Pimephales promelas* Rafinesque). *Trans. Am. Fish. Soc.* **103**, 65-72.

Solomon, D.J. (1973) Evidence for pheromone influenced homing by migrating Atlantic salmon (*Salmo salar* L.). *Nature* **244**, 231-232.

Solomon, D.J. (1977) A review of chemical communication in freshwater fish. *J. Fish Biol.* **11**, 363-376.

Sorensen P W (1984) Juvenile eels rely on odour cues for migration. *Maritimes* **28**, 8-10.

Sorensen P W (1992) Hormonally-derived sex pheromones in goldfish: a model for understanding the evolution of sex pheromone system in fish. *Biol. Bull. (USA)* **183**, 173-177.

Sorensen P W (1996) Biological responsiveness provides fundamental and unique insight into olfactory function. *Chem. Senses* **21**, 245-256.

Sorensen P W and Winn W H (1984) The induction of maturation and ovulation in American eel, *Anguilla rostrata* (Le Seur), and the relevance of chemical and visual cues to male spawning behaviour. *J. Fish Biol.* **25**, 261-268.

Sorensen P W and Scott A P (1994) The evolution of hormonal sex pheromones in teleost fish: poor correlation between the pattern of steroid release by goldfish and olfactory sensitivity suggests that these cues evolved as a result of chemical spying rather than signalling specialization. *Acta Physiol. Scand.* **152**, 191-205.

Sorensen P W and Stacey N E (1999) Evolution and specialization of fish hormonal pheromones. In: *Advances in Chemical Signals in Vertebrates* (eds. Johnston R E, Muller-Schwarze D and Sorensen P W), 15-47. Plenum Press, New York.

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 J. Mar. Freshw. Res.* **38**, 399-417.

Sorensen P W and Hoye T R (2007) A critical review of the discovery and application of a migratory pheromone in an invasive fish, the sea lamprey, *Peteromyzon marinus* L. *J. Fish Biol.* **71D**, 100-114.

Sorensen P W, Stacey, N E, Hara T J and Goetz F W (1988) F prostaglandins function as potent olfactory stimulants that comprise the postovulatory female sex pheromone in goldfish. *Biol. Reprod.* **35**, 1035-1050.

Sorensen P W, Irvine, I A S, Scott A P and Stacey N E (1992) Electrophysiological measures of olfactory sensitivity suggest that goldfish and other fish uses species-specific mixtures of hormones and their metabolites as pheromones. In: *Chemical Signals in Vertebrates* (eds: Doty R and Muller-Schwarze D), 357-364. Plenum Press, New York.

Sorensen P W, Scott A P, Stacey N E and Bowdin L (1995) Sulfated 17, 20-dihydroxy- 4-pregn-3-one functions as a potent and specific olfactory stimulant with pheromonal actions in the goldfish. *Gen. Comp. Endocrinol.* **100**, 128-142.

Sorensen P W, Maniak P J, Loomis A K and Thomas P (1997) Hormones, pheromones and sexual behaviour in the ruffe (*Gymnocephalus cernuus*). In: *Proceedings of the International Symposium on Biology and Management of Ruffe* (March 21-23, 1997) (ed: Jensen D A), 13 Ann Arbor, Michigan.

Sorensen P W, Christensen T A and Stacey N E (1998) Discrimination of pheromonal cues in fish: emerging parallel with insect. *Curr. Opinion Neurobiol.* **8**, 458-467.

Stabell O B (1987) Intraspecific pheromone discrimination and substrate marking by Atlantic salmon parr. *J. Chem. Ecol.* **13**, 1625-1644.

Stabell O B (1992) Olfactory control of homing behaviour in salmonids. In: *Fish Chemoreception* (ed: Hara T J), 249-270. Chapman & Hall, London.

Stabell O B and Lwin M S (1997) Predator-induced phenotypic changes in crucian carp caused by chemical signals from conspecifics. *Environ. Biol. Fishes* **49**, 145-149.

Stabell O B, Selset R and Sletten K (1982) A comparative chemical study on population-specific odorants from Atlantic salmon. *J. Chem. Ecol.* **8**, 201-213.

Stacey N E (1983) Hormones and pheromones in sexual behaviour. *Bioscience* **33**, 552-556.

Stacey N E (2003) Hormones, pheromones and reproductive behaviour. *Fish Physiol. Biochem.* **28**, 229-235.

Stacey N E and Hourston A S (1982) Spawning and feeding behaviour of captive Pacific herring, *Clupea herrenicus pallasi*. *Can. J. Fish. Aquat. Sci.* **39**, 489-498.

Stacey N E and Sorensen P W (1991) Function and evolution of fish hormonal pheromones. In: *Biochemistry and Molecular Biology of Fishes* (eds: Hochachka P W and Mommsen T P), 109-135. Elsevier/North-Holland, Amsterdam.

Stacey N E, Sorensen P W, Dulka J G, Cardwell J R and Irvine I A S (1991) Fish sex pheromones: current status and potential applications. *Bull. Inst. Zool., Academia Sinica (Monogr.)* **16**, 189-227.

Stacey N E, Sorensen P W and Cardwell J R (1992) Hormonal pheromones: recent developments and potential application in aquaculture. In: *Researches for Aquaculture: Fundamental and Applied* (eds. Lahliou B and Vitiello P), 242-268. Springer-Verlag,

New York.

Stacey, N.E., Cardwell, J.R., Liley, N.R., Scott, A.P. and Sorensen P W (1994a) Hormones as sex pheromones in fish. In: *Perspectives in Comparative Endocrinology* (eds: Davey K G, Peter R E and Tobe S S), 438-448. National Research Council of Canada, Ottawa.

Stacey N E, Zheng W N and Cardwell J R (1994b) Milt production in common carp (*Cyprinus carpio*): stimulation by a goldfish steroid pheromone. *Aquaculture* **127**, 265-276.

Sveinsson T and Hara T J (1995) Mature males of Arctic char, *Salvelinus alpinus*, release F-type prostaglandins to attract conspecific mature females and stimulate their spawning behaviour. *Environ. Biol. Fishes* **42**, 253-266.

Tavolga W N (1956) Visual, chemical and sound stimuli as cues in sex discriminatory behaviour of the gobid fish, *Bothygobio soporator*. *Zoologica* **41**, 49-64.

Teichmann H (1962) Die Chemorezeption der Fische. *Ergebn. Biol.* **25**, 177-205.

Teeter J H (1980) Pheromonal communication in sea lamprey, *Petromyzon marinus*. *Can. J. Fish. Aquat. Sci.* **37**, 2123-2132.

Theissen D D and Sturdivant S K (1977) Female pheromone in the black molly fish (*Mollinesnsis latipinna*). *J. Chem. Ecol.* **3**, 207-217.

Thines G and Legrain J M (1973) Effects of alarm substance on the behavior of cavefish, *Anoptichthys jordani* and *Caecobarbus geerrsi*. *Ann. Speleol.* **28**, 291-297.

Tierney K B, Baldwin D H, Hara T J, Ross P S, Scholz N L and Kennedy C J (2010) Olfactory toxicity in fish. *Aquat. Toxicol.* **96**, 2-26.

Timms A M and Kleerekoper H (1972) The locomotor responses of male *Ictalurus punctatus*, the channel catfish. *Trans. Am. Fish. Soc.* **101**, 302-310.

Thom M D and Hurst J L (2004) Individual recognition by scent. *Ann. Zool. Fennici* **41**, 765-787.

Thommessen G (1982) Specificity and distribution of receptor cells in the olfactory mucosa of char (*Salmo alpinus* L.). *Acta Physiol. Scand.* **115**, 47-56.

Thommessen G (1983) Morphology, distribution and specificity of olfactory receptor cells in salmonid fishes. *Acta Physiol. Scand.* **117**, 241-249.

Tood J H (1971) The chemical languages of fishes. *Scient. Am.* **224**, 98-108.

Tood J H, Atema J and Bardach J E (1967) Chemical communication in social behaviour of a fish, the yellow bullhead (*Ictalurus natalis*). *Science* **158**, 672-673.

van den Hurk R and Resink J W (1992) Male reproductive system as sex pheromone producer in teleost fish. *J. Exp. Zool.* **261**, 204-213.

van den Hurk R, Schoonen W G E J, van Zoelen G A and Lambert J G D (1987) The biosynthesis of steroid glucuronides in testis of zebrafish, *Brachydanio rerio*, and their pheromonal function as ovulation inducer. *Gen. Comp. Endocrinol.* **68**, 179-188.

van Weerd J H (1990) Pheromones and ovarian growth in the African catfish, *Clarias gariepinus*. *Ph.D. Thesis*. University of Wageningen, Wageningen, The Netherlands.

van Weerd J H and Richter C J J (1991) Sex pheromones and ovarian development in teleost fish. *Comp. Biochem. Physiol.* **100A**, 517-527.

Vermeirissen E L M, Scott A P and Liley N R (1997) Female rainbow trout urine contains a pheromone which causes a rapid rise in plasma $17\alpha,20\beta$ -dihydroxy-4-pregnen-3-one levels and milt amounts in males. *J. Fish Biol.* **50**, 107-119.

Vermeirissen E L M and Scott A P (2001) Male priming pheromone is present in bile, as well as urine, of female rainbow trout. *J. Fish Biol.* **58**, 1039-1045.

von Frisch K (1938) Zur Psychologie des Fisch-Schwarmes. *Naturwissenschaften* **26**, 601-606.

von Frisch K (1941) Über einen Schreckstoff der Fischhaut und seine biologische Bedeutung. *Z. Vergl. Physiol.* **29**, 46-145.

Vrieze L A, Bjerselius S and Sorensen, P W (2010) Importance of olfactory sense to migratory lampreys *Petromyzon marinus* seeking riverine spawning habitat. *J. Fish Biol.* **76**, 949-964.

Vrieze L A, Bergstedt R A and Sorensen, P W (2011) Olfactory-mediated stream-finding behaviour of migratory adult sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* **68**, 523-533.

Wabnitz P A, Bowie J A, Tyler M J, Wallace J C and Smith B P (1999) Aquatic sex pheromone from a male tree frog. *Nature* **401**, 444-445.

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 Lake. *Can. J. Fish. Aquat. Sci.* **63**, 475-479.

Wagner C M, Twohey M B and Fine J M (2009) Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? *Anim. Behav.* **78**, 593-599.

Wagner C M, Stroud E M and Meckley T D (2011) A deathly odour suggests a new sustainable tool for controlling a costly invasive species. *Can. J. Fish. Aquat. Sci.* **68**, 1157-1160.

Waldman B (1982) Quantitative and developmental analysis of the alarm reaction in the zebra danio, *Brachydanio rerio*. *Copeia* **1982**, 1-9.

Ward A J W, Webster M M and Hart P J B (2007) Social recognition in wild fish population. *Phil. Royal Soc. London* **274B**, 1071-1077.

Waring C P and Moore A (1997) Sublethal effects of a carbamate pesticide on pheromonal mediated endocrine function in mature male Atlantic salmon (*Salmo salar* L.). *Fish Physiol. Biochem.* **17**, 203-211.

Waring C P, Moore A and Scott A P (1996) Milt and endocrine responses of mature male Atlantic salmon (*Salmo salar* L.) parr to water-borne testosterone, 17,20-dihydroxy-4-pregnene-3-one-20-sulphate and urine from adult female and male salmon. *Gen. Comp. Endocrinol.* **103**, 142-149.

Watts S A, Hines G A, McClintock J B, Marion K R and Hopkins T S (1993) Chemical communication and population structure of echinoderms in marine communities: role of steroids. *J. Alabama Acad. Sci.* **64**, 96-110.

White H C (1934) Some facts and theories concerning Atlantic salmon. *Trans. Am. Fish. Soc.* **61**, 360-362.

Wisenden B D and Smith R J F (1998) A re-evaluation of the effect of shoal mate familiarity on the proliferation of alarm substance cells in ostariophysian fishes. *J. Fish Biol.* **53**, 841-846.

Wisenden B D, Chivers D P, Brown G E and Smith R J F (1995) The role of experience in risk assessment: avoidance of areas

chemically labelled with fathead minnow alarm pheromone by conspecifics and heterospecifics. *Ecoscience* **2**, 116-122.

Wisenden B D, Vollbrecht K A and Brown J L (2004) Is there a fish alarm cue? Affirming evidence from a wild study. *Anim. Behav.* **67**, 59-67.

Wysocki C J and Preti G (2004). Facts, fallacies, fears, and frustrations with human pheromones. *Anat. Rec.* **281A**, 1201-1210.

Wysocki C J and Preti G (2010). Human pheromones: what's purported, what's supported? A Sense of Smell Institute White Paper. The Fragrance Foundation, New York.

Wyatt T D (2003) *Pheromones and Animal Behaviour: Communication by Smell and Taste*. Cambridge University Press, Cambridge, United Kingdom.

Wyatt T D (2009) Fifty years of pheromones. *Nature* **457**, 262-263.

Yambe H and Yamazaki F (2000) Urine of ovulated female masu salmon attracts immature male parr treated with methyltestosterone. *J. Fish Biol.* **57**, 1058-1064.

Yambe H and Yamazaki F (2001a) Species-specific releaser effect of urine from ovulated female masu salmon and rainbow trout. *J. Fish Biol.* **59**, 1455-1464.

Yambe H and Yamazaki F (2001b) A releaser pheromone that attracts methyltestosterone-treated immature fish in the urine of ovulated female rainbow trout. *Fish. Sci.* **67**, 214-220.

Yamabe H, Shindo M and Yanazaki F (1999) A releaser pheromone that attracting males in the urine of mature female masu salmon. *J. Fish Biol.* **55**, 158-171.

Yamabe H, Kitamura S, Kamio M, Yamada M, Matsunaga S, Fusetani N and Yamazaki F (2006a) L-Kynurenine, an amino acid identified as a sex pheromone in the urine of ovulated female masu salmon. *Proc. Natl. Acad. Sci. (USA)* **103**, 1437-15374.

Yamabe H, Yamada M and Yamazaki F (2006b) Responses of immature male masu salmon parr to the urine of mature males. *Ichthyol. Res.* **53**, 182-184.

Yamazaki F (1990) The role of urine in sex discrimination in the goldfish, *Carassius auratus*. *Bull. Fac. Fish. Hokkaido Univ.* **41**, 155-161.

Yamazaki F and Watanabe K (1979) The role of steroid hormones in sex recognition during spawning behaviour of the goldfish, *Carassius auratus*. *Proc. Indian Natl. Sci. Acad.* **45B**, 505-511.

Yoakim E G and Grizzle J M (1982) Ultrastructure of the alarm substance cells in epidermis of the channel catfish, *Ictalurus punctatus* (Rafinesque). *J. Fish Biol.* **20**, 213-221.

Young M K, Micek B K and Rathbun M (2003) Probable pheromone attraction on sexually mature brook trout to mature male conspecifics. *North Am. J. Fish. Mange.* **23**, 276-282.

Yu M L and Perlmutter A (1970) Growth inhibiting factor in the zebrafish (*Brachydanio rerio*) and the blue gourami (*Trichogaster trichopterus*). *Growth* **34**, 153-175.

Yun S - S, Scott, A P, Siefkes M J and Li W (2002) Development and application of an ELISA for a sex pheromone released by the male sea lamprey (*Petromyzon marinus* L.). *Gen. Comp. Endocrinol.* **129**, 163-170.

Yun S - S, Scott, A P and Li W (2003) Pheromones of the male sea lamprey, *Petromyzon marinus* L.: structural studies on a new compound, 3-keto allocholic acid, and 3-keto petromyzonol sulphate. *Steroids* **68**, 297-304.

Zhang C (1997) Bile acids as potential pheromones in lake char, *Salvelinus namaycush*: an electrophysiological, biochemical and behavioural study. *Ph.D. Thesis*. University of Manitoba, Winnipeg, Canada.

Zheng W and Stacey N E (1996) Two mechanisms for increasing milt volume in male goldfish, *Carassius auratus*. *J. Exp. Zool.* **276**, 287-295.

Zheng W and Stacey N E (1997) A steroid pheromone and spawning stimuli act via different neuroendocrine mechanisms to increase gonadotropin and milt volume in the male goldfish, *Carassius auratus*. *Gen. Comp. Endocrinol.* **105**, 228-238.

Zheng W, Cardwell J R, Stacey N E and Strobeck C (1993) Application of sex pheromones to enhance fertility in male cyprinids: studies in goldfish (*Carassius auratus*) and common carp (*Cyprinus carpio*). In: *Proceedings of the Fifth International Symposium on Reproductive Physiology of Fish* (July 2-8, 1995) (eds: Goetz F W and Thomas P), 272. Texas A. & M. University, Austin.

Zheng W, Strobeck C and Stacey N E (1997) The steroid pheromone, 17,20-dihydroxy-4-pregnen-17,20-diol-3-one increases fertility and paternity in goldfish. *J. Exp. Biol.* **200**, 2833-2840.

Zielinski B S, Arbuckle W J, Belanger A J, Corkum L D, Li W and Scott, A P (2003) Evidence for the release of sex pheromones by male round gobies (*Neogobius melanostomus*). *Fish Physiol. Biochem.* **28**, 237-239.