

Invited review

Brief review of fish pheromones and discussion of their possible uses in the control of non-indigenous teleost fishes

PETER W. SORENSEN

Department of Fisheries, Wildlife &
Conservation Biology
University of Minnesota
1980 Folwell Avenue
St Paul, MN 55108
United States
email: Soren003@umn.edu

NORM E. STACEY

Department of Biological Sciences
University of Alberta
Edmonton, Alberta T6G 2E9
Canada

Abstract Most species of fish rely on pheromones (chemical signals released by conspecifics) to mediate social behaviours. Three categories of pheromones can be discerned based on their function: anti-predator cues, social cues, and reproductive cues. Each of these categories comprises pheromones that can induce “primer” effects (developmental and/or endocrinological changes) and/or “releaser” effects (strong behavioural changes). A handful of fish pheromones have been chemically identified and all are remarkably potent. Almost all are metabolic products whose production is seemingly unspecialised, insofar as they are not synthesised by specialised structures. Importantly, their potency and specificity makes them ideal candidates for use in control of both threatened (native) and unwanted (non-indigenous) fish species. As has been so for insect control and now sea lamprey control in the North American Great Lakes, these cues could be used in many ways as part of integrated control programmes for invasive teleost fishes. Ideally, these programmes would be designed to simultaneously exploit multiple weaknesses in species’ life histories

while being fully cognisant of stock-recruitment relationships. Generally the approach would be to use a variety of pheromones to supplement and increase the efficiencies of other control strategies including the application of poisons or fish with genetic modification, trapping for removal or sterilisation, and barriers to prevent spread. Integrated pest control using pheromones appears especially practical for the common carp (*Cyprinus carpio*) which appears to use many of the same cues as the goldfish (*Carassius auratus*) and for which half a dozen pheromones have already been identified.

Keywords pheromone; hormone; integrated pest management; carp; lamprey; goldfish; carp; steroid; prostaglandin; attractant

INTRODUCTION

The past few decades have witnessed a dramatic surge in the number of invasive fish that have become pests in various regions throughout the world. No simple solutions have emerged for this problem other than wholesale poisoning of entire ecosystems—a highly undesirable scenario. Perhaps the only successful fish control programme is that for the sea lamprey (*Petromyzon marinus*), a cartilaginous, parasitic fish that invaded the North American Great Lakes at the turn of the century. This species is presently controlled using an “integrated” approach which employs a variety of complimentary techniques including poisons, stream barriers, traps, and sterile males (see Jones et al. 2003). The sea lamprey programme benefits greatly from the fact that the unique physiology of this ancient vertebrate make it susceptible to poisons that have little affect on teleost (“bony”) fish. Still, this relatively advanced invasive control programme struggles to meet its objectives and continues to explore new techniques, especially pheromones, as it moves towards Basin-wide control. As has been proven for insect integrated pest management (IPM) programmes (Wyatt 2003), pheromones appeal to the

sea lamprey programme because they appear to offer many safe and effective options that strongly enhance extant strategies (Li et al. 2003; Sorensen & Vrieze 2003). This manuscript advocates that the same set of arguments can be applied to the control of invasive teleost fishes.

Control of invasive teleost fishes in the Great Lakes and elsewhere has been even more problematic than for the sea lamprey. For example, no coherent control strategy or control programme even exists for the two most damaging invasive teleosts in the Great Lakes, the Eurasian ruffe (*Gymnophelaus cernuus*) (Gunderson et al. 1998) and the round goby (*Neogobius melanostomus*) (Kohlar & Lodge 2002). Similarly, management of the common carp (*Cyprinus carpio*) in inland lakes and rivers in North America and Australia is a vexing problem which is presently addressed with only limited success by a “hodge-podge” of techniques including toxins and barriers (Roberts & Tilzey 1996). Finally, and most recently, the arrival of four invasive “Asian carps” (the grass carp, *Ctenopharyngodon idella*; silver carp, *Hypophthalmichthys molotrix*; bighead carp, *H. nobilis*; and black carp, *Mylopharyngodon piceus*) in the Mississippi River Basin of North America has evoked alarm because of a total lack of extant techniques to control these large destructive fishes (Chick & Pegg 2001; Brant 2004).

The ease with which invasive teleost fishes can move between systems, their high fecundity, and the size and complexity of the ecosystems in which they live create significant problems for their control. Indeed, such is the scale and complexity of this problem that even if highly specific poisons, viruses, and/or genetic technologies were to be developed and approved for use, it is doubtful whether any single approach could on its own eradicate established fishes across their entire range within a reasonable period of time. Accordingly we propose that, as has been proven for the insects and the sea lamprey, the answer to the control of invasive teleost fishes lies with the use of multiple (integrated) techniques which compliment/ amplify each other. Presumably, an IPM strategy for teleost fishes would be designed to specifically target multiple weaknesses in the pest species. Notably, IPM approaches are especially amenable to the use of pheromones (chemical signals that pass between individuals of the same species (Sorensen & Wyatt 2001)). Most fish use a variety of pheromones to effect different types of behaviours and sometimes physiological changes. Further, because these cues typically have

specific actions and are environmentally safe yet potent, they could simultaneously be deployed in multiple cost-effective ways to compliment a variety of control techniques aimed at different life history stages.

The principal objective of this manuscript is to briefly review the field of fish pheromones and then explore the possibility for using pheromones for controlling teleost fish as part of an IPM programme. Because several recent papers (Li et al. 2003; Sorensen & Vrieze 2003; Twohey et al. 2003a) have addressed the use of pheromones in non-teleosts (e.g., sea lamprey), we review the later topic only briefly. Instead, special attention is paid to the goldfish (*Carassius auratus*), for which pheromone identity and function is particularly well understood and likely very similar to that of a significant invasive species, the closely related common carp.

WHAT IS A PHEROMONE?

Karlson & Luscher (1959) first defined pheromones as “substances that are excreted to the outside by an individual and received by a second individual in which they release a specific reaction, for example a definite behaviour or developmental process”. Significantly, Karlson & Luscher (1959) state that “strict species specificity is not required” and that “the principal of minute amounts being effective holds”. Further, although they state that pheromones are involved in “communication”, they fail to define this term, but seem to imply simple passage of information, rather than use of a specialised cue with reciprocal benefits to both donor and receiver. A few years later, and after the first pheromones had been identified in a moth, Wilson & Bossert (1963) suggested that rapid behavioural and slower physiological effects be distinguished by the terms “releaser” and “primer”. These terms unfortunately have led to some confusion because some pheromones can induce both priming and releaser effects (e.g., Sorensen et al. 1989). Herein, we use these terms simply to describe what appears to be each cue’s main function.

For this manuscript, we define a pheromone as “an odour or mixture of odorous substances, released by an individual (the sender) and evoking in conspecifics (the receivers) adaptive, specific, and species-typical response(s), the expression of which need not require prior experience or learning”. This definition is closely based on the definition of Karlson & Luscher (1959) and others we have

proposed elsewhere (Sorensen & Stacey 1999; Sorensen & Wyatt 2001; Stacey & Sorensen 2002). Three corollaries of this definition warrant brief discussion. First, although pheromone detection requires specialisation within the olfactory system (cranial nerve 1) of receivers, specialisation of the donor is not required. Second, although a pheromone might comprise only a single compound, pheromones are often mixtures of chemicals (e.g., Poling et al. 2001; Sorensen et al. 1998, 2003). Third, a pheromone need not be a specialised compound. This is logical from an evolutionary perspective because pheromonal function undoubtedly arises first through specialisations in the receivers' olfactory systems, and then becomes specialised only in circumstances where selective forces can act to modify the production of the cue by the sender (see Sorensen & Stacey 1999; Stacey & Sorensen 2002).

Living in a medium that is often devoid of light but an excellent solvent, many species of fish have evolved to detect and respond to chemical cues released by conspecifics. Owing to the diversity of life histories fish use, these cues have come to serve a great variety of functions. For several reasons, they also merit serious consideration for use in control and management of both wanted and unwanted species. First, they are potent and often specific. Second, they can easily and safely be added to water. Third, if desired, pheromones of many invasive teleosts could likely be identified now that we know that many pheromones are derived from hormonal products (Sorensen & Stacey 1999; Stacey & Sorensen 2002), and bile acids (Li et al. 1995, 2002, 2003; Sorensen & Vrieze 2003). It seems especially reasonable that IPM control programmes using pheromones could be developed for Southern Hemisphere freshwater ecosystems where native ichthyofauna differs greatly from distantly related Northern Hemisphere invaders.

WHAT FUNCTIONS DO PHEROMONES SERVE IN FISH?

Fish, the oldest and largest group of vertebrates, are renowned for their diverse behaviours and lifestyles (Pitcher 1993) which appear to have favoured the evolution of many types of sensory cues including pheromones. Although recent progress understanding pheromones has been reasonably rapid, the discipline as a whole is still in its infancy, and dominated by descriptions of the actions of unpurified conspecific odours. Nonetheless, this

information, together with our limited understanding of the chemical identities of a few identified cues, is adequate to place conspecific teleost fish odours into three categories which we briefly summarise below.

Anti-predation and alarm cues

As with other aquatic organisms, fish exhibit numerous chemically-mediated responses that appear to reduce predation risk (Chivers & Smith 1998; Chivers & Mirza 2001; Wisenden 2003).

Priming responses

Unknown chemicals in conspecific skin increase body depth in crucian carp (*Carassius carassius*) (Bronmark & Miner 1992; Stabell & Lewin 1997), an effect that might reduce predation by increasing predator handling time and facilitating evasive escape during attack.

Releaser responses

Numerous studies show that fish exhibit evasive (alarm or fright reactions) responses to the odour of damaged conspecifics or predators that have eaten conspecifics. In ostariophysan fish, there is evidence that specialised epidermal club cells produce the active odour, which has been hypothesised to be hypoxanthine-3-N-oxide and/or a mixture of related compounds (e.g., Brown et al. 2002, 2003, and below).

Non-reproductive aggregation

Kin and individual recognition in dominance hierarchies and schooling

The complex social systems of some fish appears to have favoured the evolution of chemosensory mechanisms to determine relatedness of conspecifics (Brown & Brown 1992; Olsén 1999). Functions of these "familial" odours include establishment of dominance relationships, recognition of young, shoaling/schooling, and migration. In North American Ictalurid catfish at least some components of the odour used in individual recognition are L-amino acids (Bryant & Atema 1987). Studies of salmonids suggest that kin odours are released in the urine (Moore et al. 1994) and that a gene product associated with the major histocompatibility complex (MHC) might be involved (e.g., Olsén et al. 2002). There is also evidence that at least some species of fish school as kin groups (presumably to avoid predation), the recognition of which is mediated by odour (Mann et al. 2003). The identity of individual, kin-specific odours is unknown. However, it seems likely that complex mixtures are

involved, some of which may be subsets of others, and could involve learning (Olsén et al. 2002), calling into question the distinction between pheromones and general social cues.

Species recognition, aggregation, and shoaling responses

In many fishes (see Keenleyside 1955; Hemmings 1966; Courtenay et al. 1997), including goldfish and common carp (Saglio & LeMartret 1982; Saglio & Blanc 1983), conspecific odour promotes aggregation/shoaling. Apparently, this response is not based on immediate familial relationship, although this aspect has largely been ignored. Both bile acids (Selset & Døving 1980) and L-amino acids (Saglio & Fauconneau 1985) have been implicated in species-recognition but little research has been directed to this question.

Migratory attraction

At least a few species of migratory fish appear to locate feeding and/or spawning habitat by tracking conspecific odour. In some examples, such as the freshwater eel, *Anguilla rostrata*, these attractants may serve as short-range attractants and are found within a bouquet of other stimuli (Sorensen 1986; Briand et al. 2002). In other examples, such as the Arctic char (*Salvelinus alpinus*; Selset & Døving 1980) and banded kokopu (*Galaxias fasciatus*) (Baker & Montgomery 2001), pheromones evidently attract conspecifics from a distance. Easily the best understood of long distance migratory attractants is that of the sea lamprey, whose migratory adults are attracted from the ocean (or large lakes) by the odour of unique bile acids released by stream-dwelling larvae (Li et al. 1995; Sorensen & Vrieze 2003; see below). For both the sea lamprey and kokopu, these odours are unlikely to be learned or kin-related. Migratory attractants might be regarded as a special type of an aggregation pheromone.

Reproductive aggregants and stimulants

Gender recognition

Many species of fish appear to have evolved to distinguish the odour of mature male and female conspecifics well in advance of spawning (Liley 1982). For example, male goldfish increase swimming activity when exposed to the odour of vitellogenic females or estrogen-treated females, but not males (Kobayashi et al. 2002). Conversely, mature males exposed to the odour of androstenedione (an androgenic steroid released in large

quantities by other males) exhibit high levels of aggressive behavior (Sorensen et al. 2004). Although such gender-specific cues likely are common, they appear to have only been chemically characterised in the goldfish.

Priming responses before spawning

Immediately before and during spawning, many teleost fish respond to conspecific odour by increasing gonadal development and/or hormonal changes that induce final gamete maturation (Liley 1982; Stacey & Sorensen 2002). Where there is information on the chemical nature of these odours, they have been found to be gonadal steroids, prostaglandins, and/or their precursors and metabolites, hence leading to the term "hormonal pheromones" (Stacey & Sorensen 2002). The best understood examples of these cues are used by the goldfish (Kobayashi et al. 2002; discussed below), and the Atlantic salmon (*Salmo salar*; Moore & Waring 1996).

Releaser responses associated with spawning

Reproductive behavioural responses to conspecific odours provide perhaps the most well studied examples of pheromone function in teleost fish (Liley 1982; Stacey & Sorensen 2002). As with reproductive primer responses, releaser responses are commonly induced by released hormonal products, as discussed below for the goldfish. Although many behavioural responses to the "whole" odour of sexually active fish appear to be species-specific (Liley 1982), the few hormonal products that have been known to be associated with these responses are not, suggesting that, as frequently noted in insects (see Sorensen et al. 1998), specificity may result from the use of odour mixtures (Sorensen et al. 2000). More study is needed on this question.

WHAT TYPES OF COMPOUNDS DO FISH USE AS PHEROMONES?

A wide variety of chemicals have been proposed to function as pheromones including tetrodotoxin (Matsumura 1995), specific amino acids (Kawabata 1993), purines (Pfeiffer et al. 1985), bile acids (Døving et al. 1980; Polkinghorne et al. 2001), gonadal steroids (Sorensen et al. 1990), and F prostaglandins (Sorensen et al. 1988). However, only for gonadal steroids, prostaglandins, and bile acids has release, olfactory detection, and biological responsiveness been characterised. The majority of

information on identified pheromones pertains to hormonal products, and for these the goldfish model is understood best. In the two decades since Colombo et al. (1980) first reported a releaser response to a conjugated gonadal steroid (etiocolanolone glucuronide) in the black goby (*Gobius joso* = *G. niger*), much evidence has accumulated to indicate that hormonal pheromones are widespread among fish. In particular, underwater electro-olfactogram (EOG) recording has demonstrated that the olfactory epithelium of many species from many taxonomic groups (e.g., Cypriniformes, Siluriformes, Characiformes, Salmoniformes, Perciformes) exhibit remarkable sensitivity to hormonal compounds (see: Stacey & Cardwell 1995; Stacey & Sorensen 2002). Although in a small number of species hormonal odourants have been shown to have biological actions (see Table 1 for a list of the best understood cues), only in the goldfish has a hormonal pheromone been fully characterised in terms of synthesis, release, olfactory detection, and response (see section below).

Bile acids also appear to function in many teleost fishes as pheromonal attractants. Examples include migratory adult arctic charr which appear to be attracted to bile products released by juveniles (Selset & Døving 1980). Evidence also suggests that the lake charr (*Salvelinus namaycush*) uses as yet incompletely characterised bile derivatives as cues (Zhang et al. 2001). Certainly, teleost fish including the carps produce and release a vast array of bile acids, some of which are detected with great sensitivity and specificity (Sorensen & Caprio 1998;

Sorensen unpubl. data). With the exception of the sea lamprey, which use a variety of bile acids as both aggregants and sex pheromones (see below), this topic has not received much attention.

Chemically-mediated alarm responses (behaviours that appear to reduce predation risk) are common in fish (Chivers & Smith 1998), although the identity of the active chemicals has only been proposed in Ostariophysans (e.g., Cypriniformes, Siluriformes, Characiformes) which also possess epidermal club cells for their production (e.g., Pfeiffer 1977; Smith 1992). Argentini (1976) suggested that the cue used by minnows might be hypoxanthine-3-N-oxide, although neither the olfactory activity of this compound, nor its presence in fish water, have as yet been demonstrated (Kasumyan & Ponomarev 1987; Smith 1999). Recently, however, Brown et al. (2002, 2003) showed that this compound and related compounds induced alarm responses at concentrations expected of a pheromone. Perhaps hypoxanthine-3-N-oxide is one component of a more complex cue.

BILE ACID DERIVED PHEROMONES IN THE SEA LAMPREY, A NON-TELEOST MODEL FOR EXAMINING PHEROMONE APPLICATION

The ancient, jawless sea lamprey has an interesting anadromous and semelparous life history in which young lampreys hatch in freshwater streams where they spend the majority of their lives (4–20 years)

Table 1 Synopsis of our understanding of identified hormonal pheromones in teleost fish. Details are in text and Stacey & Sorensen (2002). (? , unknown; S, Suggested; E, clearly established.)

Species	Cue	Biochemical identity	Production	Release	Detection	Biological activity
Goldfish*	Female identifier	S	S	E	S	E
	Primer	E	E	E	E	E
	Releaser	E	E	E	E	E
African catfish†	Male identifier	E	E	E	E	E
	Attractant	S	E	S	E	S
Atlantic salmon‡	Primer	S	?	E	S	S–E
	Releaser	S	E	E	S	S–E
Round goby§	Male identifier	S	E	S	E	S

**Carassius auratus*.

†*Clarius gariepinus*.

‡*Salmo salar*.

§*Neogobius melanostomus*.

filter feeding. Following metamorphosis, sea lamprey first migrate into oceans or large lakes to prey on teleost fish (by rasping into their prey's body cavities), then mature 1–2 years later and migrate up streams to spawn thousands of eggs, and die. Unlike salmon, adult lamprey do not return to natal streams but seek out any suitable stream using the odour of stream resident larvae which should reflect habitat quality (Sorensen & Vrieze 2003). Their unusual life history, behaviour, and physiology have made sea lamprey relatively easy to target with poisons and barriers (Bills et al. 2003; Lavis et al. 2003). Moreover, their reliance on olfaction (the olfactory system constitutes a large portion of the sea lamprey brain) has stimulated research demonstrating that a series of bile acid derived pheromones produced by larval and adult male sea lampreys have the potential to be used in the control of this damaging species.

A plethora of field and laboratory evidence has demonstrated that the pheromone produced by larval lamprey comprises the unique bile acid, petromyonal sulfate (PS; Li et al. 1995; Polkinghorne et al. 2001) and at least two other related compounds which the adult detects at sub-picomolar concentrations (Sorensen et al. 2003). These odourants, which serve to attract migratory adults into and up rivers (Bjerselius et al. 2000), are released at such a rate that single larvae activate over 400 litres an hour (Vrieze & Sorensen 2001). The main component of the migratory pheromones is now known to have a molecular weight of 704 daltons and to attract migratory adults at a concentration of less than 0.1 pM (Sorensen et al. 2003). A synthetic version is presently being developed.

The actions of the migratory pheromone are complimented by a male sex pheromone. As adult lamprey mature during their upstream migration, they cease responding to larval pheromones and start responding to the odour of mature, spermated males (Teeter 1980; Bjerselius et al. 2000). Li and colleagues provide a variety of biochemical evidence that 3-keto-petromyozonol sulfate is part of the male sex cue (Li et al. 2002) which is released via the gill and attracts ovulated females (Siefkes et al. 2003a). Evidence suggests that other sex pheromones exist but they have yet to be identified (Teeter 1980).

Although the sea lamprey control programme sponsored by The Great Lakes Fishery Commission has succeeded in identifying remarkably specific toxins (3-trifluoromethyl-4-nitrophenol and 2',5'-dichloro-4'-nitrosalicylanilide; Bills et al. 2003) which presently kills over 90% of larvae, the high

fecundity of this species necessitates an even more effective approach. Accordingly, the sea lamprey programme has embraced IPM (Christie & Goddard 2003), seeking to suppress sea lamprey to "socially, economically, and ecologically acceptable levels" by combining complimentary techniques that target multiple stages in this species' life history. Efforts are underway to reduce toxin application (Brege et al. 2003) while blocking spawning runs with barriers (Lavis et al. 2003), and introducing sterile males (Bergstedt et al. 2003). The recent identification of pheromonal cues has led to many suggestions of how these cues might be used to effect even better controls and field trials have commenced to assess feasibility. Because these ideas have been recently reviewed in detail (Li et al. 2003; Sorensen & Vrieze 2003; Twohey et al. 2003a), we summarise only key points here.

A major strength of pheromones is the fact that they could be used in many ways to compliment other control strategies according to specific need. This has certainly been so for insects (Carde & Minks 1997; Wyatt 2003). No specific strategy has yet been developed for the sea lamprey but many are being considered. It is quite possible that multiple applications will eventually be identified and used. Sorensen & Vrieze (2003) suggest the migratory pheromone might be used to: (1) divert migratory adults from important streams to streams where they are not expected to reproduce or their young can be poisoned; (2) capture migrating adults to remove them for disposal or sterilisation; and (3) disrupt migratory patterns. Li et al. (2003) suggest that the male sex pheromone might be used to: (1) trap and remove mature females; and (2) disrupt mating processes. The migratory and sex pheromones could be deployed in complimentary ways. Likely, pheromone-based strategies will be particularly valuable in locations where sea lamprey numbers are low and stock-recruitment relationships predictable, a situation that already exists in some regions of the Great Lakes. Indeed, pheromones may represent the best hope for further suppression in these regions where other techniques have already reached their maximum potential. Although further research is required to optimise the use of pheromone(s) in sea lamprey control, their potency, versatility, and ease of application makes it likely that they will be incorporated into a truly integrated sea lamprey management programme. Of course, it seems reasonable to expect the same for teleost fishes.

PHEROMONES IN GOLDFISH AND RELATED CARPS —AN IMPORTANT MODEL SYSTEM FOR TELEOST FISH

All major types of pheromones have now been characterised in the goldfish, and in some instances these have been identified, making it one of the leading vertebrate models to understand pheromone identity and function. Further, there are indications that the common carp and crucian carp, which has been placed in the same sub-tribe as the goldfish (Cyprini; Rainboth 1991), use very similar sets of cues. Indeed, these species hybridise (Taylor & Mahon 1977). Not surprisingly, EOG recording data strongly suggest pheromone identity is inherited and that closely related species of teleost fish use similar types of hormonal and bile acid cues (Stacey & Cardwell 1995; Sorensen et al. 1999; Stacey & Sorensen, 2002 unpubl. data). Notably, the Asian carps are somewhat distantly related from Cyprini (Cucnha et al. 2002) and although EOG screening suggests they too use hormonal pheromones, initial indications are that they are somewhat different than those used by the common carp and goldfish (Stacey & Cardwell 1995). Our understanding of the goldfish pheromone system (Kobayashi et al. 2002; Stacey & Sorensen 2002) lays the foundation for further studies to understand pheromone identify, function, and application in fish.

Alarm cues

Like other Ostariophysians, the goldfish and its close relatives possess club cells and presumably produce alarm cues. Studies of both goldfish and crucian carp (Hamdani et al. 2000) appear to support this possibility, although Maniak et al. (2000) reported difficulties duplicating this finding in the goldfish. Notably, responses to alarm pheromones appear to be influenced by experience (Wisenden 2003), calling into question whether such odours should be considered pheromones in the manner that we have defined them. Several studies have documented that exposure to damaged skin odour appears to stimulate crucian carp to develop deeper bodies which might make them more difficult to consume, an apparent priming effect (Bronmark & Miner 1992). Alarm responses do not appear to have been studied in the common carp but it seems highly likely they use these cue(s), especially because all Ostariophysians are thought to use these cues (Pfeiffer 1977; Smith 1992). The species-specificity of the alarm pheromone(s) has not been rigorously explored. Nevertheless, they have considerable potential for

use in barriers designed to minimise dispersion of invading species that are completely new to an area.

Non-reproductive aggregants

There is evidence that both goldfish and carp use aggregation pheromones. Studies testing the role of skin extracts as a chemical signal illustrated that immature goldfish were attracted to skin mucus extracts, which contain free amino acids (Saglio & Fauconneau 1985; Saglio & Blanc 1989). Other candidate compounds were not examined. Recently, we (Sherman & Sorensen unpubl. data) performed similar behavioural studies with various fish odours and found evidence of conspecific attraction in goldfish. These experiments are presently being expanded to include carp and the various odorous compounds including the bile acids that they release. Under conditions in which recruitment is limiting, aggregants could be useful in an IPM programme (see below).

Reproductive pheromones

In goldfish, crucian and common carp, gonadal recrudescence begins in winter and spawning, which can occur several times over a protracted spring–summer spawning season, appears to be triggered when a combination of increasing temperature and submerged vegetation, a preferred substrate for the adhesive eggs, induces a preovulatory luteinising hormone (LH) surge in postvitellogenic females (e.g., Stacey et al. 1979). Males accompany the ovulated female for the few hours she retains ovulated eggs, and engage in intense sperm competition as she repeatedly enters aquatic vegetation to oviposit. The evolution of promiscuous mating systems evidently has favored males capable of recognising and responding to female chemicals associated with ovarian condition.

Reproductive pheromones are particularly well understood in the goldfish, in which reproductive females sequentially release at least four distinct hormonally-derived pheromones, three of which are mixtures (Fig. 1). EOG recordings as well as behavioural and endocrine bioassays (Bjerselius & Olsén 1993; Irvine & Sorensen 1993; Stacey et al. 1994; Bjerselius et al. 1995) all strongly suggest that the reproductive pheromones of common carp and crucian carp are remarkably similar to those of the goldfish.

Female recrudescence pheromone

Male goldfish are attracted to the odour of females which are experiencing vitellogenesis as a consequence of high estrogen levels (Yamazaki & Watanabe 1979; Yamazaki 1990; Kobayashi et al.

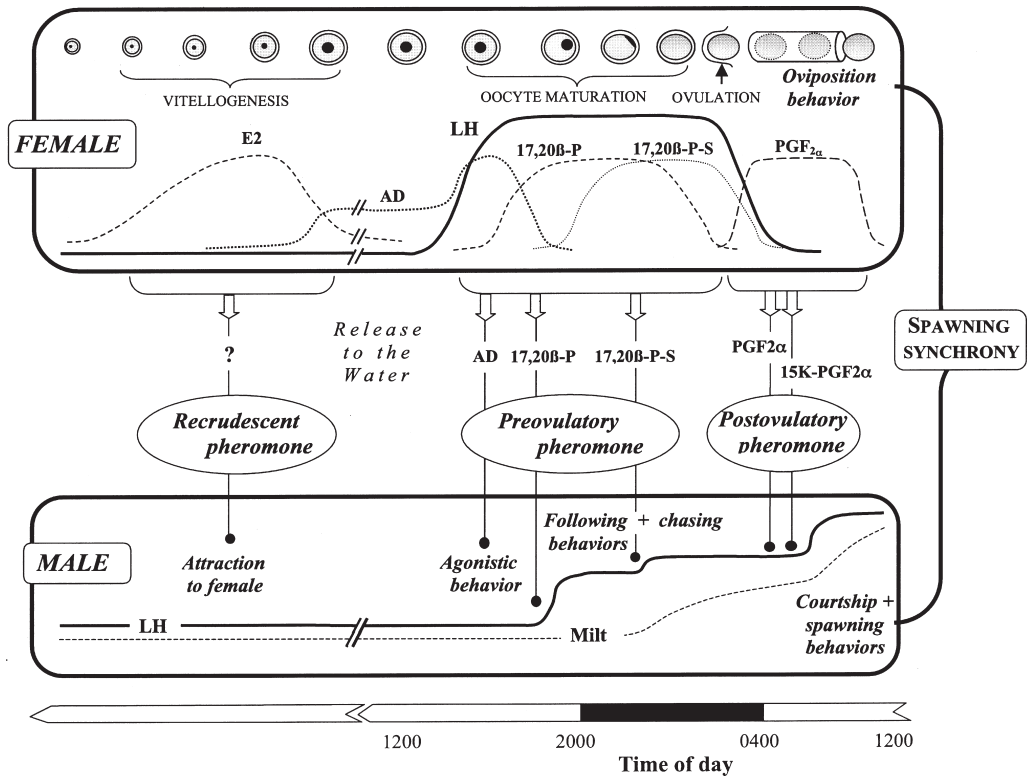


Fig. 1 Schematic model of female pheromones exerting primer and releaser effects on male goldfish, *Carassius auratus*, and presumably common carp, *Cyprinus carpio* (see Stacey & Sorensen 2002 for additional details and original sources). In vitellogenic females, plasma estradiol (E2) stimulates urinary release of an unidentified recrudescence pheromone that attracts males. In postvitellogenic females, exogenous cues induce an evening luteinising hormone surge which stimulates release of a preovulatory steroid pheromone containing a changing mixture of androstenedione (AD), 4-pregnen-17,20β-diol-3-one (17,20β-P), and its sulfated metabolite, 17,20β-P-S. Early in the LH surge, water-borne AD induces agonistic behaviours among males and inhibits male LH response to 17,20β-P. As the 17,20β-P: AD ratio increases, males increase LH and begin to follow and chase conspecifics. Later in the LH surge, 17,20β-P-S dominates the preovulatory pheromone mixture, enhancing its behavioural and endocrine effectiveness. LH increase in pheromone-exposed males increases both the quantity and quality of sperm in the sperm ducts before ovulation. At ovulation, eggs in the oviduct induce synthesis of prostaglandin F_{2α} (PGF_{2α}) which acts in the brain to stimulate female sex behaviour and is cleared to the water with its principal metabolite (15K-PGF_{2α}) to function as a postovulatory pheromone that stimulate male courtship and spawning behaviours and further LH increase. (LH, luteinising hormone.)

2002). This response presumably enables males to remain within aggregations containing females, a critical ability in a mating system where spawning can occur in turbid water at unpredictable times and places (Kobayashi et al. 1988). The putative recrudescence pheromone, also expected to exist in crucian and common carp, is apparently released in the urine but has not yet been chemically characterised (Yamazaki 1990). It might be useful as a male attractant.

Female preovulatory steroid pheromone

Following an extended vitellogenic phase of several months associated with recrudescence pheromone release, female goldfish exhibit a dramatic preovulatory LH surge when exposed to appropriate spawning stimuli (rising temperatures, spawning substrate, female pheromones) (Kobayashi et al. 1987, 2002; Stacey et al. 1979, 1989). In response to this LH surge, which lasts c. 15 h and terminates

with ovulation and spawning during late scotophase, changes in steroid synthesis lead to release of a multi-component steroid pheromone that enhances male fertility (DeFraipont & Sorensen 1993; Zheng et al. 1997).

At the onset of their LH surge, the female's steroid synthesis favours C18 steroids (estrogens), but then rapidly shifts to favour first C19 steroids (androgens), then C21 steroids (progestogens), and finally C19 steroids again at the time of ovulation and spawning. Steroid release closely parallels plasma concentrations, with the exception that conjugated metabolites are also released (Stacey et al. 1989; Scott & Sorensen 1994; Sorensen & Scott 1994). EOG and steroid release studies indicate that three steroids, androstenedione (AD), the maturation-inducing steroid 4-pregnen-17,20 β -dihydroxy-3-one (17,20 β P), and its sulfated metabolite 4-pregnen-17,20 β -dihydroxy-3-one-20-sulphate (17,20 β P-S), are "primary" components of the preovulatory pheromone which affects males, because each is effective when tested alone, and acts through specific, and sensitive (picomolar threshold) olfactory receptors (Sorensen et al. 1990, 1995b). Several other steroids (e.g., 17,20 β P-glucuronide) which function as receptor agonists appear to function as "redundant" components which augment the action of the three primary components. These details have not been explored in other carps.

As the 17,20 β P:AD ratio of the preovulatory pheromone increases during the female's LH surge, the males' initial response (aggression toward other males) is replaced by persistent inspection and following behaviours (Poling et al. 2001), and their LH increases, resulting in steroid changes that mediate increased milt (sperm and seminal fluid) production and enhanced fertility/paternity (Dulka et al. 1987; DeFraipont & Sorensen 1993; Zheng et al. 1997). Late in their LH surge, females release significant quantities of urinary 17,20 β P-S that elicit brief, acute bouts of male chasing and following and relatively small increases in LH (Sorensen et al. 1995a; Poling et al. 2001).

Significantly, the three primary components of the preovulatory pheromone are not encountered as a single odour mixture, because the free steroids (AD and 17,20 β P) are released almost exclusively across the gills and theoretically detectable only in the immediate vicinity of the female, whereas 17,20 β P-S (as with other conjugated steroids) is released as controlled urinary pulses and theoretically detectable at greater distances (Sorensen et al. 2000). Nonetheless, males appear capable of integrating gill

and urine odours, because AD suppresses behavioural responses to 17,20 β P-S, and 17,20 β P and 17,20 β P-S will synergise each other's actions (Sorensen & Poling unpubl. data).

There is some evidence that the sex steroids released by female goldfish are also detected and used as a priming pheromone by other females. Female goldfish appear to synchronise their ovulations in the laboratory (Kobayashi et al. 1988) and exposure to 17,20 β P increases the incidence of ovulation (Kobayashi et al. 2002). The function(s) of pheromonally-mediated ovulatory synchrony may be to promote predator swamping (e.g., by producing many eggs at once it is less likely that any particular egg will be eaten), and/or reducing potentially disruptive effects of male competition by reducing male : female sex ratios. Reproductive synchrony amongst female common carp has also been noted in aquaculture (Stacey et al. 1994). This complex pheromone could be used as both an attractant for trapping adult males and as a synchronising agent to control population-wide spawning of males and females in an IPM control programme. Exactly how to use this cue within the "chemical network" it controls (see section below) will, however, take some careful thought.

Female postovulatory prostaglandin pheromone

At the time of ovulation, female goldfish produce large quantities of prostaglandin F2 α (PGF2 α) which acts as hormone to trigger spawning (oviposition) behaviours (Stacey 1976; Stacey & Peter 1979) before being metabolised and released where males recognise it as a releaser pheromone (Sorensen & Goetz 1993; Sorensen et al. 1995b; Stacey & Sorensen 2002). Recently ovulated goldfish release great quantities (100 ng h⁻¹) of PGF2 α and a metabolite, 15-keto-prostaglandin F2 α (15K-PGF2 α) in urinary pulses, whose frequency changes during spawning (Appelt & Sorensen 1999). EOG and behavioural studies show that both of these prostaglandins are detected with great specificity and sensitivity (nM and pM thresholds, respectively) and are effective when tested individually (Sorensen et al. 1988, 1989). Interestingly, the mixture of PGF2 α and 15K-PGF2 α also induces LH increase in males which is dependent on social context and but is mediated by a different neuroendocrine mechanism than that of the steroidal pheromone (Zheng & Stacey 1997). So important is the prostaglandin pheromone that male goldfish generally fail to mate if their olfactory systems are disrupted (Stacey & Kyle 1983). Common and crucian carp detect F

prostaglandins with approximately the same sensitivity and specificity as goldfish and it seems likely that they use these or very similar cues (Irvine & Sorensen 1993; Bjerselius & Olsén 1993). Notably, the possible role of mixtures in the female prostaglandin pheromone and the actual identity of the prostaglandins used have only been studied in the goldfish (Sorensen et al. 1995a, 2000). Still, the potency and importance of this cue give it good potential for use as an attractant or perhaps disruptant for controlling mature male carp (see below).

Male sex pheromone

Although interactions with females are the most striking components of male reproductive behaviour, it is clear that male goldfish also engage in inhibitory and stimulatory interactions with other males. AD is released in large quantities by males (Sorensen & Scott 1994; Sorensen et al. 2004), and strongly stimulates male aggressive behaviours in the absence of other steroidal cues (Poling et al. 2001). Further, in the absence of spawning stimuli, mature males suppress each other's milt production; isolation causes their milt volume to increase (Stacey et al. 2001; Fraser & Stacey 2002). AD might be responsible for these phenomena but this has yet to be proven. Similarly, the possibility that females may detect and use male odours (such as AD which they also detect) has yet to be examined although male common carp detect AD (Irvine & Sorensen 1993). An immediate use for this androgenic cue is not clear unless an analogue without activity in mammals can be identified.

Goldfish pheromones and chemical networks

The fluid nature of goldfish and carp social aggregations and the proximity of their members makes it highly likely that these fishes live within chemically-mediated social networks (McGregor & Peake 2000; Wisenden & Stacey 2004). We believe that this network alternates between two distinct states—recrudescence and spawning. In the first state, the recrudescence pheromone promotes bisexual aggregations in which negative feedback among males maintains hormones and milt at basal levels (Fig. 2A). However, the relatively stable recrudescence state likely can rapidly shift into a transient spawning state if temperature and substrate stimuli trigger a preovulatory LH surge in female(s), thereby triggering preovulatory pheromone release and LH increase in proximate females and males, activating a positive feedback mechanism that amplifies and disseminates the original stimulus to promote

synchronous gonadal maturation and spawning within the network (Fig. 2B). The spawning state likely quickly reverts to the recrudescence state because, in the absence of cues from ovulatory females, male-male inhibition will rapidly be restored. Under conditions appropriate for spawning, this proposed network likely cycles between recrudescence and spawning states as successive waves of vitellogenesis restore female sensitivity to abiotic and pheromonal cues triggering the preovulatory LH surge. Cycles might thus be expected to be rapid or long, depending on local conditions. As mentioned above, it seems entirely reasonable that cycles could be actively manipulated using priming pheromones and perhaps other sensory cues; if managers could control the time and location of fish spawning, they could use traps, poisons, or perhaps other control agents such as viruses or genetic techniques more effectively. We elaborate on this issue in greater detail below.

HOW MIGHT PHEROMONES BE USED TO MANAGE AND CONTROL TELEOST FISHES?

Any discussion of how pheromones might be used must begin with the caveat that successful management of any species depends on understanding a suite of factors related to its life history (migratory, aggregated, or dispersed), mating system (iteroparous or semelparous), and habitat requirements (flowing or still water). Further, pheromones must be recognised as potent modulators of behaviour (and physiology) that need to be developed and deployed together with other techniques as part of an integrated approach to be truly effective. Nevertheless the advantages pheromones can bring are considerable and may even determine whether a particular strategy (e.g., trapping out sea lamprey) is viable. The experience of the sea lamprey programme suggests that administrative approval of teleost pheromones will be relatively easy, at least compared with toxicants.

A final and important consideration for pheromone application is that these cues disperse and are broken down (or removed) in natural waters such that their application can be controlled, yet sensory adaptation does not hinder behavioural responses. Although the natural distribution of these cues has not been studied in detail, some insight is available. First, both bile acids and hormonal products appear (based on laboratory studies) to have half-lives of about a day (Sorensen et al. 2000; Polkinghorne et

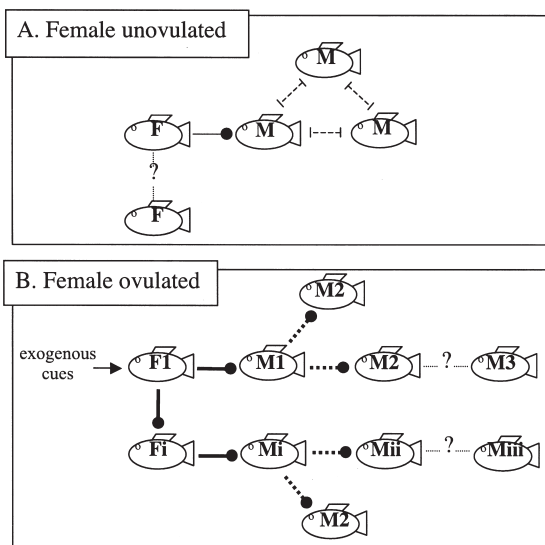


Fig. 2 Schematic model illustrating some of the reproductive interactions within groups (networks) of goldfish (*Carassius auratus*), that are either known (solid lines) or hypothesised (dashed lines) to be mediated by pheromones. **A.** In the presence of recrudescing females (F) that are not ovulatory, mature males (M) remain in a “basal” endocrine state and release unknown cues that inhibit milt production. There is presently no evidence for pheromonal interaction among vitellogenic females. **B.** If exogenous stimuli (increased water temperature and aquatic vegetation) induce an ovulatory LH surge in one female (F1), release of her preovulatory pheromone can stimulate endocrine changes in a male (M1) that increases his releasable sperm stores, and evokes the release of unknown cues inducing similar changes in additional males (M2). As well, the preovulatory pheromone can induce ovulation in additional females (Fi), whose preovulatory pheromone release will activate additional networks of males either directly (Mi), or indirectly (Mii). It is not known if males (M2 and Mii) that receive ovulatory information indirectly through other males influence additional males (M3 and Miii, respectively).

al. 2001), suggesting that they are likely to create sharp odour gradients and not to persist in ways that might be of concern. Further, in waters with high organic loads, this phenomenon would be enhanced by binding with natural humic acids (Mesquita et al. 2003). Indeed, preliminary biochemical analyses of natural waters for the sea lamprey pheromone (Fine & Sorensen 2004) note a correlation between larval abundance and PS, with PS concentrations hovering around the picomolar range, both confirming the

natural behavioral potencies of river waters and explaining the abilities of lamprey to orient within them (Vrieze & Sorensen 2001). How best to create pheromone plumes that fish can track is an important question that has not yet been studied but it is worth noting that like invertebrates, many fish appear to possess sophisticated abilities to track or otherwise orient into variable odour plumes using combinations of taxes and kineses (Atema 1995; Vickers 2000; Baker et al. 2002; Wyatt 2003). Presumably, once fish chemo-orientation mechanisms are better understood they can be manipulated.

Possible uses for pheromones in the conservation and management of rare and endangered wild fish include attracting fish populations from great distances to desirable locations to promote reproduction (e.g., Baker & Hicks 2003), guiding fish around barriers (e.g., Briand et al. 2002), and stimulating reproduction at desirable places and times. No other technique offers such potential in situations where small differences in fish recruitment can be significant. In fish culture pheromones could be used to stimulate gonadal development and spawning, and to select responsive males or females for brood stock purposes, reducing handling stress and labour costs (see Stacey et al. 1994).

Finally, an equally large number of uses can be envisaged for controlling populations of non-indigenous teleost fishes, some of which are similar to those being considered for the sea lamprey mentioned above. We believe that these applications must be considered within the context of IPM and that the best chance for the control of teleost fish likely lies with the development of multiple coordinated strategies that specifically target different life histories of species in complimentary fashions. A good place to start this discussion is to review present approaches that have achieved some success and which pheromones might therefore be used to compliment. These include: (1) removal of animals using trapping and/or poisoning (Bryrd & Crance 1965; Sanger & Koehn 1997; Brege et al. 2003); (2) reduction of reproductive potential through trapping followed by sterilisation (Twohey et al. 2003a,b); and (3) construction of barriers to prevent movement (Lavis et al. 2003). Finally, the possibility that fish might be eventually controlled through the introduction of self-perpetuating lines of genetically modified organisms with altered reproductive abilities (e.g., “Daughterless technology”; Grew 1997) must be considered. Six possible applications for pheromones are listed below, some of which could serve multiple strategic functions.

Using pheromones to facilitate trapping

Trapping might be deployed in population control either as direct strategy to simply remove organisms, and/or to collect animals for sterilisation and re-release, thereby targeting reproductive potential more directly. Certainly, most fish traps are very inefficient and pheromones could help rectify these deficiencies at low cost. The question is simply whether pheromonal traps could be effective enough to make a significant difference to the population. Accordingly, the population dynamics of the species being controlled must be carefully considered, as simply removing animals from populations whose densities are so high that their recruitment is not density-dependent may not be a valuable exercise over the short term. Notably, however, if population densities can be suppressed to levels where recruitment is density-dependent, then trapping for control becomes highly feasible, and pheromonal enhancement of trapping efficiencies reasonable. Even slight increases in trapping efficiency can be extraordinarily significant in these instances (see: Twohey et al. 2003a). Naturally, pheromone application should be considered together with the use of other attractant cues such as sound or light to get the best possible result.

Trapping for control is already a realistic possibility for many populations of invasive fishes whose densities are for some reason (e.g., effective controls already exist, or habitat is suboptimal) at levels that are density-dependent. An excellent example of such a situation is for that of sea lamprey located in the St Mary's River (the largest river in the Great Lakes Basin) where the combined use of toxicants and sterile males has already been optimised and driven lamprey populations down to a point where recruitment is density-dependent (Twohey et al. 2003a,b). Similar situations have also been described for a large number of smaller, closed bodies of water containing common carp in both North America and Australia which have been "fished" down to only a few individuals which can not be easily removed yet represent an omnipresent threat (Brown & Walker 2004). In insects, pheromonally assisted trapping has often been combined with use of poisoned baits and sometimes other sensory cues with great success (Wyatt 2003). Poisons such as rotenone have been used with great success to control common carp in North America, using simple broadcast application with as yet little effort to enhance this technique through the use of attractants, targeted applications, or oral administration (Dawson & Kohlar 2003).

Needless to say, trapping is probably best employed if it can be targeted to remove mature adults so as to remove their reproductive contribution. Here sex pheromones represent a powerful tool because they could be used to target either males and/or females. If these fish might then be sterilised, potential gain is greatly amplified. For species whose numbers are limited by female availability (e.g., common carp), it would be best to simultaneously use a male sex pheromone to attract females so that they might be removed, and/or to catch males so that they might be sterilised and re-released (a suitable technique for this has yet to be identified). For species for which male fertility is limiting (e.g., species for which males guard nests such as gobies), the opposite strategy could be attempted.

For species such as the common carp, a range of sex and aggregation pheromones could also be used to attract and remove males, females, and/or juveniles in different situations dictated by local environment and populations dynamics. Thus, F prostaglandins, which function as female cues, could be considered for use in male trapping regimes. Similarly, male odours such as androstenedione should be considered for use in schemes designed to attract and remove females. Finally, aggregants/attractants (which are likely to include the bile acid, cyprinol sulfate) might be used where simple removal will suffice, or where juveniles can be targeted on spawning beds. At present, we have little understanding of the role of pheromones and other sensory cues as long-distant attractors so study is needed. Efficient trap designs that use these cues will also be needed. A coordinated approach with repellents might also be considered. Likely other examples of sensory-mediated trapping schemes can be envisaged, some of which might be especially useful in combination with other strategies such as specific poisons, viruses, environmental manipulation (e.g., predator introduction or water draw-down), or genetic manipulation (e.g., daughterless). All of these techniques have special promise for treating residual populations of fish that are for one reason or another resistant to specific strategies yet continue to pose great threat. In conclusion, it seems reasonable that if a focused IPM programme for carps or other fish were to be developed, trapping for control would/should be an important tool, especially if used with other techniques which suppress reproductive potential.

Using pheromones to disrupt and reduce reproductive success

Pheromones play key roles in the reproductive success of many fishes just as they do for insects. Perhaps the most successful application of pheromones in insect IPM at present is a technique known as “pheromonal disruption” in which high concentrations of synthetic pheromone(s) are applied to fields to effect mass confusion (Carde & Minks 1995, 1997). Although the exact mechanisms underlying this technique are as yet unclear, often the pest experiences total reproductive failure at little environmental or financial cost (Wyatt 2003). Conceivably, pheromonal disruption could also be used on fishes such as common carp although considerable quantities of pheromone might be needed. This might be possible if/when synthetic analogues are identified. An alternative to the direct application of pheromone would be to stimulate pheromone production in sexually immature fish (perhaps by implanting pheromonal precursors), thereby creating a significant sensory distraction within spawning aggregations. Pheromonal disruption might also be evoked by applying the preovulatory steroidal pheromones to trigger (or inhibit) spawning at times and locations that benefit fish managers but not the fish.

Using pheromones to disrupt movement and migration

Migratory fishes species such as the lampreys and charrs appear to use pheromones to find spawning grounds from some distance (Selset & Døving 1980; Baker & Montgomery 2001; Vrieze & Sorensen 2001). It is conceivable that pheromones could be used to divert migrations of invasive fishes to regions unsuitable for spawning or habitation. Pheromones along with related attractive odours might also be used to disrupt short-range movements of species such as carp which perform short-distance, directed movements to specific types of spawning habitat that can have limited distributions. Migration could also conceivably be blocked if pheromonal antagonists can be identified or natural mixtures/concentration altered, essentially another form of disruption.

Using hormones and their pheromones to promote the success of sterilised fishes

For strategies that use sterile fishes, the fertility of these fishes and their ability to attract or find mates is critical. Sex steroid hormones and the pheromones associated with them are known to greatly enhance individual reproductive success (Oliveira et al. 2002; Stacey & Sorensen 2002). In male goldfish, for example,

exposure to the priming pheromone, 17,20 β P increases hormone levels, competitiveness, sperm quality, and pheromone production—leading to several-fold increases in individual spawning success (DeFraipont & Sorensen 1993; Zheng et al. 1997). Presumably, this increase is related to a combination of increased male competitiveness and the ability of females to discern more fertile individuals. Likely this phenomenon is hormonally-driven and common amongst fishes, especially those that spawn in large groups. Accordingly, if hormone and pheromone production could be increased in sterilised (or genetically altered) fish through physiological or genetic manipulations, the efficacy of sterilisation might be greatly enhanced. Although Siefkes et al. (2003b) have explored the possibility that sterilisation might impair pheromone production, there appear to have been no attempts to boost pheromone production.

Using pheromones to repel

Many species of fish release alarm pheromones which have potential for keeping invasive fish away from areas of special concern such as optimal spawning habitat, canals that connect key waterways, or regions where ballast water is taken up. Preventing spread is a key objective to all invasive control programmes, whether it be related to a new invader or simply preventing organisms from re-invading a recently treated area. Repulsive odours such as alarm pheromones can easily be applied to prevent spread and will work in most situations, even relatively high currents. Other sensory cues such as sound and bubble nets in barriers might significantly boost these effects at very low cost. When using repellents, one must consider where the affected animals might move, but in the important example of barriers connecting waterways this is not an issue. These possibilities have all been proposed and discussed for the Eurasian ruffe whose alarm pheromone survives freezing, enabling it to be easily collected and deployed (Maniak et al. 2000). Of course, identifying the chemical component(s) of alarm pheromones would be very useful and might even lead to the development of synthetic species-specific repellents.

Using pheromones to assess population size and distribution

Integrated pest control requires that managers have an excellent understanding of the numbers and locations of the fish they are managing. Traditionally, these aims have been met by labour-intensive and expensive techniques such as electro-shocking, creel

census, and trapping. These efforts often take a very significant portion of the budget available for control. However, if species- or even gender-specific pheromones could be accurately measured in natural waters, their concentrations could serve as useful and inexpensive measures of population abundance (or simply presence-absence), saving a great deal of money. Indeed, this possibility is presently being pursued for the sea lamprey migratory pheromone which can be detected in natural stream waters using electro-spray mass spectrometry (Fine & Sorensen 2004). The lamprey, however, is somewhat of a special example, insofar as its migratory pheromone is released in great quantity at an effectively constant rate and into a directional flow. Clearly, aggregational cues such as bile acids have the greatest utility in this regard for both lampreys and teleost fishes.

CONCLUSIONS

Pheromones serve prominent roles in the life histories of a great many species of fish. Many of these cues have now been identified and laboratory studies have found them to strongly influence critical physiological and behavioural processes relevant to basic fish biology. Some of the signals used by the goldfish have now been elucidated and techniques developed to facilitate identification of the remaining cues. Ongoing studies on the sea lamprey demonstrate that fish control needs to consider simultaneous use of multiple techniques based on an IPM model to achieve control. Indeed, even highly effective techniques such as lampricide treatment can and need to be improved upon. Pheromones offer the potential to significantly enhance the efficiencies of many strategies in safe and affordable ways that the public finds acceptable. Statistical modelling and field trials suggest that they will be useful and although the path forward is unlikely to be simple or straightforward, few other alternatives with such promise seem to exist. Finally, further understanding of pheromones will almost certainly benefit the conservation of native fishes.

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