J. Appl. Zool. Res. (2005) **16** (2): 210-216

RECENT ADVANCES IN FISH PHEROMONE RESEARCH WITH EMPHASIS ON THEIR POTENTIAL APPLICATIONS IN FISHERIES

A. K. PANDEY
Central Institute of Freshwater Aquaculture, Kausalyaganga, Bhubaneswar-751002

ABSTRACT: Most of the vital activities of fish like alarm communication, individual identification, group cohesion, parent-offspring recognition, territorial markings, sex attraction and synchronization of reproductive processes as well as migration are shaped by pheromones. Our knowledge in this field is still fragmentary because involvement of pheromones is known mainly by the behavioural responses, chemically they are largely unknown. Aspects pertaining to fright reaction and alarm substances, social structure and individual recognition, sex pheromones, and fish migration have been discussed in this review. Problems associated with chemoreception under environmental pollution have been discussed. Possibilities of utilizing pheromones in advancing maturation and breeding of cultivable species as well as in fishery management are also highlighted

Keywords: Alarm pheromones, sex pheromones, migration, aquatic pollution.

Pheromones are externally secreted semiochemicals employed in intercommunications between individuals of the same species. There exist convincing evidence that such system is widely operative among the organisms ranging from protozoans to mammals. There are instances of chemical communication in aquatic plants especially for the attraction of gametes. Recent studies have demonstrated that most of the vital activities in fish like alarm communication, individual identification, group cohesion, parent-offsprings recognition, territorial markings, sex attraction as well as synchronization of the reproductive processes, and migration are shaped by the pheromones (LILEY, 1982; PFEIFFER, 1982; PANDEY, 1984, 1998; CHIVERS and SMITH, 1998). Pheromones of the terrestrial organisms are volatile having low molecular weight ranging from 50-300 while such semiochemicals in the aquatic species appears to be of larger size (high molecular weight) and soluble in water (SMITH, 1992; SORENSEN *et al.*, 1998; PANDEY, 2003).

Alarm Pheromones: Alarm substance cells (ASC) of the ostariophysan and other groups of fish release alarm pheromone from their skin on mechanical injury presumably by a predator that elicits alarm behaviour among the conspecifics and members of the closely-related species. Depending upon the biology of the species, the alarm reaction includes dashing, c-turn, immobility, forming of tight school, hiding and avoidence of the area (PFEIFFER, 1982; SMITH, 1992). There are instances that the predator northern pike (*Esox lucius*) consuming the preys (*Pimephales promelas* and *Culaea incostans*) containing the ASCs in skin, releases the alarm pheromone in the faecal matter which are detected by the members of the prey or closely related species. 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. This phenotypic change appears to be due to primer effect of the alarm pheromone.

The alarm substance of minnow was suggested to be purine- or pterine-like (double-ringed compounds usually associated with pigments), non-volatile and extremely soluble in water. Histamine was also implicated to be alarm substance of certain cyprinids. PFEIFFER and LEMKE (1973) reported the alarm substance of the European minnows (*Phoxinus phoxinus*) to be pterine (isoxanthopterine), which might be conjugated with protein for water solubility and to denote species specificity. However, KASUMYAN and LEBEDEVA (1979) showed that the alarm pheromone of *P. phoxinus* possesses molecular weight approximately 1100, behaves in alkaline medium (pH 8-9) as anion and breaks down when heated. They have suggested it to be a carbohydrate or related compound containing amino groups. PFEIFFER (1982) found several heterocyclic compounds to induce effective alarm response. Hypoxanthine-3-N-oxide has been reported to be an active component of the ostariophysan alarm signaling system (PFEIFFER *et al.*, 1985; BROWN *et al.*, 2000, 2003). Laboratory as well as field studies have revealed that the traps labelled with the fathead minnows skin extract, hypoxanthine-3-N-oxide, or pyridine-N-oxide caught significantly fewer fish than did those labelled with distilled water. The central bundles in both tractus olfactorii of the medial olfactory tract of the fish conduct the nervous excitation elicited by alarm substance to the brain (PFEIFFER *et al.*, 1984) resulting in the elevation of plasma cortisol, glucose, potassium (K^+) and sodium (Na^+) levels. Plasma calcium (Ca^{2+}) recorded an initial increase followed by a decline to the below normal level. These changes suggest that alarm pheromone functions as stressor in fish (LEBEDEVA *et al.*, 1994).

Individual and Species Recognition: Varying degrees of socialism have been recorded in fish, however, such tendency is more marked among the visually-deficient species. The school of roach (*Ritulus ritulus)* does not disintegrate during night because members of the school maintain contact through chemical cues. There exist records that individuals of *Ictalurus natalis, Clupea herrangus pallasi, Caecobarbus geertsi, Haplochromis burtoni, Astyanix jordani, Salmo alpinus, Notropis lutrensis, Anguilla anguilla, Oncorhynchus kisutch, Oncorhynchus nerka, Ictalurus nebulosus, Astyanax mexicanus, Phreactichthys andruzzi, Carassius auratus* and *Heteropneustes fossilis* are attracted towards the waters of the tank previously occupied by their conspcifics. Even broods and youngs are recognizable to their parents by the odours. The parents of Midas cichlid fish (*Cichlasoma citrinellum*) recognize to their youngs by means of pheromone. BARNETT (1981) reported that fry of Midas cichlid fish discriminates even between mother and father on the basis of urine odour and suggested that the steroid titers in urine could provide information on sex and that of peptide chains could indicate species. It appears that the secretions in the skin mucus, urine as well as metabolites of bile acids (voided in faecal matter) are involved in individual identification and group cohesion in these fishes (TODD, 1971; SELSET, 1980; BARNETT, 1981; ZHANG, 1997).

Benficial conditioning of the waters by conspecifics and inhibition of growth under over-crowded condition are assumed to be mediated through pheromones (SOLOMON, 1977). Eels (*Anguilala anguilla*) are usually caught in the traps dripped with conspecific skin extracts (SAGLIO, 1982). TODD (1971) found that fighting as well as stress does alter chemistry of the pheromones of the yellow bullhead (*Ictalurus natalis*) secreted in the mucus. Diets also appear to modify body odour of the catfish. Interestingly, COLYER and JENKINS (1976) have indicated the presence of an aggression-suppressing pheromone(s) in the Siamese fighting fish, *Betta spendens*. CARR and CARR (1986) have observed that the aggression-suppressing pheromone of the brown bullhead (*I. nebulosus*) gets inactivated by heat and protease treatments and have suggested it to be a protein with molecular weight less than 10,000.

During reproductive period, the males of some species deposit a layer of mucus on the spawning surface which may serves as chemical signals marking the breeding sites and may perhaps communicate the status of the occupants. There exist reports on the substrate marking behaviour in fishes and secretions of mucus, urophysis and urine have been implicated in the production/release of the territorial marking pheromones (STABELL, 1987). Possibly, these marks bear the same biological significance as marking fluid (MF) of the mammals.

Sex Pheromones: There exist reports on congregation of salmonid males around the cages/pens of the mature females during breeding season. Fishermen of Mississippi usually catch large number of male channel catfish, *Ictalurus punctatus*, by placing ripe females in cages in the river. In some regions of France, male lamprey nearing sexual maturity is placed by the fishermen in the traps to attract females. Behavioural studies have revealed the occurrence of sex pheromones in lamprey (*Petromyzon marinus*), sharks (*Carcharhinus melanopterus* and *Traenodon obesus*) and a number of teleostean species such as *Lebestes reticulatus, Bothyogobius soporator, Hypsoblennius jenkinsi, H. genitilis, H. robustus, Mollinesia letipinna, Gasterosteus aculeatus, Pimephales promelas, Plotosus lineatus, Gobius jozo, Ictalurus punctatus, Pterophyllum scalare, Carassius auratus, Poecilia chica, P. melanogester, P. sphenops, Xiphophorus helleri, Salmo gairdneri* (=*Oncorhynchus mykiss*), *S. salar, Misgurnus anguillicaudatus, Rhodesus ocellatus ocellatus, Plcoglossus altivelis, Acheilognathus laneolatus, Oncorhynchus rhodurus, Anguilla rostrata, Cottocomephorus grewingki, Corgonus automnalis migratorius, Blennius pavo, Trichogaster trichopterus, T. pectoralis, Catastomus catastomus, C. commersoni, Colisa labiosa, C. lalia, Brachydanio rerio, B. albolineatus, Hypsomesus olidus, Haplochromis burtani, Clupea herrengus pallasi, Cyprinus carpio communis, Oreochromis niloticus, Fugus niphobles, Astyanax mexicanus, Gymnocephalus cernuus, Salvelinus alpinus, Clarias gariepinus, C. batrachus, Heteropneustes fossilis* and *Barilus bendelisis* (LILEY, 1982; SORENSEN and STACEY, 1999; SORENSEN *et al.*, 1998; PANDEY, 2003). Both releaser as well as primer sex pheromones appear to operate in fishes. 17α, 20β-dihyroxy-4-pregnen-3-one, its sulphate/glucuronid metabolites, metabolites of $F_{2\alpha}$-prostaglandin and steroid glucuronides (etiocholanolone glucuronide and 5β-pregnene-3α,17α-diol 20-one-3 glucuronide) seem to be involved in the attraction of sexes, courtship and spawning of the goldfish, zebrafish, guppies, catfishes, salmons and trouts. Further, there are evidences that the male pheromone (s) accelerate ovarian recrudescence among female conspecifics, probably by enhancing plasma 17β-estradiol (E_2), 17α,20β-dihydroxy-4-pregnene-3-one (17,20-P), 5β-pregnene-3α,17α,20β-triol and 11-ketotestosterone (11-KT) levels and vitellogenic activities (VAN WEERD, 1990; DEGANI and SCHREIBMAM, 1993). Out of the nine steroid hormones (dehydroepiandrosterone, testosterone, dihydrotestosterone, progesterone, androstenedione, estrone, oestradiol, corticosterone and cortisol) tested, only testosterone elicited the preference respones (attraction) in spawning-run female sea lamprey. Testosterone or a closely related structural derivative has been suggested to be sex pheromone of the male cyclostome (ADAMS *et al.*, 1987). Further, pheromones have also been implicated in the reproductive isolation of sympatric species such as zebrafish (*Brachydanio rerio* and *B. albolineatus*), gourami (*Trichogaster trichopterus* and *T. pectoralis*), suckers (*Catastomus catastomus* and *C. commersoni*) and masu salmon/rainbow trout (*Oncorhynchus masau* and *O. mykiss*).

The male three-spined stickleback (*Gasterosteus aculeatus*) gets stimulated by smelling odours of its own nest during breeding season. LOSEY (1969) demonstrated that the males of *Hypsoblennius jenkinsi, H. robustus* and *H. genitilis* secrete a chemical during high courting and mating periods that releases sexual appetitive behaviour and sexual receptivity in 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. SHERWOOD *et al.* (1991) reported that this pheromone shows hydrophobic properties similar to those of polar steroids, prostaglandins, or other conjugate forms, and atleast one form appears to contain a sulphate or glucuronide group. The male pheromone appears to play role in synchronization of spawning in the school of herrings. Recently, CAROLSFIELD *et al.* (1997) have shown that elevated levels of plasma 3α,17α-dihydroxy-5β–pregnen-20-one and 17α-hydroxyprogesterone coincided with responsiveness to the spawning pheromone in this species. Since unisexual groupings of the females (without males) inhibit the ovarian development, it offers an opportunity to explore the female-female priming pheromones in fishes (PANDEY *et al.*, 2000).

Pheromones and Migration: How migratory fish locate their pathways from sea to freshwater and *vice versa* remains a mystery. Work done on homing of the salmonids has demonstrate 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). It was 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 metablic products of a specific population (pheromones) as homing cues for the salmonids was proposed in 1924 and 1934 but this hypothesis was totally eclipsed by the concept of olfactory imprinting propounded by HASLER (1983). 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 brain and they "retain the olfactory memory" during the interim period of homeward migration.

NORDENG (1971) realised the pheromone odour tracks to help guide homing of the Arctic char (*Salmo alpinus*). SOLOMON (1973) demonstrated that the migrating Atlantic salmon (*S. salar*) prefers the river in which youngs of its own populations were living. After exhaustive studies on *S. alpinus*, *S. trutta* and *S. salar*, NORDENG (1977) rejuvenated the pheromone hypothesis. He remarked that 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 the anadromous rainbow trout (*O. mykiss*) and sea lamprey (*P. marinus*). MILES (1968) has demonstrated that elvers of the catadromous European eel (*A. rostrata)* are attracted towards the water of the streams containing the conspecific adults. While working at Rhode Island, SORENSEN (1984) has also confirmed this finding. Recently, 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 the concept of chemical ecology in management of salmonid fisheries.

Our knowledge regarding the chemical nature of these navigational cues is still fragementry. MILES (1968) found that the compound(s) involved with attraction of the elvers in *A. rostrata* to be biodegradable, unaffected by autoclaving and non-volatile. ATEMA *et al.* (1973) reported that the alwife (*Alosa pseudoherengu)* homing pheromones are heat-stable, non-volatile, polar and having molecular weight less than 1000. DOVING *et al.* (1980) demonstrated the presence of migratory cues of *S. alpinus* in the faecal matter of the smolts and suggested it to be derivatives of bile salts like taurolithocholate, taurolithocholic sulphate, sulphotaurolithocholate or taurochenodeoxycholate which may convey the information to the brain through medial portion of the olfactory tract. By employing electrophysiological, biochemical and behavioural approaches, ZHANG (1997) has also confirmed the chemostimulatory roles of 9 out of 38 authentic bile acids in lake char (*Salvelinus namaychush*) and remarked that the olfacory sensitivity and specificity of bile acids are affected by (i) position and orientation of hydroxyls, (ii) hydrosulphation, (iii) side chain length and (iv) side chain substituents of the molecules. LI and SORENSEN (1997) have identified peteromyzonol sulphate and allocholic acids as migratory pheromone in *P. marinus.*

Chemoreception and Water Pollution: Four groups of chemicals such as (i) amino acids, (ii) steroids, (iii) prostaglandins and (iv) bile acids (and their derivatives) 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 in the olfactory system. HARA (1992) has given a hypothetical three dimensional model to show the mode of interaction of amino acids which serve as feeding stimulants in fish with olfactory receptor sites. It has been observed that detergents even at the concentration of 0.5 ppm (much lower value that inflict lethal damage) impaired functioning of the receptor by causing erosion in the chemosensory organ. BLOOM *et al.* (1978) showed that sublethal (0.5 ppm) exposure of zinc affected the behaviour to the sexual aggregating pheromones in the zebrafish. Linear alkylbenzene sulphate (LAS) significantly depressed chemoattraction of water conditioned by conspecifics to juvenile *Salvelinus fontinalis.* Laboratory studies have revealed that the freshwater spawning migration of salmons is being impaired by acidification of rivers. Electrophysiological recordings of the olfactory epithelium of the adult male *S. salar* to testosterone and urine of the ovulated femals significantly reduced at pH 5.5-4.5 and abolished at pH 3.5. Exposures to sublethal concentrations of diazinon and carbofuran significantly reduced the ability of mature Atlantic salmon parr to priming pheromone of ovulated females. The pernicious effects of an anionic detergent (sodium lauryl sulphate), pH, mercury (Hg), silver (Ag), cadmium (Cd), copper (Cu), nickle (Ni) and zinc (Zn) on the olfactory system are now well established. By calculating IC_{50} value (concentration which inhibits electroolfactographic response by 50%), it has been found Ag, Hg, Cu and Cd to have most depressive effects on the chemoreception in salmonids. The whitefish (*Coregonus clupeaformis*) and rainbow trout (*O. mykiss*) exposed to 2.4 μm copper sulphate ($CuSO_4$) solution for two weeks exhibited loss in the phospholipid stainable granules in the receptor neurones of the olfactory mucosa, however, recovery in the granules were observed when the fishes were transferred to freshwater for 12 weeks. Phospholipids have been reported to be involved in the electrophysiological (electrolfactogram, 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 like hydrocarbons and heavy metals. Since the present trends of rapid industrialization and increase in population have drastically changed the aquatic environment, it is imperative to undertake the studies regarding the interactions of various pollutants with the pheromonal communication system in fishes. BARNETT (1981) remarked that a chemically polluted environment might interfere with the success of parent care.

Conclusions: Earlier fishes were viewed as leaky bags that slowly release various chemicals which can serve as a chemical picture of the animal that others can smell and identify as to species, sex, stress level and perhaps size as well as individuality (ATEMA, 1980). Though the chemical nature of pheromones and sites of their biosynthesis (except alarm substances) are not clearly identified, there are growing evidences that therse chemicals do have communicative roles among these class of vertebrates. Since sex pheromones are widely distributed among fish, a better understanding of their role is *sine qua non* to understand their role in reproductive physiology (DEFRAIPONT and SORENSEN, 1993). Interestingly, GnRH has been identified as a potent olfactory stimulant in fish but its role in synchronization of reproductive process is not known.

Since these signals are species-specific and operate at molecular levels, it is imperative to utilize them for management and conservation of fisheries. In pisicultural operations, they may be employed to advance puberty and accelarate ovarian recrudescenc as well as selective stimulants to induce spawning at a time and place convenient to the managers. Since they are externally active, their delivery would eliminate the stress associated with the hormone or drug administration. They may also be employed as artificial baits, selective attractants, growth stimulators and inhibitors of aggression as well as cannibalism. Recent studies point to the potential exploitation of semiochemicals in propagating the migratory fishes in new rivers and streams.

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.

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 (G.E. GLASS, ed.). Ann Arbor Scient. Pub., New York.* pp. 177-197.

BARNETT, C., 1981. The role of urine in parent-offspring communication in a cichlid fish. *Z. Tierpsychol.* **52** : 173-182./

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.

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., 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.

CAROLSFIELD, J.M., SCOTT, A.P. and SHERWOOD, N.M., 1997. 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., 1986. Characterization of an aggression-suppressing pheromone in the juvenile brown bullhead (*Ictalurus nebulosus*). *Copeia* **1986** : 540-545.

CHIVERS, D.P. and SMITH, R.J.F., 1998. Chemical alarm siganalling in aquatic predatory-prey systems : a review and prospectus. *Ecoscience* **5** : 338-352.

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

DEFRAIPONT, M. and SORENSEN, P.W., 1993. Exposure to the pheromone 17α,20β-dihydroxy-4-pregnen-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.

DOVING, K.B., SELSET, R. and THOMMESEN, G., 1980. Olfactory sensitivity to bile acids in salmonid fish. *Acta Physiol. Scand.* **108** : 123-131.

HARA, T.J., 1992. *Fish Chemoreception*. Chapman & Hall, London.

HASLER, A.D., 1983. Synthetic chemicals and pheromones in homing salmon. In : *Control Processes in Fish Physiology* (J.C.RANKIN, T.J. PITCHER and R.T. DUGGAN, eds.). Croom-Helm, London. pp. 103-116.

KASUMYAN, A.O. and LEBEDEVA, N.E., 1979. New data on the nature of the alarm pheromone in cyprinids. *J. Ichthyol.* **19** : 109-114.

LEBEDEVA, N.Y., LEBEDEVA, V.I. and GOLOVKINE, T.V., 1994. Pheromone of the trout stress inducer. *Biophysics* **39** : 527-530.

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.

LILEY, N.R., 1982. Chemical communication in fish. *Can. J. Fish. Aquat. Sci.* 39 : 22-35.

LOSEY, G.S., 1969. Sexual pheromone in some fishes of the genus, *Hypsoblennius* Gill. *Science* 163 : 181-183.

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.

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.

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

PANDEY, A.K., 1998. Chemical cimmunication in fishes : an overview. *Fishing Chimes* 18 (2) : 15-20.

PANDEY, A.K., 2003. Current status and potential applications of fish pheromones in aquaculture and fishery management. In : *Aquaculture Medicine* (I.S. BRIGHT SINGH, S.S. PAI, R. PHILIP and A. MOHANDAS, eds.). School of Environmental Sciences, Cochin University of Science & Technology, Cochin pp. 271-292.

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). Central Institute of Freshwater Aquaculture, Bhubaneswar. p. 83.

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

PFEIFFER, W. and LEMKE, J., 1973. Untersuchungen zur Isolierung und Identifizierung des Schreckstoffes aus der Hault 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., RIEGELBAUER, G., MEIER, G. and SCHEIBLER, B., 1985. 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.

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.

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.

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.

SMITH, R.J.F., 1992. Alarm signals of fishes. *Rev. Fish Biol. Fish.* 2 : 33-63.

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. and STACEY, N.E., 1999. Evolution and specialization of fish hormonal pheromones. In : *Advances in Chemical Signals in Vertebrates* (R. E. JOHNSTON, D. MULLER-SCHWARZE and P. W. SORENSEN, eds.). Plenum Press, New York. pp. 15-47.

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 discimination 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* (T. J. HARA, ed.). Chapman & Hall, London. pp. 249-270.

STABELL, O.B. and LWIN, M. S., 1997. Predator-induced phenotypic changes in crucial carp caused by chemical signals from conspecifics. *Environ. Biol. Fish.* 49: 145-149.

TOOD, J.H., 1971. The chemical languages of fishes. *Scient. Am.* 224(5) : 98-108.

VAN WEERD, J.H., 1990. Pheromones and ovarian growth in the African catfish, *Clarias gariepinus*. *Ph.D. Thesis*. University of Wageningen, Wegeningen, The Netherlands.

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.