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Minireview

Use of chemical communication in the management of freshwater aquatic species that are vectors of human diseases or are invasive

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Abstract

Chemical communication occurs when both originator (signaller) and one or more receiver(s) possess specializations for chemical exchange of information. Chemical information can be used by a wide variety of species to locate food and mates, avoid predators and engage in social interactions. In this review, we focus on chemical signalling between mates or cues from nest sites or hosts by selected aquatic pest species and indicate how chemical information can be used to manage pests. The pests are vectors of disease (blood-sucking insects) or invasive species (crayfishes and fishes) that have exhibited detrimental effects on indigenous species. Pheromones released by females attract and stimulate males in some taxa (insects, crayfish, goldfish, and crucian carp), whereas pheromones released by males attract females in others (round goby, sea lamprey). Other chemicals (e.g., habitat odours or odours given off by developmental stages of conspecifics) can affect oviposition decisions of pest species. In areas of aquatic environments where other cues may be limited (e.g., visual), freshwater organisms may rely solely on chemical signals or in concert with environmental cues for reproduction. Once the chemical structure of odour attractants are identified and shown to lure conspecifics to traps, odorants or their blends can be used to control the aquatic pests. There is promise for the application of pheromone traps to control the malarian vector (*Anopheles gambiae*) or invasive species such as signal crayfish (*Pacifastacus leniusculus*), sea lamprey (*Petromyzon marinus*) and the round goby (*Neogobius melanostomus*) by disrupting the reproductive behaviours of these species.

Keywords: Behaviour; Chemical communication; Freshwater; Pheromones; Reproduction; Vectors; Invasive species; Management

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1. Introduction

Chemical signalling among organisms affects the behaviour and physiology of species (Liley, 1982) and may be particularly important in relaying specific information to species in aquatic environments where visibility may be limited. Chemicals that mediate interactions between either inter- or intraspecific organisms are called semiochemicals (Table 1) and may be subdivided into interactions between individuals of the same (pheromones) or different (allelochemicals) species (Nordlund, 1981). Pheromones have been defined as substances, or mixtures of substances, that are released by individuals into the environment where they induce specific, adaptive and largely innate biological responses in conspecifics; i.e., pheromones are mutually beneficial to both the sender and receiver within the same species (Karlson and Lüscher, 1959). Pheromones can include sex attractants, trail marking odours and others. Allelochemicals are compounds secreted by an individual of one species and received by individuals of another species. Allelochemicals that travel between individuals of different species are subdivided into synomones (both sender and receiver benefits) and kairomones (receiver benefits) on the basis of which species benefits from the message (Wyatt, 2003) (Table 1).

In nature, chemical communication between sexes of a given species often involves individuals of one sex releasing

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Table 1
Definition of information-bearing chemical compounds secreted outside of animals, resulting in communication

Term	Description
Semiochemicals	A generic term for compounds secreted from one individual to another, either inter- or intraspecific, modifying behaviour
Pheromones	Compounds secreted (often at a certain stage in development) by an individual to a conspecific with benefits to both sender and receiver
Contact pheromones	Sex pheromones produced by females and recognized by conspecific males once the male contacts the body surface of the female; i.e., the male will not attempt to mate with a female until contact is made
Allelochemicals	Compounds secreted by an individual of one species and received by individuals of another species and are further defined on the basis of which species benefits (the sender or receiver)
Kairomones	Allelochemicals released by individuals of one species and detected by a second species to the benefit of the receiver (e.g., CO_2 or carboxylic acid released by a host to the benefit of mosquitoes)
Synonomes	Allelochemicals released by individuals of one species and received by individuals of a second species, resulting in a benefit to both sender and receiver

Definitions are modified from Evenden et al. (1999), Wyatt (2003), Sonenshine (2004), and Wisenden and Stacey (2005).

odour(s) to attract a receptive mate. A classic example from the 1870s is Jean–Henri Fabre's observation of male peacock moths flying through his open door to a recently emerged female conspecific (www.rsnz.org/education/alpha/Alpha119.pdf). Observations of such interactions led to several approaches in understanding chemical signalling. Laboratory experiments are conducted to examine effects of holding water or washings from reproductive individuals of one sex on the opposite or same sex (Liley, 1982). Histological studies, often using immunofluorescence, reveal the source of the chemical substances in cells of glands e.g., Leydig-like cells in the testes or seminal vesicles of fish (Arbuckle et al., 2005). Identification of chemicals, such as bile acids, peptides or steroids, is achieved by comparing thin-layer chromatography and high-performance liquid chromatography (HPLC) fractions with known standards or by HPLC analysis and electrospray mass spectrometry (Arbuckle et al., 2005). Once compounds within species are identified, physiological (electro-olfactogram, EOG, recordings) and behavioural (typically responses of individuals in a Y-maze to conspecific odours) assays are used to examine the efficacy of synthesized steroids. If results of these tests support a specific response to identified odours, field manipulations are conducted using pheromone traps in natural settings (e.g., Johnson et al., 2005). Alternatively, some researchers characterize the olfactory system of a species by testing its responses to a suite of commercially available steroids or prostaglandins (Murphy et al., 2001). Others typically use EOG studies as a physiological bioassay to test responses of males or females to fractions of stimulus water to identify potent compounds (Belanger et al., 2004). Although the process of identifying putative pheromones is most challenging (Sorensen et al., 2005), behavioural assays are the key to understanding chemical communication between and among individuals. Given the diverse expertise required in these analyses, a multidisciplinary approach is needed to understand chemical communication between and among organisms.

Specific compounds, including cuticular hydrocarbons, peptides, steroids, prostaglandins, and bile acids, are linked to reproductive behaviour in freshwater organisms (Tables 2–4). In insects, females typically release signals to which conspecific males respond (Birch and Haynes, 1982). In the case of blood-sucking insects, male insects are attracted to females through a combination of visual, chemical, and auditory cues (depending on species), but females respond to odours that are emitted from human hosts, aggregations of eggs or from the water in which eggs dwell (Qiu, 2005; Yuval, 2006). Invasive species such as crayfish and fishes may use pheromones for mate attraction as well as for oviposition cues. Therefore, once the chemical structure of sex pheromones of invasive species have been identified, the compounds could be used in the control of such species.

In this paper, we focus on the chemical exchange of information (e.g., that affecting oviposition, spawning, courtship displays, and mate choice) of reproductive freshwater organisms (i.e., organisms in which at least one life history stage has been spent in freshwater) that are pests, and suggest ways that this information can be used in the control of aquatic pest species. Although pheromone secretions (sex and aggregation pheromones) have been studied in other aquatic groups such as caddisflies, Trichoptera (Löfstedt et al., 1994), an insect order closely related to Lepidoptera, this group (and others) were ignored because they are not pests. We arbitrarily selected aquatic species that are vectors of diseases (blood-sucking insects) or invasive species (crayfishes and fishes) that have exhibited detrimental effects on other species. Once chemical signals (often sex pheromones, but also habitat or oviposition cues) are identified, baited traps can be used to capture designated species. Control techniques, such as trapping, decrease the abundance of gravid females or reproductive males, thereby reducing the reproductive potential of the pest, while increasing the recruitment potential of co-habiting native species. Understanding the information content of a signal and its function in mate attraction and courtship behaviour will help in the potential management of species.

2. Olfactory organization and chemoreception

Chemosensory information is initially received at peripheral sensory organs where chemical signals or

Table 2
A summary of the behavioural responses by insects to test odours, Genus and species names are listed alphabetically within a family

Family	Genus species	Adult sex or Life stage	Test substance	Behavioral response	Reference
Culicidae	*Aedes aegypti*	F	Matrone	Stimulates oviposition; prevents females from remating	Gillotte (2003)
		F	Dodecanoic acid (Z)-9 hexadecenoic acid	Ovipositional behaviour	Ganesan et al. (2006)
		L	Larval conditioned water: heneicosane, docosane, nonacosane, octadecanes and isopropyl myristate	Egg laying enhanced	Mendki et al. (2000)
	Aedes triseriatus	F	2-Methylphenol	Oviposition	Bentley et al. (1981)
	Aedes triseriatus	F	4-Methylphenol, *p*-cresol	Oviposition stimulant	Bentley et al. (1979)
	Aedes, *Armigeres*,*Culex*	F	Tri-methyl phenols	Oviposition	Ikeshoji et al. (1975)
	Anopheles gambiae	F	Ammonia, CO_2, lactic acids	In a field study, more mosquitoes were attracted to test substances than to human odour	Qiu (2005)
	Culex cinereus	F	6-Acetoxy-5-hexadecanolide	Oviposition attractant	Mboera et al. (1999)
	Culex pipiens fatigans	F	Erythro-6-acetoxy-5-hexadecanolide	Oviposition attractant	Laurence and Pickett (1982)
		F	(-)-(5R,6S)-6-acetoxy-5-hexadecanolide	Oviposition attractant	Laurence et al. (1985)
	Culex quinquefasciatus	F	Erythro-6-acetoxy-5-hexadecanolide	Oviposition attractant	Mboera et al. (1999)
	Culex tarsalis	F	Extracts from egg rafts	Oviposition attractant	Osgood (1971)
Glossinidae	Several species of tsetse flies	M and F	Acetone, CO_2, octenol, 3-*n*-propylphenol, 4-methyl-phenol	Field tests showed that adults were attracted to test substances and visual cues	Leak (1999)
Simuliidae	*Simulium leonense*	F	Unidentified compound emitted from conspecific eggs	Oviposition attractant	McCall et al. (1997)
	Wilhelmia equine	M and F	Cuticular washings	Contact pheromones	Būda et al. (2003)
Tabanidae	*Tabanus sudeticus*	F	Acetone, octenol, horse urine	Canopy traps baited with acetone and horse urine attracted more flies than traps with octenol or unbaited traps in Eastern Croatia	Krčmar et al. (2005)
	Several species	F	Ammonia, CO_2, octenol	Significant numbers were attracted to canopy traps with test odours compared to control traps	French and Kline (1989)
	Several species	F	Acetone, cow urine, CO_2, octenol, phenol	Odours and visual cues were effective in attracting flies to traps	Milhok (2002), Milhok et al. (2007)

Adult sex, male (M) or female (F) and immature stage, larva (L). See website (www.pherobase.com) for other examples.

odorants bind the extracellular surface of G-protein coupled receptors, located on the dendrites of bipolar neurons. Bipolar neurons are specialized at one end for chemical detection and at the other end for chemically signalling (Firestein, 2001). Most olfactory sensory neurons can be found beneath the cuticle of sensory hairs (invertebrates) or on the apical surface of olfactory sensory neurons in the olfactory epithelium of the nares (vertebrates). Following odorant binding, a cascade of events is initiated that transforms the chemical energy of binding into a neuronal signal, changing the membrane potential of the receptor neuron. An action potential is initiated and is propagated along nerves where the sensory information is integrated in the high order brain centres of the central nervous system and where the signal may trigger some behavioural or physiological output in the animal (for reviews see Firestein, 2001; van der Goes van Naters and Carlson, 2006).

The peripheral olfactory system of invertebrates is organized into a large number of distinctive sensilla (specialized sensory hairs or setae) that are specialized for a chemosensory function and/or touch (Fig. 1). Chemosensory sensilla are peripherally located and are found on the antennae, maxillary palps, and other sensory appendages. Odorants can enter the sensillum lymph via pores or permeable membranes of the cuticle and cross the lymph, binding to the dendrites of sensory neurons and activating G-proteins. This causes a cascade of events potentially leading to the generation of an action potential (for review, see Rützler and Zwiebel, 2005). Insects appear to have relatively few odour receptor genes, when compared to other animals, as shown in the recent discovery of the genome sequence (Adams et al., 2000) and the complete repertoire of olfactory receptors (Jacquin-Joly and Merlin, 2004) in the fruit fly *Drosophila melanogaster*, and in the genome sequence of the mosquito, *Anopheles gambiae* (Holt et al., 2002).

Table 3
A summary of conspecific chemical communication in crayfish

Order	family	Genus species	Sex	Test substance	Behavioural response	Reference
Decapoda	Astacidae	*Austropotamobius* (= *Potamobius*) *pallipes*	M	Conspecific female	Males passed through five stages of attraction to females, with the peak occurring when reproductive females were most receptive to copulation	Gaudioso and Cabello (1979)
			M	Receptive and non-receptive females	Males attempted copulation with the receptive females only	Villanelli and Gherardi (1998)
			M	Female conditioned water plus a visual stimulus	Males required both chemical and visual stimuli in order to obtain a behavioural response. Males spent more time moving and less time hiding in a shelter	Acquistapace et al. (2002)
		Pacifastacus leniusculus	M	Mature female odour	Conspecific males attracted to a sex pheromone baited trap	Stebbing et al. (2003a)
				Mature female conditioned water	Males exhibited significantly increased levels of motile activity and handling behaviour	Stebbing et al. (2003b)
	Cambaridae	*Orconectes propinquus*	M	Female conditioned water	Males spent significantly more time within 3 cm of the stimulus inflow hole when conspecific female conditioned water was released	Tierney and Dunham (1984)
		Orconectes rusticus	M	Female conditioned water	Reproductive males with intact major chelae spent significantly more time handling the female odour source than non-reproductive males and reproductive males with blocked chelae	Belanger and Moore (2006)
		Orconectes virilis	M	Female conditioned water	Males spent significantly more time within 3 cm of the stimulus inflow hole when conspecific female conditioned water was released	Tierney and Dunham (1984)
		Orconectes virilis	M	Female conditioned water	A submissive response to cues released by the opposite sex	Hazlett (1985)
		Procambarus acutus	M	Female conditioned water	Displayed a preference for female conspecific odour in a Y-maze	Bechler et al. (1988)
		Procambarus clarkii	M	Females located in perforated test containers and female conditioned water	Males showed submissive behaviours when females were in the test containers and blinded males searched longer when females were in the test containers. Males showed submissive behaviours when female conditioned water was introduced	Ameyaw-Akumfi and Hazlett (1975)
		Procambarus clarkii	M	Conspecific female	Males spent an extended amount of time in the area of receptive females	Gaudioso and Cabello (1979)
		Procambarus clarkii	M	Female conditioned water	Displayed a preference for female conspecific odour in a Y-maze	Bechler et al. (1988)
		Procambarus clarkii	M	Female conditioned water	Less aggressive postures were visualized when males presented with female stimulus water	Dunham and Oh (1992)
		Procambarus clarkii	F	Male conditioned water	Intact females displayed significantly more aggressive behaviours in the presence of stimulus water from the same sex	Dunham and Oh (1992)

The taxonomic classification scheme follows Taylor (2002). Genus and species names are listed alphabetically within each family.

Drosophila melanogaster has 62 odorant receptors encoded by 60 genes (Robertson et al., 2003). The *Anopheles* mosquito has 79 odour receptor genes (Hill et al., 2002). In contrast, *Caenorhabditis elegans* nematodes possess >1500, mice possess ca 900 and humans have 350 functional odorant receptor genes (Bargmann, 2006).

In vertebrates, chemoreception also occurs via the binding of odorants to G-protein coupled receptors; however, these receptors are contained within the olfactory epithelium of the nares. All life cycle stages of teleost fishes are aquatic and fish lack a vomeronasal organ. The olfactory organ of fish is located peripherally in the dorsal part of the snout (Fig. 1). Each olfactory organ consists of an olfactory chamber connecting to the aquatic environment through two openings (except in cichlids and damselfishes that have one opening): the anterior and posterior nares. Flow of

Table 4
Summary of chemical communication in fishes

Order	Family	Genus species	Sex	Test substance	Behavioral response	Reference
Petromyzontiformes	Petromyzontidae	*Petromyzon marinus*	Ad	Larval washings	In a two-choice maze, adults stay longer on the side with larval washings than control side; M and F are attracted to odours of opposite sex	Teeter (1980)
			M	Spermiating and non-spermiating males	Field study: ovulating females caught in traps with spermiating males	Johnson et al. (2005)
			Ad	Larval washings petromyzonal sulfate (PS) and allocholic acid (ACA)	Adult sea lamprey were more attracted to larval washings than to a mixture of PS and ACA	Li et al. (1995), Vrieze and Sorensen (2001)
			Ad	Petromyzonamine disulfate (PADS), petromyzosterol disulfate (PSDS), PS and larval extract	In a two-choice maze, adult migratory sea lamprey were attracted to PADS at lower concentrations than PSDS or PS, but PADS alone was less effective than the entire larval extract	Sorensen et al. (2005)
Cypriniformes	Cyprinidae	*Carassius auratus*	M	Prostaglandin $F_{2\alpha}$	10^{-8}M threshold evoked chasing behaviour	Sorensen et al. (1988)
			M	15-keto prostaglandin $F_{2\alpha}$	10^{-10}M evoked chasing behaviour and courtship behaviour; males are attracted to females	Sorensen et al. (1988), Stacey and Sorensen (2002)
			M	AD	Steroid induces agonistic responses in males	Poling et al. (2001)
		Carassius carassius	M	Preovulated females injected with 17,20βP	Males increased lutenizing hormone and milt	Olsén et al. (2006)
Perciformes	Gobiidae	*Neogobius melanostomus*	M	Estrone	Increased gill ventilation in osmic males	Belanger et al. (2006)
			M	Female gonadal tissue extracts	Increased gill ventilation in osmic males	Belanger et al. (2006)
			M and F	Etiocholanolone (ETIO), ETIO-glucuronide (ETIO-g), androsterone-sulfate (ANDR-s)	Increased ventilation rates of both sexes	Murphy et al. (2001)
			M and F	Estrone, estradiol-glucuronide (E2-3g),	Increased ventilation of males, but not females	Murphy et al. (2001)
			Implants	Estrone	Increased gill ventilation in methyl testosterone treated females	Murphy and Stacey (2002)
			M	Washings from reproductive males	Gravid females spent more time near male odour than odours from non-gravid females and control water	Gammon et al. (2005)
			F	Washings from reproductive females	Non-reproductive females spent more time near odour of reproductive females than control	Gammon et al. (2005)
			M	Washings from reproductive and non-reproductive males and females	Non-reproductive males were more active than reproductive males, but no response to odours	Marentette and Corkum (2007)
			F	Free steroids (11-oxo-T, Androstendione (AD), 11β-OH-AD), ETIO, 11-oxo-ETIO); conjugated steroids (11-oxo-ETIO-s, 11-oxo-ETIO-g, ETIO-s, ETIO-g) and total (free + conjugated) steroids	Reproductive and non-reproductive females spent more time in the steroid than control arm of a Y-maze; Reproductive females were more active when exposed to conjugated and total steroids than non-reproductive females. Non-reproductive were more active than reproductive females when exposed to free steroids	Moscicki et al., unpublished

The taxonomic classification scheme follows Nelson et al. (2004). Genus and species names are listed alphabetically within each family. Adult (Ad), male (M), female (F).

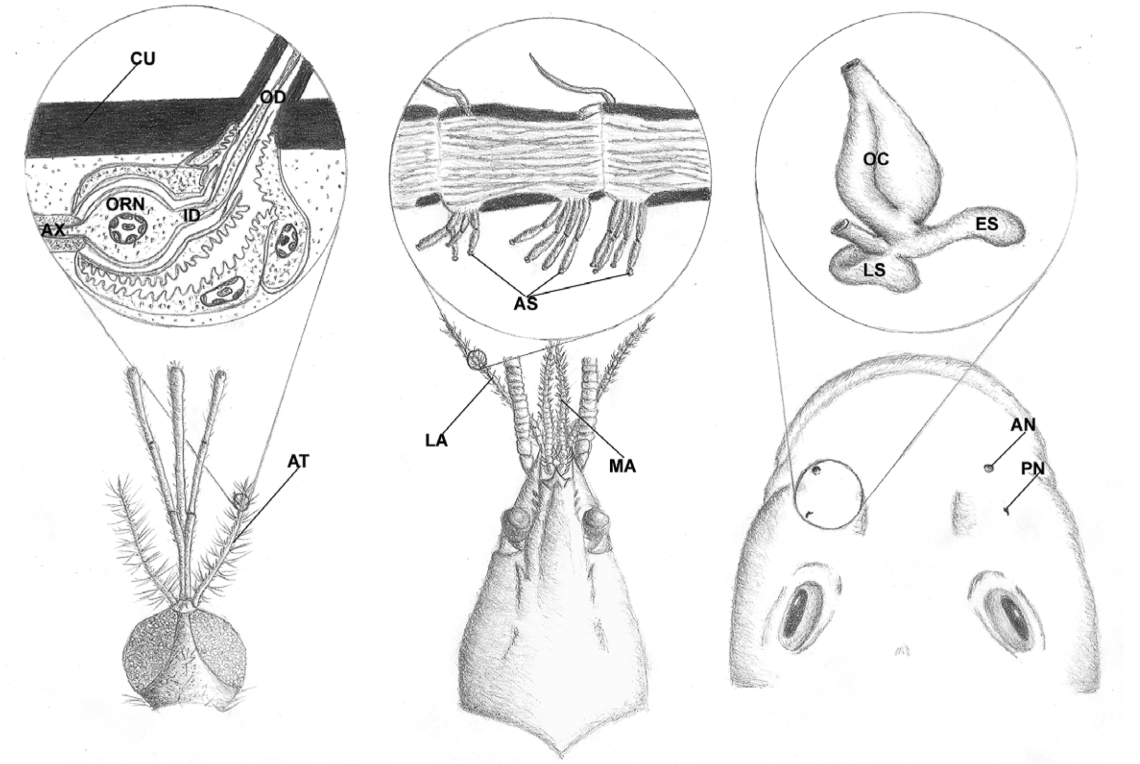

Fig. 1. Drawings of the olfactory structures in the female mosquito, *Anopheles gambiae* (Left), the crayfish, *Astacus fluviatilis* (Middle), and the round goby¸ *Neogobius melanostomus* (Right). Left: antennae (AT) of an adult mosquito (lower panel) and the olfactory sensilla (upper panel), showing CU, cuticle; OD, outer dendritic segment; ID, inner dendritic segment; ORN, olfactory receptor neuron; AX, axon (modified from Qiu, 2005). Middle: crayfish cephalothorax, showing MA, medial antennule and LA, lateral antennule (lower panel) and a portion of the LA enlarged with aesthetasc hairs (AS) (upper panel) (modified from Huxley, 1879). Right: the head of the round goby, showing the anterior nostril (AN) and posterior nostril (PN) (lower panel). The three components of the nasal cavity include OC, olfactory chamber; and two accessory nasal sacs, ES, ethmoidal sac that is positioned medially, and the LS, the lachrymal sac that is positioned laterally (Drawing was prepared by Yolanta Kita).

water is directed through the olfactory organ as the fish swims and nasal sacs may aid by pumping water over the olfactory epithelium (Johnson and Brown, 1962), which is contained in a series of lamellae. Lamellae are raised from the floor of the olfactory cavity, forming a rosette (Kleerekoper, 1969; Yamamoto, 1982). The lamellae consist of olfactory sensory neurons and non-sensory epithelia. Sensory neurons extend a dendrite to the surface of the epithelium, where odorant binding and peripheral processing occurs (for review see Laberge and Hara, 2001).

In fishes, there are three different types of olfactory sensory neurons (OSN), including ciliated, microvillus, and crypt neurons, each of which project into a different region of the olfactory bulb (Hamdani and Døving, 2006). In fishes, axons of ciliated neurons project into the medial olfactory tract, mediating alarm reactions (Hansen et al., 2003); axons of microvillus neurons of several species project into the lateral olfactory tract, mediating feeding behaviour (Hamdani and Døving, 2006); and, axons of crypt neurons in channel catfish project into the ventral midline of the olfactory bulb, mediating reproductive behaviour (Hansen et al., 2003; Hamdani and Døving, 2006). Hamdani and Døving (2006) suggest that crypt cells express olfactory receptors for sex pheromones in crucian carp, *Carassius carassius*.

3. Blood feeding insects with an aquatic stage: Diptera

Olfactory signals used in locating mates are widespread among terrestrial insects, particularly moths, but information on chemical signalling is not readily available in aquatic insects, including the blood-feeding aquatic Diptera. Aquatic insects differ from invasive aquatic species such as crayfish and fish in that most spend their immature feeding stages in the water, but emerge to the terrestrial habitat for reproduction. Therefore, any chemical signalling occurs in the terrestrial rather than the aquatic habitat. The pherobase website (www.pherobase.com) is a database of insect pheromones and semiochemicals for over 700 species, mostly terrestrial. Pheromones within the order Lepidoptera have been the most widely studied in terrestrial insects, and have been reported in >400 species, representing 44 families (Arn et al., 1992). Within the order Diptera, pheromones are known from “a few dozen species” in 12 different families, namely Agromyzidae, Calliphoridae, Ceratopogonidae, Culicidae, Drosophilidae, Glossinidae, Muscidae, Sarcophagidae, Scaridae, Simuliidae, Tabanidae, and Tephritidae (Būda et al., 2003; Roberts and Janovy, 1996; Tamaki, 2001; Yuval, 2006). Several of these families have members that are blood-sucking disease vectors, and of these, four are aquatic (Ceratopogonidae, biting midges or sand flies; Culicidae, mosquitoes; Simuliidae, black flies; Tabanidae, horse flies, deer flies) and one is associated with vegetation along the banks of lakes and rivers (Glossinidae, tsetse flies).

Blood-sucking dipterans are vectors of many diseases. For example, some Ceratopogonidae are vectors for bluetongue and encephalitis (Roberts and Janovy, 1996). Culicidae transmit malaria (*Anopheles gambiae*), yellow fever and dengue (*Aedes aegypti*), as well as encephalitis (Japanese encephalitis, St. Louis encephalitis virus, west Nile virus, western equine encephalitis) and filarial worms (*Culex* spp.) (Lampman et al., 2006; Roberts and Janovy, 1996). Female Simuliidae (black flies, e.g., *Cnephia pecuarum, Prosimulum mixtum*, *Simulium arcticum, S. colombaschense*, and *S. vittatum*) are best known for causing weight losses and death from anaphalaxis in livestock and poultry (Roberts and Janovy, 1996), but *Simulium damnosum* is a common vector of human onchoceriasis (river blindness), resulting from a filarial infection caused by *Onchocerca volvulus*. Female blood-sucking Tabanidae (*Chrysops* and *Tabanus*) transmit bacterial infections (tularaemia and anthrax); however, the likelihood of anthrax transmission in cattle is low. In contrast to most dipteran blood-suckers, where only females require a blood meal, both sexes of tsetse flies (*Glossina* spp.) are blood-suckers. Tsetse flies transmit the *Trypanosoma* blood parasite, responsible for sleeping sickness in humans and nagana (animal counterpart) in African ungulates, leading to weight loss and anemia (Roberts and Janovy, 1996).

The potential to carry diseases has led to considerable research into the management of these blood-sucking flies. Control of insect disease vectors has traditionally relied on a variety of mechanisms, including some that involve chemical cues. These include the release of sterile insects for mating, residual and non-residual spraying of pesticides and repellents, and pheromone traps to act as attractants or deterrents/repellents (Fredeen, 1987). Sterile insect release requires a method to attract one of the sexes, which may or may not rely on pheromones and residual spraying of repellents makes use of chemicals that interrupt or interfere with normal host cues. Pheromone traps have been widely used in insect management to attract and remove males from the reproductive pool, as well as for monitoring populations for pesticide-based control programs. The development of species-specific pheromone traps for aerial adults has the potential for controlling aquatic blood-sucking dipterans that transmit diseases and rely on pheromones for mating.

In most species, ovarian development must be initiated by a blood meal (which provides protein for the developing egg) (Yuval, 2006), and so host-finding cues also are important in disease transmission. In vector species, pathogen acquisition requires at least one blood meal to pick up the pathogen in the host blood, then transmission of disease requires additional blood meals from different hosts (Hayes et al., 2005); all of which relate to the ability of the vector to distinguish and locate their vertebrate host. For example, many *Culex* mosquitoes are mainly ornithophilic (bird-feeders) and are attracted to birds by host odours (Molaei et al., 2006). When diseases such as eastern equine, western equine, and west Nile encephalitis are present, they are found primarily in birds, and only spill over into human and other non-target hosts later in the breeding season, when the vectors can switch to other hosts (Hayes et al., 2005).

In contrast to encephalitis vectors, human malaria vectors are anthropophilic, i.e. attracted to human odours from a distance, and both sexes may be attracted to the host. Years ago, McIver (1982) reported that males were attracted to nylons worn by humans, suggesting that the males may use human odours to find conspecific females at their blood hosts. Several studies have shown that the attraction of mosquitoes to humans is based on a blend of compounds in specific proportions rather than a single compound (Qiu, 2005). Female *An. gambiae* are sensitive to many human odours, including ammonia, carboxylic acids, CO_2, lactic acids, and others (Qiu, 2005; van der Goes van Naters and Carlson, 2006). Field studies at a site on the River Gambia, West Africa, showed that a control odour (lactic acid, ammonia, and CO_2) attracted more mosquitoes of all species than odour from humans alone (Qiu, 2005), suggesting that odours are important in malaria management strategies.

Blends of compounds also have been shown to be effective in attracting tsetse flies. Leak (1999) reports that odour traps containing volatiles from cattle and urine such as acetone, CO_2, octenol (1-octen-3-ol), 3-*n*-propylphenol and 4-methyl-phenol were effective in attracting tsetse flies to screens with insecticides in Africa. Similarly, ammonia, CO_2 and octenol have increased the efficacy of tabanid traps (French and Kline, 1989). Both 1-octen-3-ol and aged horse urine are effective attractants for tabanids in Europe (Krčmar et al., 2005). Performance of a simple, cost-effective Nzi (Swahili for fly) blue–green traps baited with acetone, cow urine, CO_2, octenol, and phenols capture tsetse, stable and tabanid species in Africa and North America (Milhok, 2002; Milhok et al., 2006, 2007).

Mating pheromones may be less important in aquatic blood-sucking Diptera than chemical cues that drive other reproductive behaviours, such as searching for hosts or oviposition sites, but there is evidence that they exist. Sex pheromones in insects can be long-range volatile chemicals, or short range contact chemicals, and are derived from chemicals with a variety of uses. Cuticular hydrocarbons (CHC), which cover the body surface of terrestrial arthropods to prevent loss of water, are used as contact pheromones. These hydrocarbons, often fatty acids, have been shown to be important semiochemicals in insect recognition and mating (Howard and Blomquist, 1982). Female tsetse produce high molecular CHC (sex attractants) that lure males (Carlson and Langley, 1986). More recently, Carlson et al. (2005) report the isolation and identification of dimethylalkenes (13,17 dimethyltritriacont-1-ene and 13,17-dimethylpentatriacont-1-ene) in *Glossina austeni* females that stimulate conspecific males. Full copulatory responses were detected in males to dead unwashed females (and to the alkene fraction at doses as low as one female equivalent), but not to solvent washed decoys (Carlson et al., 2005). The type of chemical used may be a function of the breeding ecology so that those nesting or mating in a localized site may have short-distance low volatile signals (e.g., CHC) and those species with widely distributed landmark sites might have long-distant, highly volatile signals (Ayasse et al., 2001).

Chemical secretions by male mosquitoes may also be important in influencing female behaviour. Almost 40 years ago, researchers identified a secretion (matrone) from male accessory glands of *Aedes aegypti* that induced monogamy in females (Craig, 1967; Fuchs et al., 1969). This secretion also influences female behaviour with respect to fecundity, oviposition and the protection of eggs (Gillotte, 2003). Matrone was originally identified from whole body extracts of *Aedes aegypti* and included two fractions, α and β. Both fractions prevented females from re-mating; however, fraction α also stimulated oviposition (Gillotte, 2003).

Mate acquisition in many species of blood-feeding Diptera occurs when males swarm near potential oviposition sites (Yuval, 2006) so that attraction to these sites is important both for mating and for the deposition of fertilized eggs. Environmental factors (rainfall, humidity, water temperature) typically initiate ovipositional flight in mosquitoes, but the selection of oviposition sites is a function of visual, tactile and olfactory cues (Bentley and Day, 1989). Mosquitoes use a variety of oviposition strategies, including deposition of individual eggs on soil that is likely to flood (*Aedes, Ochlerotatus* and *Psorophora)*; laying eggs singly (*Anopheles*, *Sabethes, Toxorhynchites* and *Wyeomyia* spp.) or in rafts (*Coquillettidia*, *Culex* and *Culiseta* sp.) on the water, or in rafts attached to vegetation below the water surface (*Aedeomyia* and *Mansonioides*) (Bentley and Day, 1989). There is great variability in the density of mosquito eggs and in the manner by which ovipositing adults respond to conspecifics (Prokopy and Roitberg, 2001), as well as to habitat odours. Preference for oviposition sites may be attributed to both attractants and repellents in natural habitats such as decomposition of organic material, soakage pits, or grass infusions (Bentley and Day, 1989). Ikeshoji et al. (1975) showed that trimethyl phenols from wood creosote extracts induced oviposition behaviour in *Aedes, Armigeres* and *Culex*. Chemicals identified from infusions such as 4-methylphenol, 4-methyl cyclohexanel, and para-alkyl groups were shown to be attractants, while ortho or meta-alkyls were stimulants for *Aedes triseriatus* (the eastern tree-hole mosquito) (Bentley et al., 1979, 1981). *Aedes aegypti* adults were attracted to hay infusions with 3-methylindole. Mendki et al. (2000) identified chemicals (heneicosane, docosane, nonacosane, octadecanes, and isopropyl myristate) from larval conditioned water. Of these chemicals, egg-laying by *A. aegypti* was significantly increased when exposed to heneicosane treated water compared with control water. Ganesan et al. (2006) concluded that kairomones present at natural oviposition sites contain either phenols or indoles, the latter of which is typically associated with mammalian waste products and has an intense fecal smell.

Osgood (1971) was the first to demonstrate the presence of an oviposition pheromone from egg raft extracts of *Culex tarsalis*, a mosquito implicated in the transmission of several types of encephalitis. In a subsequent study, an oviposition attractant, later identified as erythro- 6-acetoxy-5-hexadecanolide, was isolated from apical droplets of day-old eggs of *Culex quinquefasciatus* (Laurence and Pickett, 1982; Laurence et al., 1985). A synthetic oviposition pheromone (SOP) 6-acetoxy-5-hexadecanolide when added to water in pit latrines in Tanzania received more egg rafts of *Culex quinquefasciatus* and *Cx. cinerus* than untreated water (Mboera et al., 1999). *Culex tigripes* and *Cx. pipiens molestus* responded to the olfactory cues of *Cx. quinquefasciatus* eggs. This may be a common strategy for predaceous mosquitoes to find prey. For example, *Cx. tigripes* feed on the larvae of hatched *Cx. quinquefasciatus* and other species (Mboera et al., 1999) The SOP and soakage pit water appears to have a synergistic effect by attracting ovipositing female mosquitoes. The applied benefit is that oviposition chemicals can be used in odour-baited traps for control of mosquitoes known to be disease vectors.

Mosquitoes may respond to odours produced by other mosquitoes, as well as those relating specifically to the habitat. Gravid females of several species of *Culex* respond to pheromones emitted from conspecific eggs, and these will reduce oviposition by females that arrive at oviposition sites later than others. In contrast, evidence of female *Aedes* (most of the species previously referred to as *Aedes* are now *Ochlerotatus;* Reinert, 2000) responding to oviposition sites with conspecific eggs has been inconclusive. Recently, Ganesan et al. (2006) identified the compounds in egg extracts of *Aedes aegypti* to which gravid females were sensitive; the compounds were fatty acids with chain lengths C_{16}–C_{18} and their methyl esters (e.g., dodecanoic acid and (*Z*)-9-hexadecenoic acid). Previous reports also demonstrate neutral or negative responses by this species when exposed to esters of lower fatty acids ($C < 6$) (Ganesan et al., 2006). The authors suggest that these chemicals may reduce overcrowding of conspecific *Aedes aegypti* eggs at sites.

In black flies (Simuliidae), visual cues are thought to be more important than chemical cues in mating (Adler et al., 2004). Thus, visual attractant oviposition traps have typically been used to capture adults (Bellec, 1976). However, chemical cues may influence oviposition behaviour. In several black fly species, females deposit their eggs in aggregations of conspecifics (Crosskey, 1990). In both *S. leonense* (McCall, 1995) and *S. damnosum* (McCall et al., 1997), two compounds detected by gas chromatography but unidentified, were shown to originate from freshly laid eggs. McCall (1995) also showed the presence of oviposition attractants in these species, suggesting that “egg (gravid) traps” could be used to attract female black flies. Females, lured to these traps, will be gravid and larval black flies that hatch in such traps could be discarded before the adults emerge and take a blood meal. The existence of an oviposition aggregation pheromone in *S. damnosum*, the important vector of human onchoceriasis (river blindness), suggests that a potential for the control of the disease vector exists (McCall et al., 1997).

Cuticular washings of the black fly, *Wilhelmia equine* (a vector of human and cattle diseases), showed differences in the composition of these washings between sexes (Būda et al., 2003). Most of the 27 compounds, analysed by gas chromatography/mass spectrometry, identified in male washes were branched hydrocarbons with chain lengths of 11–19 carbon atoms and 24–36 carbon atoms, while most of the 11 chemicals found in female cuticular washes were fatty acids; some compounds were found in both sexes (Būda et al., 2003). These compounds might serve as contact pheromones i.e., sex pheromones, perceived only by direct contact between male and female. Swarms of *W. equine* males fly up and down, increasing both the release of low volatiles from the body surface of males and the distance of odour detection by females that are lured to enter the mating swarm (Būda et al., 2003). These results are important because they are the first to demonstrate sexual dimorphism in CHC, supporting the existence of sex pheromones and chemical communication in black flies.

This brief summary describes some insect vectors of disease and the potential for using traps baited with blends of sex attractants or odours emitted from hosts and oviposition sites to capture insect pests. The problem of insect pests is one of devastation on human health. Malaria, alone, is responsible for more than one million deaths each year, mostly children in Africa (van der Goes van Naters and Carlson, 2006). Given the isolation and identification of sex pheromones in tsetse species (Carlson et al., 2005) and development of the genome sequence in *An. gambiae* (Holt et al., 2002), it is likely that pheromone traps, as well as new drugs and vaccines will be developed to capture and control insect pests, reducing the spread of disease (Sachs, 2002). An increased focus in chemosensory research will help control the spread of disease by blood-sucking Diptera.

4. Crayfishes

Crayfish are benthic aquatic macroinvertebrates that are found in most every type of freshwater habitat except glacial and thermal effluents (Hobbs, 2001). Crayfish are nocturnally active, hiding under rocks during the day. Given this, crayfish rely heavily on chemical and mechanical stimuli in their environment and have several sensory appendages containing chemo- and mechanosensory setae (Dunham and Oh, 1996; Hazlett, 1985). Crayfish use chemosensory-mediated behaviours for food acquisition and orientation (Kraus-Epley and Moore, 2002), identification of conspecific social status (Bergman et al., 2003; Schneider et al., 2001), localization and sex recognition for mating purposes (Belanger and Moore, 2006; Dunham and Oh, 1992; Stebbing et al., 2003a), and detection of alarm cues (Hazlett, 1990, 1994; Schneider and Moore, 2000) and predators (Keller and Moore, 1999; Willman et al., 1994). Because crayfish and other crustaceans are considered “leaky bags” (Atema, 1986), information about their internal physiological state may be transmitted to conspecifics. This creates the potential for active or passive chemical communication regarding sex or social status.

Sex recognition and information about reproductive status has been documented in several crayfish species exposed to conspecific conditioned water (Ameyaw-Akumfi and Hazlett, 1975; Bechler et al., 1988; Belanger and Moore, 2006; Hazlett, 1985; Stebbing et al., 2003a; Tierney and Dunham, 1982, 1984; Villanelli and Gherardi, 1998). Chemical cues are released in the urine of crayfish (Schneider and Moore, 2000; Stebbing et al., 2003a). Urine is released almost exclusively during social interactions (Bergman and Moore, 2005; Breithaupt and Eger, 2002; Schneider et al., 2001) and fan organs (feathered flagella of the mouthparts) send and receive signals in habitats with stagnant flow conditions (Breithaupt, 2001). Bergman et al. (2005) and Breithaupt and Eger (2002) showed that more urine is released by winners than losers in dominance interactions. Additionally, reproductive males are attracted to receptive females, but not to non-receptive females. It is unknown if the same or different chemicals are released during aggressive interactions and mating behaviour.

Male crayfish show alterations in aggressive behaviour in the presence of females or mating pairs. Agonistic bouts between male crayfish have been shown to be more intense when a female was present. When the female was removed, inter-male aggression decreased (Berrill and Arsenault, 1984). Also, Villanelli and Gherardi (1998) suggested that a copulating pair might release a pheromone that both reduces aggression and induces mating. Several studies have investigated the use of sex pheromones by female crayfish and behavioural responses by conspecific males (for review see Dunham, 1988) (Table 3). These include attraction (Ameyaw-Akumfi and Hazlett, 1975; Bechler et al., 1988; Gaudioso and Cabello, 1979; Stebbing et al., 2003b; Tierney and Dunham, 1982, 1984), attempted copulation (Gaudioso and Cabello, 1979; Villanelli and Gherardi, 1998), decreased aggression (Ameyaw-Akumfi and Hazlett, 1975; Dunham and Oh, 1992; Hazlett, 1985), increased motility (Acquistapace et al., 2002; Stebbing et al., 2003a), and increased time spent with a conspecific female conditioned water source (Belanger and Moore, 2006; Stebbing et al., 2003a). Chemical information alone may not be enough to elicit mating behaviours or attraction. Acquistapace et al. (2002) showed that male *Austropotamobius pallipes* need visual, as well as chemical cues to respond to a female. When both cues are present, males spend less time in shelters and more time searching for potential mates. Thorp and Ammerman (1978) and Itagaki and Thorp (1981) could not demonstrate sex recognition in *Procambarus acutus acutus* and *P. clarkii*. However, their methodology has been debated in the literature (Dunham, 1988; Hazlett, 1984; Rose, 1982, 1984). Although pheromones are likely involved in crayfish mating behaviour (Bechler, 1995), the chemical structure of these signals is unknown and despite considerable efforts, no crustacean sex pheromone has yet been fully characterised (Dunham, 1988).

Reception of chemical cues occurs via peripheral chemoreceptors located within sensory setae, which are typically located on the cuticle of cephalothoracic appendages (Laverack and Ardill, 1965) (Fig. 1). Mate odours are believed to be detected by antennae and antennules (Tierney et al., 1984; Dunham and Oh, 1992); however, other peripheral appendages, such as the major chelae, may also be responsible for detection of these odours (Belanger and Moore, 2006).

Courtship and mating typically progress from an initial aggressive interaction between a pair to a ritualized submissive behaviour by the female, leading to copulation. Stebbing et al. (2003a) described seven distinct stages of mating behaviour in the signal crayfish, including orientation, contact, seizure, turning, mounting, spermatophore deposition, and dismounting. Although these mating stages are likely similar among crayfish species, the duration of each activity differs between individuals and species.

Generally, male crayfish are attracted to female odours e.g., *Austropotamobius* (= *Potamobius*) *pallipes* (Gaudioso and Cabello, 1979); *Orconectes propinquus* (Tierney and Dunham, 1982, 1984); *O. rusticus* (Belanger and Moore, 2006); *Pacifastacus leniusculus* (Stebbing et al., 2003a,b; *P. clarkii* and *P. acutus* (Bechler et al., 1988). However, female *P. clarkii* recognize and respond to conspecific male odours (Dunham and Oh, 1992). Female conditioned water induces increased activity levels in reproductive male crayfish (Stebbing et al., 2003a) and handling time of female conditioned water source when compared to a control (water) or conspecific male odours (Belanger and Moore, 2006; Stebbing et al., 2003a). Male crayfish may become submissive in the presence of conspecific female odours (Ameyaw-Akumfi and Hazlett, 1975; Dunham and Oh, 1992; Hazlett, 1985) and may attempt copulation with a receptive female or female odour source (Gaudioso and Cabello, 1979; Stebbing et al., 2003a; Villanelli and Gherardi, 1998).

Aggressive same-sex behavioural displays (e.g., meral spread) are frequently observed in males and females (Ameyaw-Akumfi and Hazlett, 1975; Dunham and Oh, 1992; Hazlett, 1985). These aggressive behaviours change when conspecific odours are released from individuals of the opposite sex. Both, male and female *P. clarkii* showed submissive behaviours (major chelae down) when presented with odours of conspecifics of the opposite sex (Ameyaw-Akumfi and Hazlett, 1975; Dunham and Oh, 1992). Odours from same sex conspecifics resulted in a continuation of aggressive posturing. Given the differential aggressive behaviours displayed by male and female conspecific crayfish to conditioned water or individuals located within perforated test containers, sex pheromones may be used to alter aggressive behaviours and facilitate mating.

Crayfish introductions (e.g., *P. leniusculus*, *O. rusticus*, and *P. clarkii*) produce alterations in freshwater environments and are responsible for declines and extinctions of native species worldwide (Lodge et al., 1998, 2000). Signal crayfish (*P. leniusculus*), native to North America, escaped from farm ponds in England and have colonized rivers throughout southeastern England (Lodge et al., 1998), negatively affecting the native white-clawed crayfish (*Austropotamobius pallipes*). Signal crayfish also carry a "crayfish plague" that is decimating the native white-clawed crayfish population (Alderman et al., 1987). *Procambarus clarkii*, originating from North America, has been introduced in all continents except Antarctica and Australia. The introduction of *P. clarkii* is has had negative impacts on ecosystem organization and function, as well as modulation of resources to other species (Hobbs et al., 1989).

In North America, *O. rusticus* are native to the Ohio River valley but have invaded portions of Minnesota, Wisconsin, and Ontario where they have caused a variety of negative environmental impacts. They have been shown to be a very aggressive aquatic inhabitants often displacing native species (e.g., *O. virilis* and *O. propinquus*) and destroying aquatic plant beds, reducing aquatic plant abundance and species diversity (Lodge et al., 2000).

Environmentally-sound ways (e.g., the use of pheromone traps) to control introduced populations of invasive crayfish in areas where they causing negative environmental impacts needs to be explored. Recently, Stebbing and colleagues tested the idea of using pheromone traps to control the invasive signal crayfish in the UK (Stebbing et al., 2003b, 2004). Laboratory observations demonstrated that urinary sex pheromones stimulated mating behaviour in mature males (Stebbing et al., 2003a). Their preliminary field trials are promising, demonstrating that sex pheromone baited traps, containing water conditioned from mature females, are attractive to conspecific males during the breeding season (Stebbing et al., 2003b, 2004). Because of the species specificity of sex pheromones, pheromone traps can be used in the presence of native crayfish. This would allow for trapping of the target crayfish species in a mixed population, resulting in only the targeted species being removed. Stebbing et al. (2003a) state that the long term advantage of the use of male specific pheromone traps is to leave a non-breeding population of females, ultimately leading to a decline in crayfish invaders. This would have a positive impact on the native populations of crayfish and aquatic flora.

In summary, crayfish commonly modify their behaviour in the presence of conspecifics or conspecific conditioned water. In the presence of a female or female odour source, males become less aggressive, exhibit increased searching behaviour, and attempt copulation. Because male crayfish are attracted to female odour sources (see references within and Table 3), the use of a sex pheromone trap has been used and tested in the UK to control invasive crayfish population. With the success of baited traps for attracting male conspecifics, further studies on the use of these traps in areas where invasive crayfish affect native populations need to be investigated. Future research should focus on the isolation and identification of sex pheromones in crayfish and explore their use in pheromone trapping in other species of crayfish.

5. Fishes

Olfaction in fishes is among the most highly developed sense of all vertebrates (Kleerekoper, 1969). Chemical signals, received and processed by the olfactory system, are released and received between conspecifics. These signals have been linked to predator avoidance and alarm cues (Chivers and Smith, 1998; Wisenden, 2003), gender recognition (Liley, 1982), kin recognition in dominance hierarchies and schooling (Olsén, 1998), aggregations prior to reproduction (Teeter, 1980), and in feeding and spawning migrations, as well as reproductive processes (Sorensen and Stacey, 2004; Stacey and Sorensen, 2006).

Chemical communication has been demonstrated in at least ten teleost families with freshwater species, including Petromyzontidae, Cyprinidae, Catostomidae, Cobitidae, Ictaluridae, Clariidae, Gasterosteidae, Salmonidae, Cottidae, and Gobiidae (Sorensen and Stacey, 2004). Recent studies document the importance of chemical communication in catadromous species (e.g., European eels) as well (Huertas et al., 2006). Although odorants are commonly used by fishes, their importance is not well known. For example, over 120 fishes have been tested for their response to odours (typically electrophysiological assays), yet behavioural responses are less often studied (Poling et al., 2001). Results of electrophysiological assays show that precursors and derivatives of bile acids, sex steroids and prostaglandins are detected by fishes, providing evidence that they use these compounds as pheromones (Stacey and Sorensen, 2006). This section will focus on chemical communication associated with reproductive behaviour of fishes in fresh water, specifically mating signals in invasive fishes (Table 4).

Invasive fishes such as common carp (*Cyprinus carpio*), goldfish (*Carassius auratus*), sea lamprey (*Petromyzon marinus*) and the round goby (*Neogobius melanostomus*) have become established in new regions often because of their prolific reproductive habits. Pheromone manipulations that interrupt reproductive cycles of fishes might prove to be an effective control strategy for invasive species (Corkum, 2004; Sorensen and Stacey, 2004). The following is a summary of progress on chemical communication between reproductive males and females for these species. The research strategy could potentially be used to control these and other invaders such as species of Asian carp (bighead carp *Hypophthalmichthys nobilis* and silver carp *Hypophthalmichthys molitrix*). Pheromone traps may be explored as a new management strategy for fisheries.

5.1. Common carp and goldfish

Reproductive pheromones are probably best understood in goldfish, a species that is typical of other non-territorial cyprinids. In goldfish, females release hormonal pheromones, attracting males that compete for spawning access (Sorensen and Stacey, 1999). Sorensen and Stacey (2004) present a model of female pheromones exerting both primer and releaser (behavioural responses) effects. In vitellogenic females, estradiol stimulates the urinary release of an unidentified pheromone that attracts males (Stacey and Sorensen, 2006). In the postvitellogenic phase, females respond to environmental cues (water temperature and vegetation for attachment of their adhesive eggs) that induce a surge in luteinizing hormone (LH) in preovulatory females, stimulating the release of a pheromone mix, including androstenedione (AD), 17α,20 β-dihydroxy-4-pregnen-3-one (17,20 βP), and sulfated 17,20 βP (17,20 βP-S) (Stacey and Sorensen, 2006). Both AD and 17,20 βP are released through the gills of females (detectable nearby); 17,20 βP-S is released in the urine (detectable at greater distances). AD released by females early in the LH surge induces agonistic behaviour among males (Poling et al., 2001). The release of the pheromone 17,20 βP during the mid-surge of LH in females results in an increase in LH in the blood plasma of males (Zheng and Stacey, 1997). In response, males elicit courtship behaviour with low levels of nudging and chasing (Poling et al., 2001). The release of the pheromone 17,20 βP-S during the late surge in LH by females exhibits strong courtship behaviours by males (Poling et al., 2001). Post-ovulatory females release prostaglandin $F_{2\alpha}$($PGF_{2\alpha}$), which acts in the brain to promote female sexual behaviour, and releases $PGF_{2\alpha}$ and 15 keto-$PGF_{2\alpha}$ into the water via urine, which then stimulates spawning behaviour in the males (Stacey and Sorensen, 2002). Perhaps it is the relative ratios of these chemicals in pre- and post-ovulatory females that represent the signal to which mates respond. Moreover, female synchrony in ovulation in goldfish and common carp likely promotes predator swamping, increasing the likelihood of egg survivorship.

Olsén et al. (2006) conducted a field test in which they confirmed that, as previously observed in male domesticated goldfish, male wild crucian carp responded to preovulated females. In this study, male crucian carp increased LH and milt when conspecific females were injected with the goldfish pheromonal steroid 17,20 βP and followed a time course in LH release and milt production that matched goldfish under lab conditions. Because of the similarities in chemical communication between sexes in both crucian carp and goldfish, crucian carp can serve as an ideal model to conduct field experiments.

Closely related species typically have similar pheromone systems, facilitating hybridization. This can be a concern for the conservation of native species. Goldfish and the common carp are both sensitive to AD, 17,20 βP and 17,20 βP-S (Irvine and Sorensen, 1993). These two species have been introduced in many regions and both hybridize with native species. For example, about 38% of crucian carp populations, native to the British Isles, hybridize with introduced goldfish and common carp in that region, leading to competition between pure species and hybrids and the ultimate decline of native species, as well as introgression between F1 hybrids and pure species (Hänfling et al., 2005). In salmonids, brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) are both sensitive to $PGF_{2\alpha}$, suggesting that their sex pheromones may be similar; these two species also hybridize (Essington and Sorensen, 1996).

5.2. Sea lamprey

Sea lamprey are ancient, jawless fish that as adults are parasitic on fish, having had a devastating effect on fisheries (Jones et al., 2003). Chemical control (pheromone) strategies have been sought to replace the lampricide program in the Laurentian Great Lakes drainage basin of North America. Sea lamprey hatch as ammocoetes and live from 3 to 20 years in streams before they metamorphose into the parasitic stage, migrating downstream to a lake. In spring, adult male sea lamprey migrate upstream from lakes or oceans into tributaries (Bjerselius et al., 2000). At the time of upstream migration, adult sea lamprey are sexually immature, but sexual maturation progresses during migration, culminating in spawning activities. Sea lamprey upstream migration occurs in darkness, but nest building and spawning occurs in daylight (Teeter, 1980 and references within). Once eggs are fertilized, the adults die. Unlike salmon, sea lamprey do not return to their natal stream (Bergstedt and Seelye, 1995).

The understanding of chemical communication in sea lamprey and the identification of key pheromones for their ultimate management has taken over 25 years to develop. Teeter (1980) showed that sexually immature male sea lamprey, captured at the beginning of a spawning migration, were attracted to larval washings (mucus scraped from skin of adults of either sex was not attractive); males were attracted to washings from ovulated and sexually mature females, but not unovulated females; and, females were attracted to male washings, but not to milt. These early experiments showed that males and females release pheromones that stimulate the aggregation of the opposite sex (Teeter, 1980). Later, Li et al. (1995) established that adult sea lamprey rely on pheromones, petromyzonal sulfate (PS) and allocholic acid (ACA), released from developing larvae to identify suitable spawning streams. In behavioural experiments, adult sea lamprey were more attracted to larval washings than to a mixture of PS and ACA, suggesting that other key components of the pheromone mixture were missing (Vrieze and Sorensen, 2001). Recently, Sorensen et al. (2005) identified the key components of the sea lamprey migratory pheromone: petromyzonamine disulphate (PADS), petromyzosterol disulphate (PSDS) and PS; and, each of these compounds is discerned by a different olfactory receptor. PADS attracted adult migratory sea lamprey, but it had less behavioural activity than the whole larval extract (Sorensen et al., 2005).

Sea lamprey males arrive at spawning sites before females; males build a nest and emit a sex attractant to which females respond (Li et al., 2002). In a field experiment, Johnson et al. (2005) demonstrated that ovulating females (individuals and groups) were attracted to traps baited with spermiating males. Spermiating males release 3-ketopetromyzonal sulfate (3kPZS) to which ovulating females are attracted (Li et al., 2002). This compound functions as a sex pheromone and is released through the gills of spermiating males (Siefkes et al., 2003). Moreover, Siefkes et al. (2005) has shown using a 2-choice maze that ovulating females, but not males or preovulating females, are attracted to 3kPZS and washings from spermiating males. These studies also offer opportunities for the control of an invasive species using pheromones.

5.3. Round goby

The round goby is a bottom-dwelling fish of the family Gobiidae and native to the Ponto-Caspian region. The species was first reported in June 1990 in both the Baltic Sea (Skora and Stolarski, 1993) and in the Laurentian Great Lakes (Jude et al., 1992). Females may spawn up to six times a year and males provide parental care (MacInnis and Corkum, 2000). The round goby out-competes native fishes for nest sites and feeds on the eggs of native fishes (Janssen and Jude, 2001; Corkum, 2004). Kulikova (1985) suggested a possible link between pheromones and the reproductive state of the round goby, when it was found that males were stimulated to become reproductive merely by the presence of females made gravid through hormone injections. Male round gobies also were found to increase gill ventilation rates when exposed to either gonadal extracts of gravid females or estrone (E1) (Belanger et al., 2006) and these responses have been shown to increase during the reproductive season (Belanger et al., 2007). In laboratory studies, gravid females respond to reproductive male odour, and non-reproductive females to gravid female odour, by increasing swimming velocity and remaining near the odour source (Gammon et al., 2005). This demonstrates that both genders are capable of releasing pheromones detected by conspecifics, but thus far only in a reproductive state. Marentette and Corkum (2007) showed that male round gobies, regardless of reproductive status, did not respond to conspecific odours, but reproductive males preferred to stay inside shelters, and transitional males swam less than non-reproductive males. This finding is not unexpected because parental males are territorial and establish nests in shelters, from where they will court females and tend eggs. What is surprising is the complete lack of a vigorous response on the part of male gobies to conspecific females or males, given contrasting reports in marine gobiids (Tavolga, 1956; Locatello et al., 2002). Shorey (1973) argues that behavioural responses such as decreased locomotion may result in aggregation in the same manner that attraction does in other species.

Several studies on the round goby support the view that this species releases steroids with pheromonal properties. Murphy et al. (2001) examined olfactory epithelial EOG responses of mature male and female round goby to over

100 steroids and prostaglandins. The prostaglandins were all inactive; however, 19 steroids elicited responses. Cross-adaptation studies with these steroids revealed that there were four classes of olfactory receptor that Murphy et al. (2001) named: E1, E2-3-g, ETIO and DHEA-s, after the steroids that were the most potent odorants for each class of receptor (E1, 17β-estradiol 3-glucuronide [E2-3g], etiocholanolone [ETIO] and 17-oxo-androst-5-en-3β-yl sulfate [dehydroepiandrosterone sulfate; DHEA-s]. Murphy et al. (2001) discovered that males markedly increased their gill ventilation rate in response to steroids that acted on the E1, E2-3g and ETIO receptors, while females only responded to steroids that acted on the ETIO receptor. In a subsequent study (Murphy and Stacey, 2002), females responded to E1 and E2-3g following treatment with methyl testosterone, suggesting that these classes of receptors were involved in female-to-male communication. This study showed that an androgen (methyl testosterone) implanted in adult females induces behavioural typical of males (i.e. the masculinisation of females).

Building on the research of Murphy et al. (2001), Arbuckle et al. (2005) showed that a suite of steroids, both free and conjugated, are synthesized in the testes of sexually mature male round gobies. Several steroids were successfully identified: testosterone (T), 11-oxo-testosterone (11-oxo-T); AD; 11β-hydroxy-androst-4-ene-3,17-dione (11β-OH-AD); ETIO; 3α-hydroxy-5β-androstane-11,17-dione (11-oxo-ETIO); and 11-oxo-ETIO-s. Two of these steroids, 11-oxo-ETIO and 11-oxo-ETIO-s, had not been previously identified in teleost gonads (Arbuckle et al., 2005). Moscicki et al. (University of Windsor, unpublished) grouped the compounds into free (11-oxo-T, Ad, 11β-OH-Ad, ETIO and 11-oxo-ETIO), conjugated (11-oxo-ETIO-s, 11-oxo-ETIO-g, ETIO-s, ETIO-g) and free+conjugated steroids and tested the behavioural responses of ripe and non-ripe females to each of the steroid blends against an ethanol control. With all three blends, ripe and non-ripe females spent 37% more time than expected ($P < 0.003$) in the treatment arm than in the control arm, but there was no significant difference in the response between ripe and non-ripe females ($P = 0.654$). In previous experiments, where females were exposed to the water conditioned by reproductive males ('natural' pheromone blend), only ripe females responded. At present, it is not clear whether the response by the non-reproductive females to the synthetic blends is due to inappropriate amounts (or proportions) of steroids in the blends, the presence of a particular steroid that is probably not released by ripe males or if there is another compound that remains to be identified.

The control of invasive species will likely arise from multiple strategies. Sorensen and Stacey (2004) suggest that pheromone traps used in concert with acoustic and light attractants would be an effective option to control invasive species if directed at ripe fishes. Depending on the species, male or female odours could be used to attract and remove members of the opposite sex. Additionally, pheromones could be used to disrupt reproductive success, to disrupt or divert migrations, to promote the success of sterilized fishes, to repel fishes and to assess population size and distribution (Sorensen and Stacey, 2004).

6. Conclusions

Chemical communication has evolved independently in many diverse organisms. Signals released from organisms relay specific information to species in aquatic environments where species are nocturnally active or where visibility is often limited. In blood-sucking Diptera, mating pheromones may be less important than other cues that are emitted from hosts or ovipostion odours that attract insects to areas where hatching may be maximized. Traps baited with enhanced host odours appear to be successful in trapping mosquitoes, tsetse and stable flies. In crayfishes, the structures of chemical compounds have yet to be identified, but it seems clear that the signal is released in the urine of females to which reproductive males respond. Chemical communication in fishes may involve compounds such as steroids, prostaglandins or bile acids. Depending on the compound, the signal may be released in the urine or feces or via gills. Female fishes may respond to males as in sea lamprey and round goby or males may respond to females as in goldfish. There is promise for the application of pheromone traps to control invasive species such as signal crayfish, sea lamprey or the round goby by disrupting the reproductive behaviours of these species. Understanding the information content of a signal is gleaned from behavioural experiments in nature.

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