

# Theory and Application of Semiochemicals in Nuisance Fish Control

Peter W. Sorensen<sup>1</sup> · Nicholas S. Johnson<sup>2</sup>

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**Abstract** Controlling unwanted, or nuisance, fishes is becoming an increasingly urgent issue with few obvious solutions. Because fish rely heavily on semiochemicals, or chemical compounds that convey information between and within species, to mediate aspects of their life histories, these compounds are increasingly being considered as an option to help control wild fish. Possible uses of semiochemicals include measuring their presence in water to estimate population size, adding them to traps to count or remove specific species of fish, adding them to waterways to manipulate large-scale movement patterns, and saturating the environment with synthesized semiochemicals to disrupt responses to the natural cue. These applications may be especially appropriate for pheromones, chemical signals that pass between members of same species and which also have extreme specificity and potency. Alarm cues, compounds released by injured fish, and cues released by potential predators also could function as repellents and be especially useful if paired with pheromonal attractants in “push-pull” configurations. Approximately half a dozen attractive pheromones now have been partially identified in fish, and those for the sea lamprey and the common carp have been tested in the field with modest success. Alarm and predator cues for sea lamprey also have been tested in the laboratory and field with some success. Success has

been hampered by our incomplete understanding of chemical identity, a lack of synthesized compounds, the fact that laboratory bioassays do not always reflect natural environments, and the relative difficulty of conducting trials on wild fishes because of short field seasons and regulatory requirements. Nevertheless, workers continue efforts to identify pheromones because of the great potential elucidated by insect control and the fact that few tools are available to control nuisance fish. Approaches developed for nuisance fish also could be applied to valued fishes, which suffer from a lack of powerful management tools.

**Keywords** Invasive species · Monitoring · Judas fish · Trapping · Removal · Disruption · Re-direction · Sea lamprey · Carp

## Introduction and General Overview of Semiochemicals and Nuisance Fish

Most freshwater and marine ecosystems and fisheries are in serious decline (Mullon et al. 2005). Challenges to aquatic ecosystems and their inhabitants are complex and include increased turbidity, eutrophication, warming and acidification, changing food webs, overfishing, and the arrival of exotic species from other locations. Populations of many unwanted exotic fish species are becoming excessively abundant, as in some cases are native species. In this manuscript, fishes that are considered overly abundant and troublesome by fisheries managers are termed “nuisance,” and if they are also from another location and established, we term them “invasive” (Simberloff 2013). Challenges associated with nuisance fish control are great because of the enormous size and complexity of many water bodies and our inability to accurately sample fish to characterize movement and distribution. At present, efforts to

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✉ Peter W. Sorensen  
soren003@umn.edu

<sup>1</sup> Department of Fisheries, Wildlife & Conservation Biology,  
University of Minnesota, 324 Skok Hall, St Paul  
Campus, MN 55108, USA

<sup>2</sup> U.S. Geological Survey, Hammond Bay Biological Station, Great  
Lakes Science Center, 11188 Ray Road, Millersburg, MI 49759,  
USA

control nuisance fishes focus on large-scale migration blockades (dams, electric barriers), water draw-downs and large-scale poisoning, and removal using trapping or poisoning; all these approaches have serious limitations. For example, migratory barriers often block both nuisance and valued fishes and can be expensive and difficult to build and maintain (McLaughlin et al. 2013). Similarly, removal using netting is typically nonspecific, expensive, inefficient, and limited by bottom terrain. Further, extant fish poisons are relatively nonspecific and expensive to apply safely. New solutions are urgently sought to address nuisance fish control including semiochemicals (i.e., naturally released chemicals that mediate interactions between and within species [Wyatt 2014]), which this manuscript will review. We address the theory underlying the function and identity of semiochemicals used by fish while focusing on recent applications of these products. This review expands on a recent review of applications for fish pheromones (Sorensen 2015a) and another that reviewed the breadth of useful fish cues (Sorensen and Stacey 2004).

Semiochemicals play key roles in many fishes (Sorensen 2015b) and are typically specific, potent, and easily and safely added to water. Potential applications of these compounds in fish control are myriad because of the diverse array of biological functions that semiochemicals have in fishes. These functions include attraction/arousal, repulsion, and endocrine synchrony. Like semiochemicals used by insects, fish semiochemicals typically appear to function as mixtures of chemical compounds (Sorensen and Baker 2015; Wyatt 2014). Sets of compounds that have come to be employed through some type of specialization may be considered “signals,” while those that are not specialized typically are called “cues.” Unfortunately, this distinction is not well understood in fishes and difficult to make as most, if not all, semiochemicals identified to date in fishes are bodily metabolites whose production and release is not well understood. Exactly what specialization might be for metabolites also is somewhat unclear and likely varies. Pheromones, or “molecule(s) that are evolved cues which elicit a specific reaction, for example a stereotyped behavior and/or behavioral process in a conspecific” (Sorensen 2015b; Wyatt 2014), have especially great promise for controlling fish because of their greater specificity. Notably, while many workers suggest that pheromones need to be highly evolved signals with high species-specificity, these requirements were not part of the original definition (Karlson and Luscher 1959). Furthermore, these requirements do not seem relevant in fishes, whose most potent infochemicals are mixtures of bodily metabolites that may also have other (perhaps even primary) specialized functions such as endocrine function in the carps (Stacey 2015) or antimicrobial protection in the lampreys (Sorensen et al. 2005). Because the production and detection of these types of body metabolites is specialized, adaptive, often species-specific, and used species-wide, we consider them to be pheromones. Other classes of semiochemicals with potential use in wild fish control

include the allelochemicals, or chemicals that convey information between different species, and which may be themselves be categorized as allomones, which benefit the emitter; kairomones, which benefit the receiver (sometimes to the detriment of the emitter) (Brown et al. 1970); and synomones, which benefit both the emitter and receiver (Wyatt 2014). While a wide variety of individual semiochemicals including pheromones have been described and shown to have activity in fishes (Stacey 2015), no complete pheromone mixture (signal) has been completely identified (i.e., the odor of no fish has yet been completely isolated, identified, synthesized, and tested in the field and shown to have exactly the same activity as natural odors). Nevertheless, since all fish semiochemicals appear to be discerned by the olfactory sense, they are considered “odors” (Sorensen and Caprio 1997). Herein, we broadly define “fish” as all finned vertebrates that live in water and note that this amazing group includes over 30,000 species as well as the ancient sea lamprey, *Petromyzon marinus*.

Fish have been moved all over the world both accidentally and purposefully, and dozens of species have now become invasive. Several native fish species also have reached unusually high numbers because of ecosystem imbalances (e.g., stunted northern pike, *Esox lucius*, in many inland North American lakes). The problem of invasive fishes seems especially acute in freshwater ecosystems, perhaps because many are highly disturbed and are also less diverse and therefore less resilient than marine systems (Moyle and Light 1996). Species of special concern in freshwater include the walking catfish (*Clarius batrachus*) in North America, the common carp (*Cyprinus carpio*) in most temperate regions of the world, the sea lamprey in the Laurentian Great Lakes, the round goby (*Neogobius melanostomus*) in the Great Lakes, the bigheaded (Asian) carps (*Hypophthalmichthys sp.*) in the Mississippi River, the brown trout (*Salmo trutta*) in many temperate regions of the world, the Mozambique tilapia and its hybrids (*Oreochromis spp.*) in many tropical areas of the world, the snakehead (*Channa micropeltes*) in North America, the rudd (*Scardinius sp.*) in the southern hemisphere, the mosquitofish (*Gambusia sp.*) in many sub-tropic regions of the world, and the smallmouth bass (*Micropterus dolomieu*) in Asia (<http://www.issg.org/database/species/search.asp?st=100ss&fr=1&str=&lang=EN>, <http://www.environmentalgraffiti.com/news-invasive-fish>). In marine waters, the lionfish (*Pteriois volitans*) from Australia is invasive in the Caribbean Sea and Atlantic Ocean. With few exceptions, pheromones have been at least partially identified in all the species listed above. Additionally, with the possible exception of the mosquitofish and lionfish, all invasive species are social, lack obvious visual sexual dimorphisms and thus appear to rely on semiochemicals to mediate reproductive and other social interactions.

Controlling nuisance and invasive fish is proving to be a formidable task. Only two invasive fishes are presently

controlled on a large scale: the sea lamprey in the Laurentian Great Lakes and the common carp in some inland lakes in North America. Both species are controlled primarily by using pesticides that are expensive and not entirely species-specific, although semiochemicals are now being actively considered and investigated (Sorensen and Hoye 2007) as well as gene driven technologies that can be used to alter organisms' genotypes to make them less fit (Webber et al. 2015). The large volumes of water that fishes typically inhabit present a challenge to the application of semiochemicals especially because most waters are open to the public and highly regulated. Integrated pest management (IPM), the practice pioneered in insects in which numerous approaches are brought to bear to control (Sorensen 2015a), also is seen as a possible solution for invasive fish control by many agencies. However, to be useful, IPM requires accurate assessment of pest populations and effective strategies that can target multiple life stages. IPM also usually needs to be customized to fit local situations. Many opportunities appear to exist to use semiochemicals in both monitoring and controlling fish abundance because of their diverse functions. Herein, we cover several topics, including: (1) an overview of the promise and challenge of using semiochemicals to control nuisance fish; (2) an overview of the types of semiochemicals that fish use and their potential for application; (3) an overview of the ways semiochemicals have been applied to date; and (4) lessons from studies of invasive fish that apply to conservation of valued fish. We address possible uses of pheromones in IPM including monitoring, attraction, mating disruption and redirecting migratory nuisance fishes.

### The Promise and Challenge of Using Semiochemicals to Control Nuisance Fish

Partly because of their potency, specificity, and lack of peripheral effects, and partly because few other options exist, semiochemicals are thought by many to have promise for controlling unwanted fishes. Unfortunately, this promise is offset by numerous challenges, in particular a poor understanding of their chemical identities in fishes as well as regulatory issues. Developments in pest insect management have inspired much of the work on fish semiochemicals and pheromones in particular. Fish and insects have much in common as they both typically inhabit huge, three-dimensional environments, are difficult to manage, and rely heavily on chemical cues including pheromones to mediate many aspects of their lives (Sorensen et al. 1998; Sorensen 2015b). Over the past few decades, pest insect control has shifted from a reliance on pesticides to IPM that often includes pheromones (Howse et al. 1988). Targeting can be species- and situation-specific. Often IPM in insects has wedded pheromonally-mediated targeting with selective insecticides. Similar approaches are

now being considered and tested to control invasive fish using semiochemicals and pheromones in particular (see section below). Pheromone-related research in fish is being accelerated while development of new piscicides (fish toxins) is not being actively explored owing to the high development and licensing / registration costs for aquatic pesticides for use in public waters. Although all life stages of insects including recruitment (introduction of young individuals into populations), adult survival, reproductive success, and immigration have been targeted in insect IPM, accurate data on population abundance have proven to be key, and sex pheromones are commonly used as lures in small monitoring traps in fields and orchards worldwide (Witzgall et al. 2010). Remediation and control often is a second key component of most insect IPM programs once insects have been located, and farmers often employ pheromones either as baits in mass removal (that may include insecticides) or to disrupt mating. All of these approaches are also being considered for nuisance fishes (Sorensen 2015a).

Researchers and managers testing and using semiochemicals in nuisance fish control as part of IPM strategies face several challenges. The primary challenge is that fish semiochemical signals appear to have multiple components, and no signal has been completely identified and then synthesized (Sorensen and Hoye 2010), so we only have a few components to test. Further, identification and synthesis of individual semiochemicals has proven to be both difficult and expensive (Stewart and Sorensen 2015). In addition, a very large quantity of signal/cue is typically needed for use in open waters. Quantities needed must exceed those present naturally, and exposure protocols must be biologically relevant, which can be challenging because the natural active space of most teleost fish sex pheromones appears relatively small and requires steep concentration gradients (Stacey and Sorensen 2009; Stacey 2015). Added to this challenge is the fact that experiments with fish semiochemicals are difficult and expensive and that fish pheromone research does not have the financial backing of large companies (agribusiness). Fish research also needs to be conducted in public waterways where regulatory issues can be challenged. Further, while insects often can be propagated in the lab and tested in quasi-natural bioassays throughout the year, fishes are long lived, exhibit complex behaviors, and occupy large and complex habitats that cannot be easily recreated in the laboratory (Johnson and Li 2010). Field experiments often can only be conducted a few weeks per year when fish are sexually active and observation of fish behavior in deep, fast, and the turbid waters that characterize freshwater and estuarine environments can be difficult without advanced telemetry technologies. In marine environments, which may be less constrained by season and water quality, the large scale may be a significant challenge. Finally, regulatory agencies in the United States and Canada broadly define pesticides according to their intended use (i.e., they define a

pesticide as any substance whose intended use is for pest control; <https://www.epa.gov/minimum-risk-pesticides/what-pesticide>). Accordingly, all field experiments testing semiochemicals require experimental use permits from the U.S. Environmental Protection Agency (EPA) and sometimes other agencies, and must be conducted in compliance with “good” laboratory practices (i.e., a very rigorous data management system; Garner et al. 1992). Full-scale use requires registration by the EPA, a multiple-year process that is expensive and that has only recently been granted for one component of the sea lamprey sex pheromone (Johnson et al. 2015a), which is now the only vertebrate pheromone to have this distinction.

### Overview of Fish Semiochemicals that Could Theoretically be Applied to Fish Control

Fishes are a diverse and huge group of vertebrates that employ a wide variety of semiochemicals in many ways. While this collection of cues and signals can be categorized by evolutionary function or chemistry, they also can be grouped based on the biological responses they elicit: attractants/stimulants, repellents, and physiological synchronizers (primers). Below, we briefly review these categories of semiochemicals, while listing and then describing the types of cues and signals that fall within them and how they might be used. Another section describes those few that are currently being considered for use.

#### Semiochemicals that Attract and/or Arouse

**Reproductive Releasing Pheromones** Like many organisms, fish rely heavily on sex pheromones to mediate attraction and mating behavior in the often dark, turbid, and extensive waters that they inhabit. Fish exhibit an enormous variety of reproductive behaviors, so these signals are extremely diverse and include odors released by both males and females. Most of those for teleost (bony) fish seem to have short-range actions (ex. a few body lengths in goldfish [Stacey and Sorensen 2009]), but the sex pheromones used by sea lamprey have larger active spaces (Johnson et al. 2009). While many sex pheromones stimulate tracking behaviors (i.e., they are attractive), many also simultaneously stimulate sexual arousal and searching (e.g., prostaglandin-based sex pheromone released by ovulated goldfish [Sorensen et al. 1988]) and seemingly some do both (Lim and Sorensen 2012). Pheromones that drive behavior are known as “releasers.” Examples of sex pheromones exist for open water and nest spawning species as well as for live bearers. Among teleost fishes, there is strong evidence that the vast majority of sex pheromones are mixtures of hormonally derived compounds and function as “hormonal sex pheromones” (Stacey 2015). Many of these also seem to be complex mixtures that include common body

metabolites. When the latter convey species information, such signals are known as “pheromone complexes” (Levesque et al. 2011; Lim and Sorensen 2012; Sorensen and Baker 2015). Other species may use pheromonal blends in which the precise mixtures of hormonal components convey species information (Sorensen, University of Minnesota, unpublished results). The sea lamprey male sex pheromone is derived from seemingly specialized biliary steroids. Sex pheromones have potential for controlling nuisance fish by either attracting them for trapping or disrupting them, and these possibilities have all been tested in the carps, sea lamprey, and char. The somewhat specialized nature of pheromonal compounds also makes them useful as indicators of fish abundance and reproductive state, and we will review key ongoing work in this area.

**Kin and Species Recognition Odors** Recognition of species identity is important to most fishes to facilitate shoaling and other forms of attraction and aggregation (see Sorensen and Baker 2015). Usually odors appear to be involved in this process, although with the exception of the migratory pheromone used by the sea lamprey, they have not been identified (Sorensen et al. 2005). In some cases, recognition seems to be extremely sophisticated and allows fish to even discern kin groups (Olsen et al. 2002). Although there has been speculation that major histocompatibility complex-derived (MHC) peptides may serve this role in sticklebacks (Milinski et al. 2005), other studies appear to show that a complex assortment of unidentified polar and nonpolar products are involved (Levesque et al. 2011; Lim and Sorensen 2011; Sorensen 2015b). Kin-specific odors appear to be innately recognized in teleost fish, but these also could be learned via a highly prescribed process and likely should be considered pheromonal signals. These signals may have roles in reproductive attraction as well (i.e., mediating kin/species-recognition in mature fish also releasing more generic hormonal cues as sex pheromones), perhaps as combined signals or “complexes” (Sorensen 2015b; Sorensen and Baker 2015), but here we focus on their roles in sexually inactive fish. Many of these types of pheromones seem to be involved with attraction and aggregation, specifically driving aggregation in shoaling fish. In some species, including the sea lamprey, their role may include long-distance migration (Sorensen and Baker 2015). In both cases, use in nuisance species control is plausible; however, only its use for long-distance migration in the sea lamprey has been explored for use.

**Ornamental Odors** Many species of fish are highly territorial and advertise their presence and status using chemical signals (see Corkum and Cogliati 2015). They even may have specialized glands (although this is as yet unproven) to produce these apparent signals, which may be accompanied by visual or acoustical signals. Many of these chemical signals could be considered a type of sex pheromone. Recently one



hormonally-derived product was identified in male Mozambique tilapia that appears to facilitate recognition of especially dominant males which build nests (Keller-Costa et al. 2014). This tilapia species is highly invasive, and the pheromone might have use in its control if it were also attractive or if it could be used to disrupt mating by adding large quantities to the waters they inhabit. Neither of these options has been explored so we do not review them further.

**Imprinting Odors** During larval development, Pacific salmonids (*Oncorhynchus spp.*) learn the odors of their natal streams to which they return as adults to spawn (Dittman and Quinn 1996; Dittman et al. 2015). The complete identity of these odors is not known, although some suggest amino acids play a role (Shoji et al. 2003). Because these fishes spawn in mass, it also is possible that conspecific odors (which contains amino acids as well as bile acids) might also be part of the imprinted odor. If so, these odors could be considered kairomones. Kairomones might be added to spawning sites of invasive lake trout, *Salvelinus namaycush*, to disrupt imprinting but this has not been evaluated yet.

**Signature Odors** Many species of vertebrates learn the odors of individuals and employ them to facilitate social interactions; these are known as signature odors (Sorensen 2015b). These odors can be learned and influenced by diet and probably should be considered kairomones (Bryant and Atema 1987). While there is evidence that amino acids play a role, the identities of these complex cues presumably vary and are as yet unknown; it is therefore difficult to imagine how they might be employed in fisheries management will not be considered.

### Semiochemicals that Repel

**Alarm Cues** When injured, many fishes release cues that cause conspecifics and, in some cases, related heterospecifics to avoid areas and reduce activity seemingly to reduce predation risk (Brown 2003; Chivers and Smith 1998; Wisenden 2015). Some alarm cues also seem to have priming effects and influence endocrine function; the odor of damaged Crucian carp, *Carassius carassius*, causes conspecifics to change how they grow to make them less susceptible to predation (Brönmark and Miner 1992). Because these cues often pass between species and some are clearly learned, we consider them kairomones, although some may be pheromones. No alarm cue has been fully identified although two compounds, hypoxanthine 3-*N*-oxide (Brown et al. 2003; Pfeiffer et al. 1985) and the glycosaminoglycan, chondroitin (Mathuru et al. 2012), have both been suggested to have roles in cyprinid fishes. Likely these cues vary by species, are complex, and are comprised of multiple components. There is evidence that they can be released by both the skin and/or intestine (Wisenden 2015). Many alarm cues are not species-specific

and can be learned; perhaps they are mixtures of several types of cue that vary by taxon. Alarm cues have been considered to keep invasive Eurasian ruffe, *Gymnocephalus cernuus*, from entering ballast water (Maniak et al. 2000), and to deter invasive sea lamprey, which seem to release an alarm-type cue when dead (Wagner et al. 2011). The latter use is discussed further because it has recently been field tested for possible application.

**Predator Odors** Many fish species recognize predators using odor (Wisenden 2015). These odors may be found on their skin/fur, or in sweat, saliva, urine, or feces. A taxonomically diverse group of fishes has been documented to respond to fish, bird, reptile, and even mammalian predator odors (Kats and Dill 1998). In some cases, these odors seem to be innately discerned, but their identity is poorly understood. Some suggest polyamines may have a role in sea lamprey (Imre et al. 2014), but their full biochemical identity could be quite complex. Species-specificity also has not been explicitly examined to date but it seems unlikely, and there is evidence these cues can also be learned (Brown 2003). As such, these enigmatic cues may be considered kairomones. Two potential predator cues, human saliva and 2-phenylethylamine (present in mammalian urine; Ferrero et al. 2011), have been seriously considered for use as a repellent to control invasive sea lamprey and are reviewed below.

**Disturbance Cues** Several accounts suggest that some species of teleost fish release cues when stressed and disturbed (Bryer et al. 2001). These probably should be considered kairomones and may be bodily metabolites and likely lack specificity. It is difficult to imagine how they could be used in fish management and they have not been considered so we do not review them further.

### Semiochemicals that Drive and Synchronize Physiology

**Reproductive Priming Pheromones** In addition to using sex pheromones to mediate reproductive behaviors, many fishes appear to use pheromones to synchronize reproductive endocrinology of the sexes so they mature and spawn together. This makes sense in unpredictable temperate waters where reproduction may be difficult to time. In the carps, these products have been clearly elucidated and are mixtures of hormonal products including the maturational hormone, 17 $\alpha$ , 20 $\beta$ -dihydroxy-4-pregene-3-one and derivatives (Stacey 2015). Similarly, compounds released by sexually mature sea lamprey have stimulatory (7 $\alpha$ , 12 $\alpha$ , 24-trihydroxy-5 $\alpha$ -cholan-3-one 24-sulfate, 3kPZS; Chung-Davidson et al. 2013a) or inhibitory (7 $\alpha$ , 12 $\alpha$ -dihydroxy-5 $\alpha$ -cholan-3-one-24-oic acid, 3kACA; Chung-Davidson et al. 2013b) priming functions. In Crucian carp, *Carassius carassius*, alarm cues seem to modify growth rates and types, and they too might be

considered primers, a term that refers to pheromones with largely physiological (vs. behavioral) effects. Priming pheromones could be used to track the presence of fish in waters or perhaps be added to waters to disrupt mating synchrony. Although this use of these semiochemicals does not appear to have been field tested yet, it is potentially difficult to test and apply and is not considered further.

### Overview of Semiochemicals that Are Being Considered and / or Tested for Application

Although types and possible uses of semiochemicals abound, only a few nuisance fish semiochemicals have been identified and synthesized to make application possible. Herein, we discuss these few applications. Applications being considered include monitoring, removal, disruption, and redirection, while focusing on the sea lamprey and the carps because great effort is presently being spent on their control. The sea lamprey model is especially well developed because the sea lamprey causes great and indisputable economic damage in the Laurentian Great Lakes (it preys on valued game fish) and it performs spawning migrations into limited sets of tributaries, making it susceptible to study and control at those locations. It is noteworthy that this ancient jawless vertebrate has a physiology and life history that is fundamentally different from more advanced bony (teleost) fishes. Most applications to date consider pheromones because they are best characterized and tend to be the most specific.

### Using Semiochemicals for Monitoring the Distribution and Abundance of Fish

Sustainable IPM management programs require accurate data on the number of fish, their distribution, and ideally their sex and maturity. Collecting this information is extremely difficult in large and/or flowing water-bodies where trapping, netting, and electrofishing often are of little value because fish move, are not evenly distributed, and often are “trap-shy.” Even a simple presence-absence measure, which is the minimum needed for assessing the distribution limits of invasive species, is often difficult and expensive to obtain by using conventional methods such as netting. Monitoring is especially important at invasion fronts where invaders are present at low densities or may be absent. An example of this need is the sea lamprey whose spawning streams in the Great Lakes are monitored by cumbersome electrofishing for re-invasion after pesticide (lampricide) treatment (Sorensen and Vrieze 2003). Lampricide treatments are expensive and have effects on other organisms (notably some aquatic insects), and must be targeted: the managers need the best possible information on larval lamprey abundance (Sorensen and Bergstedt 2011). Another example are the bigheaded Asian carps which are

presently invading the upper reaches of the Mississippi and Illinois rivers, but whose precise abundance and distribution cannot accurately be determined (Jerde et al. 2011). This information is needed to guide lock and dam operations upstream and to attempt fishing-out and other control in one of the world’s largest rivers. However, monitoring for fish could potentially be performed by measuring the presence of species-specific pheromones or using pheromones to lure fish into traps for counting, or even tracking pheromone-releasing fishes as they locate and swim into groups of conspecifics where they might then be captured and counted. All three possibilities, which employ pheromones, are reviewed below. None has been implemented at the management level, but all are being considered.

### *Measuring Pheromone Concentration as an Index of Population Abundance and Distribution*

The possibility of measuring the presence of invasive fishes using biochemical techniques that assess the presence of species-specific semiochemicals is appealing mainly because it is relatively easy and inexpensive to collect water samples. This approach is similar to that of measuring the DNA (environmental or “eDNA”) that is released by fishes and can now be measured with extreme sensitivity (Eichmiller et al. 2014; Gingera et al. 2016; Jerde et al. 2011). The two techniques could complement each other. Like eDNA, measuring pheromone concentrations could provide valuable information on fish distribution and relative abundance while adding new information on reproductive condition. Further, while DNA can be transported by non-fish vectors (ex. fish-eating birds that can defecate traces of DNA), pheromones are not expected to be transported by non-fish vectors and may be less prone to “false positives”, if most fish release taxon-specific mixtures of hormonal products and only for brief periods associated with spawning as presently appears to be the case (Stacey and Sorensen 2009). However, both the eDNA and pheromone approaches are susceptible to the variable effects of dilution and degradation (“false negatives”). Another complication of using pheromone concentrations to monitor species abundance is that fish pheromones appear to be mixtures of relative common taxon-specific metabolites (Sorensen and Baker 2015; Sorensen and Hoyer 2010), so measurement techniques ideally should examine multiple components in situations where multiple fishes spawn at the same time and degradation is slow. Context also is likely to be important. For instance, different carp species including the goldfish, common carp and the bigheaded carps release slightly different, but overlapping mixtures of hormonal and nonhormonal products as species-specific sex pheromones (Lim and Sorensen 2012; Sorensen unpublished results). As such, when pheromones are measured as an index of the abundance of one of these species, it should be helpful to know which species might be present in

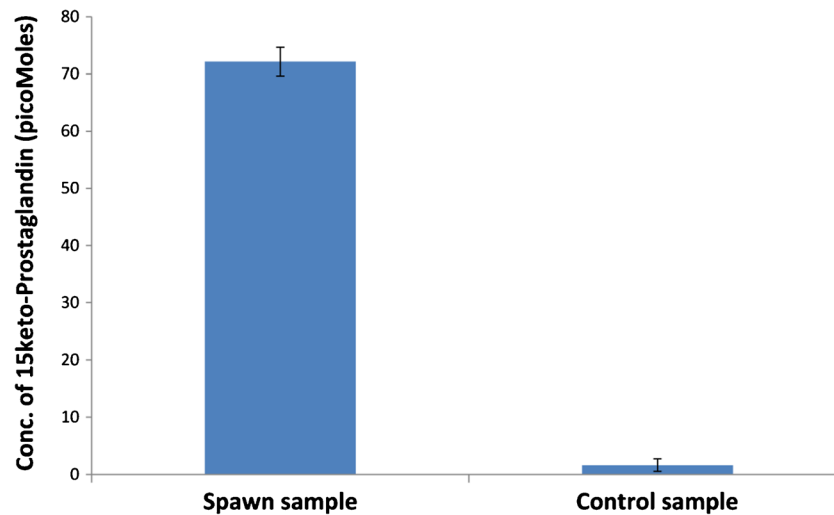
the area (and spawning), and then measure a combination of products relevant to the species of interest. Measuring a few specific component(s) is not difficult with advanced mass spectrometry (Stewart and Sorensen 2015), and this prospect has merit. For example, although petromyzonamine disulfate (PADS) is released by many species of lamprey including the invasive sea lamprey as a migratory (aggregant) pheromone (Sorensen et al. 2005), sea lamprey dominate some Great Lakes tributaries so measuring PADS could nevertheless serve as a quick and meaningful assessment tool that then might be followed up by eDNA or stream assessment surveys. Further, understanding the distribution of PADS may have value as a predictive migratory cue for determining where adult lamprey are likely to migrate, and assist in schemes that add pheromones for trapping (see below). Another example is prostaglandin  $F_{2\alpha}$  ( $PGF_{2\alpha}$ ) and its metabolites that serve as part of a releasing hormonal sex pheromone mixture in many carp species, which spawn as single-species groups and whose spawning females release large quantities of it (Lim and Sorensen 2011, 2012; Stacey 2015). The invasive bigheaded carps appear to use mixtures of F prostaglandins (PGFs) as both hormones and pheromones (Sorensen, unpublished results), which because they spawn mid-river – a location not used by other fish for spawning, could then be measured in ways that help managers track them. Some invasive fishes may also produce novel products such as MHC-derived peptides (Milinski et al. 2005) that could be measured but this is not well understood.

Several techniques are being developed to measure pheromones released by invasive fishes in natural waters and proof-of-concept studies have had some success (Fine and Sorensen 2005). These techniques, which are reviewed in detail by Stewart and Sorensen (2015), and which are continuing to evolve (Fine and Sorensen 2005; Stewart et al. 2011; Xi et al. 2011; Wang et al. 2013), employ liquid chromatography to isolate products from their natural matrix and then use mass spectrometry to identify and quantify them even at low concentrations where measurement can be difficult because of shifting, noisy baselines. For example, tracers including synthesized deuterated compounds, are often added to fish water samples to precisely quantify recovery and measurement (Sorensen and Hoye 2007; Wang et al. 2013). Immunoassay (ex. ELISA) also has been examined as an alternative and has potential because it can be performed quickly and easily (Stewart and Sorensen 2015). Further, passive sampling devices can be placed into water bodies to quickly extract larger quantities of pheromones (Stewart et al. 2011). The sea lamprey sex and migratory (larval) pheromones that already have been detected in natural waters but quantification can be difficult because of varying baselines and extraction efficiencies (Fine and Sorensen 2005;

Wang et al. 2013). Recently, however, we were able to measure and quantify 15keto- prostaglandin  $F_{2\alpha}$ , one of the primary components of the common carp female sex pheromone in lake waters with spawning carp by using tracers (Fig. 1). Further information on individual release rates as well as timing, degradation, and dispersal rates is needed to make these techniques genuinely useful. Advances isolating and quantifying the presence of low levels of compounds in complex matrices will be helpful as would new simpler and more targeted measurement techniques.

**Using Pheromone-Laden Traps to Monitor Fish Abundance** Traps baited with pheromones have proven to be useful in monitoring insect pests at invasion fronts (Witzgall et al. 2010), and some wonder if this approach could be used for invasive fish (Corkum and Belanger 2007; Sorensen 2015a). Utility will depend on the behavior of the species in question (i.e., whether the targeted species is attracted to pheromones, under what conditions, if they will enter traps [many fish will not]) and whether high quantities of pure pheromone are available. Our recent experiences with the common carp have shed some light on this question. Our experiment is described below.

The common carp is highly invasive across much of world (Sorensen and Bajer 2011) and a variety of its hormonally-derived sex pheromones now have been partially identified (Irvine and Sorensen 1993; Stacey 2015). Capturing carp in a quantitative manner by electrofishing is extremely difficult, especially in low density lakes. Pheromonally-mediated trapping for common carp in Midwestern lakes recently was tested and found to have potential (Lim and Sorensen 2012). This proof of concept study assessed attraction using radio-tagged conspecifics as subjects and used prostaglandin  $F_{2\alpha}$  ( $PGF_{2\alpha}$ )-implanted carp as pheromonal bait. Laboratory studies have shown that female common carp continuously release the complete  $PGF_{2\alpha}$ -derived sex pheromone complex that contains unknown polar bodily metabolites, which cannot be synthesized (Lim and Sorensen 2012). This study found that sexually mature male carp, but not females, were attracted to such a trap-based source from up to a distance of 40 m although none entered the traps (Fig. 2). Further, the study demonstrated behavioral activity of  $PGF_{2\alpha}$ -derived sex pheromones (Stacey 2015) in the field and showed that such a scheme, with improvements to trap design, might be used to monitor invasive carp distribution. A version of this monitoring scenario paired with more effective traps also could be deployed for other fishes such as the bigheaded carps, which are presently difficult to locate. A better understanding of whether and how carp orient to pheromone plumes, and how carp respond to traps would be extremely helpful to guide possible improvements. This concept perhaps could be applied to bigheaded carps but almost certainly smaller fish such as the

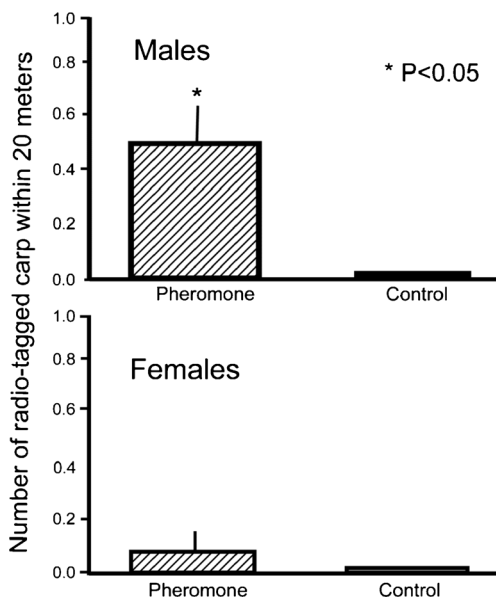


**Fig. 1** The concentration of 15-Keto-Prostaglandin  $F_{2\alpha}$ , a pheromonal component used by mating female common carp, measured in water samples collected within a few meters of a spawning aggregation of common carp in a Minnesota (USA) lake ( $N = 3$ ). Control samples were collected 100 m away from the aggregation. Water samples were collected amongst spawning groups (or not), extracted by C18 columns and then measured using high resolution mass spectrometry and

deuterated standards. Prostaglandin  $F_{2\alpha}$  was not measurable suggesting less was present. Samples were analyzed using Applied Biosystems (Foster City, CA, USA) 4000 QTRAP hybrid, triple-quadrupole, Linear ion trap mass spectrometer. The concentration of 15Keto-Prostaglandin  $F_{2\alpha}$  was determined using a linear standard curve with a range of concentration from 20 to 0.019 ng/5  $\mu$ l. (Ghosal and Sorensen, unpublished results)

round goby in the Great Lakes or the oriental weatherloach, *Misgurnus anguillicaudatus*, in the southern United States or

Australia that might be easier to trap, and the cue could include nonreproductive pheromones.



**Fig. 2** Distance of free-ranging, radio-tagged male and female common carp from female implanted with Prostaglandin  $F_{2\alpha}$  and releasing pheromone placed into a lake trap (from Lim and Sorensen 2012). In this study, male and female carp were radio-tagged just after natural spawning had ended for that year (to ensure maximal responses) and then released into lake into which traps containing carp implanted with Prostaglandin  $F_{2\alpha}$  had been added. The latter treatment is known to reliably trigger natural pheromone release and sexual receptivity. Common carp are trap-shy and did not enter the traps but with improvements in trap design, this technique might allow quantification in low density areas that are difficult to sample otherwise

**Using Pheromone-Laden Judas Fish to Locate Others for Monitoring** Experiences with the common carp demonstrate that behavioral and environmental context are important to pheromone function: female fish releasing pheromones are more attractive than the pheromones themselves. The “Judas fish technique” in which fish are remotely tracked as they locate and are located by conspecifics, which they thus “betray,” takes advantage of this. We and others have employed this technique to find and remove over-wintering aggregations of invasive common carp in lakes (Bajer et al. 2011) but this technique could be improved with other cues including sex pheromones during spring-time mating. The  $PGF_{2\alpha}$ -derived female sex pheromone used by the carps is especially amenable to this application because when carp are implanted with slow-release capsules of  $PGF_{2\alpha}$  they become both sexually active (circulating  $PGF_{2\alpha}$  drives sexual receptivity) and attractive ( $PGF_{2\alpha}$  is metabolized and released as sex pheromone; Lim and Sorensen 2012; Stacey 2015). These Judas carp might even be surgically sterilized. Recent tests of this technique in lakes (Sorensen, unpublished results) show it has promise for locating and counting groups of feeding and sexually-active common carp using eDNA and pheromones. The Judas fish technique also might be deployed with bigheaded carps because they also use PGFs and shoal tightly (Ghosal et al. 2016). An advantage of the technique is that it does not appear to require EPA permits because the pheromone is released by the fish themselves.



## Using Semiochemicals for Mass Removal of Nuisance Fishes

Many fishes use shoaling, migratory, and/or sex pheromones to find each other (Sorensen and Baker 2015; Stacey 2015). These types of pheromones are either species- or taxon-specific and are especially important to both migrating and reproductively-active fishes. While pheromone-mediated mass trapping of insects has shown great promise, results to date for fish have been mixed, with the sea lamprey migratory and sex pheromones receiving the most effort and described below.

### Using Fish Aggregation Pheromones for Mass Trapping

Fish aggregate for reasons that include avoiding predators, enhancing food search, for migratory orientation, and reproduction. These behaviors tend to be mediated by semiochemicals including pheromones. Here, we focus on proposed applications for pheromones not directly associated with reproduction (reproductive pheromones are reviewed below) while recognizing that some of these may nevertheless be closely associated with reproduction in pheromonal complexes (Sorensen and Baker 2015). Although many types of nonreproductive pheromonal aggregants could be used to enhance trapping for removal, none has been identified, and a lack of effective trapping techniques for wild fishes has slowed progress. The only example we know of a nonreproductive semiochemical is the migratory pheromone that prespawning sea lamprey use to find spawning streams.

Several hundred species of fish perform spawning migrations guided by odors that likely include pheromones and other semiochemicals (Sorensen and Baker 2015). For migratory nuisance species, pheromones have great potential for use in targeted trapping programs. Migratory fish exhibit driven behaviors that also make them easier to trap than pelagic species. The sea lamprey migratory pheromone is the only one that is well-understood and also the only one that has been tested. The sea lamprey is an ancient, jawless and parasitic fish that entered the Laurentian Great Lakes during the construction of canal systems and which rapidly destroyed its fisheries (Smith and Tibbles 1980; Sorensen and Bergstedt 2011). This species spends 12 to 18 months in the Great Lakes parasitizing fish before maturing and entering streams to spawn and die. Resulting larvae then may spend many years before metamorphosing and returning to lakes (Applegate 1950). Field and laboratory studies show that stream choice by migratory adult sea lamprey is guided by its odor (Moore and Schleen 1980; Vrieze et al. 2010, 2011), a major component of which is a migratory pheromone released by larval lamprey (Sorensen and Hoye 2007). Other studies show that larval extract can direct sea lamprey migration in small rivers (Fine et al. 2006; Wagner et al. 2006). Both biochemical and physiological studies demonstrated that this larval pheromone is comprised of at

least three steroidal components, petromyzonamine disulfate (PADS), petromyzosterol disulfate (PSDS), and petromyzonol sulfate (PS), and that these compounds elicit behavioral activity equivalent to that elicited by larval odor in the laboratory (Sorensen et al. 2005). Although challenging and expensive, synthesis also has been achieved (Hoye et al. 2007). These are among the most potent odorants identified in fish ( $10^{-13}$  M detection threshold; Sorensen et al. 2005), and they appear to be innately discerned and have additional specialized roles as antimicrobial agents: they can be considered pheromones. Nevertheless, when synthesized and added to free-flowing streams, the three-component pheromone mixture has not been fully attractive, whereas larval odor seemingly was (Meckley et al. 2012). Application of two of these synthesized pheromone components to a river plume emptying into Lake Huron did increase sea lamprey search time in the plume, although it did not increase the probability of sea lamprey entering the river (Meckley et al. 2014). The likely explanation is that the migratory pheromone contains additional unidentified component(s) whose presence is required for full activity. Indeed, laboratory experiments previously had hinted that the pheromone is synergized by unknown natural stream odors (Vrieze and Sorensen 2001) and that there is at least one other pheromonal component (Fine and Sorensen 2008). Additional putative pheromone components recently were identified but their behavioral activity is still unknown (Li et al. 2013a, 2015). The lesson seems to be that complete pheromonal mixtures will be required if they are to be useful in the field where natural cues are present and competing for animals. The search continues for the missing component(s), while some advocate looking for super-active analogues (Burns et al. 2011). Whether artificial analogues might present challenges for EPA registration is not known. The potential is clear, but the road forward is not an easy one.

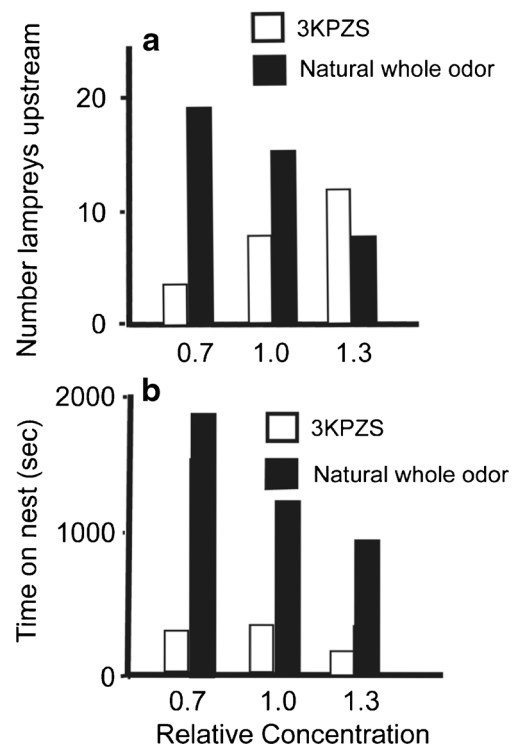
**Using Fish Sex Pheromones for Mass Trapping** Behavioral recognition of sexually mature fish by conspecifics appears to be mediated by sex pheromones in most fish species. These pheromones can serve many functions from short-range recognition of reproductively-active individuals to recognition of status and long-range attraction. While pheromones with the first two functions are likely to be of limited utility (except perhaps with Judas fish), long-range cues are more promising. Two of the latter have been tested and are described below.

The brook trout, *Salvelinus fontinalis*, and lake trout, *S. namaycush*, are char (salmonid) species of conservation concern in eastern regions of North America but are highly invasive in many lakes, including iconic Yellowstone Lake in the western United States. Both species have proven difficult to control with traditional tactics but both can smell bile acids and hormones that appear to function as pheromones (Buchinger et al. 2014, 2015; Essington and Sorensen 1996). To test the possible use of sex pheromones for brook

trout control, Young et al. (2003) conducted an experiment using hoop nets baited with mature male brook trout. Traps baited with males caught more sexually mature brook trout than did controls, suggesting a potential for using pheromones to enhance mass trapping of this species. No studies of lake trout have yet been conducted. Studies of char pheromone identity combined with synthesis and more extensive field tests now are needed to determine their full potential for control.

The sea lamprey presently provides the best example of how sex pheromones might be used in natural settings for mass trapping (Li et al. 2007; Twohey et al. 2003; Wagner et al. 2005). After finding a stream using larval pheromones and migrating upstream, adult sea lamprey mature, then males build nests and release a sex pheromone that is attractive to females. Initial stream-side maze and laboratory bioassays and electrophysiological recordings strongly suggested that 3-keto petromyzonal sulfate (3kPZS) and 3-keto-allocholic acid (3kACA) were key components of the pheromone released by spermiating males (Brant et al. 2013; Li et al. 2002; Siefkes et al. 2003; Yun et al. 2003). However, subsequent tests in the field found that while 3kPZS is a powerful attractant (Siefkes et al. 2005), neither it alone, nor in combination with 3kACA attracts ovulated females as effectively as the natural odor of spermiating males (Fig. 3; Johnson et al. 2009, 2012; Luehring et al. 2011). The missing component(s) likely arrest upstream movement of sea lamprey and/or increase search activity, increasing the probability of a sea lamprey entering and being retained in a trap (Johnson et al. 2015b). More recently, natural instream bioassays were used to characterize another bile acid 3,12-diketo-4,6-petromyzonene-24-sulfate (DKPES). When DKPES is mixed with 3kPZS, the number of females approaching the source increased, but the mixture of 3kPZS and DKPES was still less attractive than the full male odor (Li et al. 2013b). Research to identify the complete pheromone mixture continues by using in-stream bioassays.

While the sea lamprey sex pheromone contains additional components not predicted from initial laboratory studies, management tactics using 3kPZS alone are ongoing because the compound is available and is the first vertebrate pheromone registered as a biopesticide anywhere. A series of tests recently was conducted for management scenarios across the Great Lakes Basin. Specifically, 3kPZS was applied at existing sea lamprey traps to reach a final in-stream concentration of  $10^{-12}$  M in 18 streams over three years, and catch rates were compared between paired 3kPZS-baited and unbaited traps and with historic trap efficiency data. 3kPZS-baited traps captured more sexually immature and mature sea lamprey than did unbaited traps (Johnson et al. 2013). While overall trapping efficiency increased by 20 % to 30 % on wide streams (30 m + wide) where 3kPZS application rate was high (10 mg/h), 3kPZS application did not increase trapping efficiency on



**Fig. 3** The response of ovulated female sea lamprey to a synthesized component of the male sex pheromone, 3kPZS, and the odor of spermiating males (entire pheromone). The odors were tested in competition with each other in a natural stream while varying the relative concentration of 3kPZS (a value of 1.0 denotes that each cue was at the same overall concentration with respect to the other). Panel A shows that 3kPZS is almost as attractive as the natural pheromone at stimulating upstream movement toward a baited river channel over long distances (~45 m). By contrast, Panel B shows that while 3kPZS can lure females into baited channels similar to that of natural male odor, 3kPZS is much less able to hold females at the application location for long periods of time. These experiments were conducted in a natural stream using ovulated female sea lamprey fitted with tracking devices. Pheromone mixtures were pumped onto nest sites. Data were redrawn from Johnson et al. (2009) using additional data from Johnson et al. (2012). Taken from Sorensen (2015a)

narrow streams that had 3kPZS application rates lower in absolute quantity, although similar on a relative scale (~1 mg/h; Johnson et al. 2015a). These results raise the question whether the greater observed response to 3kPZS in wide streams is because these streams provided a greater void in attractant on the side away from the trap and further downstream (allowing sea lamprey to better exhibit search behavior and distinguish among activated versus regular stream water) or because of differences in behavior near the trap. Interestingly, insect pheromone application rates always have been standardized by the amount at the application location (number of drops or grams of active ingredient) because activating an unconstrained medium to a specific concentration is not possible (i.e., the atmosphere is unbounded; El-Sayed et al. 2009). Presumably, lakes and oceans may be similar to the atmosphere and are unbounded and dynamic. However, in rivers,

where water is bounded by a relatively small river channel and the flow is generally unidirectional, the entire medium can be consistently activated to a specific concentration over long distances. Because this was the first time a pheromone was tested to control an invasive fish, it was the first time the question of how to standardize pheromone application among differing sized rivers was encountered, so more research is needed to understand how best to standardize pheromone application rates. Although increases in catch rates associated with this one component have been relatively low compared to those increases observed in insect pheromone traps (El-Sayed et al. 2009; Mitchell et al. 1976), these tests demonstrated the potential of the sea lamprey sex pheromone to increase trap catch in lamprey management contexts. Additional research is required to understand how and why effectiveness varies among streams and thus optimize both the 3kPZS application rate and where 3kPZS trapping might be used most effectively. Work also continues to identify the entire sex pheromone. A lesson is that despite the great potential for pheromones to be used in nuisance and invasive fish control, these signals are more complex than most would have imagined, and they must be fully elucidated using field assays before application can be seriously considered at a management level.

### Using Semiochemicals to Disrupt Mating

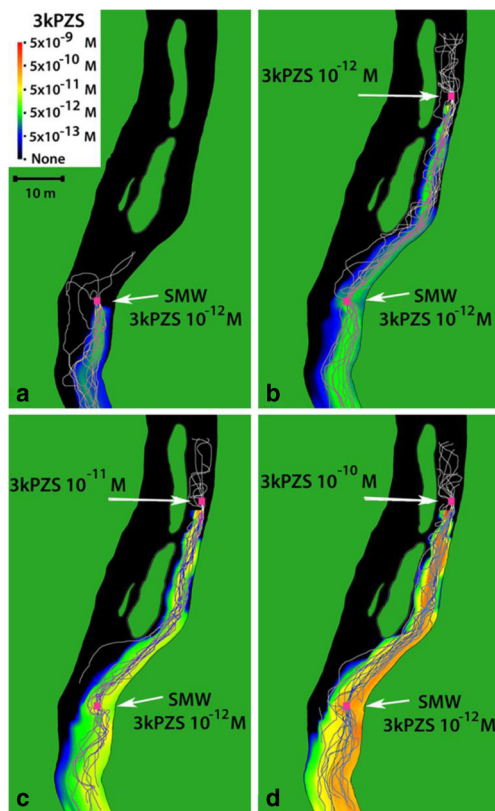
Social odors play key roles mediating reproduction in many fishes so it follows that they could be used to disrupt mating and reproductive success. Pheromones are commonly employed to severely disrupt mating in insects such as the cotton boll weevil, *Anthonomus grandis*, that employ precise pheromonal blends (i.e., highly precise mixtures) using a scheme known as pheromonal disruption in which vast quantities of artificial pheromones are released among mating insects to alter their blends (Witzgall et al. 2010). Although the precise mechanism by which this strategy works is unclear, it is possible that by adding large quantities of pheromone to the environment, managers create a great deal of odorous noise that both overwhelms and/or distorts the functioning of insect sensory systems. One advantage of this strategy is that it does not require intimate knowledge of a species' sex pheromone systems as only specific components need be added. Notably, most insects employ highly specific blends of volatile hydrocarbons as pheromones whose ratios drive different behaviors, so if these are altered by just a few percent (Vickers et al. 1991), they disrupt behavior (Sorensen et al. 1998). Although it is not yet clear how fish pheromone mixtures work, many appear to work differently from the blends used by insects. For example, the ratio of PGFs present in the common carp sex pheromone system seems unimportant, while overall composition is key (Lim and Sorensen 2011). Specific ratios of bile sterols also appear to be relatively

unimportant in the sea lamprey migratory pheromone (Fine and Sorensen 2008); however, recent work on bigheaded carps suggests that these species may be different and use pheromonal blends opening up the possibility of pheromonally-mediate spawning disruption in this genus (Sorensen, unpublished results).

Regardless, mating disruption using synthesized pheromones, and pheromone antagonists may have promise in nuisance fish control. For example, if pheromone components can be synthesized at low cost, mating disruption may be particularly useful in riverine systems because it would be fairly simple to activate the entire discharge of a river to overwhelm natural sources of pheromones. A field test of mating disruption in sea lamprey showed that application of 3kPZS upstream at 100 times the concentration of a natural male pheromone source located downstream ( $10^{-10}$  M vs.  $10^{-12}$  M; Fig. 4) disrupted near- and far-source effects of the natural male pheromone blend released by the lamprey themselves (Johnson et al. 2009). An alternative approach to mating disruption in fishes is to develop pheromone antagonists that prevent the target species from detecting the pheromone component. This work is underway in sea lamprey and seems promising, but field results are not yet published. Pheromone antagonists may be especially useful for sea lamprey control because previous studies show that naris-occluded (i.e., their olfactory organ is blocked and unavailable to sample the environment) sea lamprey generally do not locate spawning streams (Vrieze et al. 2010) or mates when released in streams (Johnson et al. 2006). It also is conceivable that priming pheromones might be added in skewed ratios and quantities to disrupt sexual maturation in both teleost fish, including carps that use multiple sex steroid components to facilitate maturation (Stacey 2015) and sea lamprey. This scheme is particularly appealing for invasive carps in North America, which like many invasive fishes, have no close relatives nearby that could be inadvertently influenced by this activity. In addition to disrupting pheromonal communication, other semiochemicals such as alarm cues might be employed to disrupt spawning. Great potential exists, but questions about signal specificity, the role of mixtures (which likely vary with species), inexpensive synthesis pathways, and regulatory approval will have to be addressed.

### Using Semiochemicals to Redirect the Movements of Migratory Invasive Fishes

Over a thousand species of fish migrate (i.e., perform highly directed movements) from one place or another at one point in their lives, and most appear to use innately discerned odorous cues to guide them (McDowall 1988; Sorensen and Baker 2015). Some of these movements are fixed but others are flexible, and not all of the population necessarily moves every year, depending on environmental cues (Chapman et al.



**Fig. 4** A field test of mating disruption in sea lamprey using a synthesized pheromone (3kPZS) in small Michigan stream. The figures show ovulated female sea lamprey movement tracks (lines) when only spermated male washings (SMW, natural pheromone source) was applied to achieve a natural 3kPZS concentration of  $10^{-12}$  M (a) and when synthesized 3kPZS was applied 40 m upstream of the natural male source at  $10^{-12}$  M (b),  $10^{-11}$  M (c), and  $10^{-10}$  M (d) to overwhelm the natural pheromone source. Color scale illustrates estimated 3kPZS molar concentrations from both sources of 3kPZS throughout the stream when fully mixed with the stream discharge. Taken from Johnson et al. (2009) with permission

2012), a process known as partial migration. Although sometimes less directed, these partial migrations can still be aggressive and important to range expansion as well as invasiveness (ex. bigheaded carps). Odors mediating migration can be placed into two groups, those that rely on innately recognized cues such as pheromones, and those that are learned and can include various types of semiochemicals (ex. imprinting odors that may include body odors of conspecifics and should be considered kairomones). Attractive semiochemicals could be used to redirect fish movements to places where these fish cause little harm or can be easily controlled. Additionally, many fishes also employ aversive damage-released alarm cues and predator cues (Imre et al. 2014; Wagner et al. 2011; Wisenden 2015) that could be used in combination with attractive odors in what is known as a “push-pull” strategy (Cook et al. 2007). Redirection could be over short (i.e., within a stream or lake) or long distances (i.e., between tributaries). Although these strategies could be employed on many

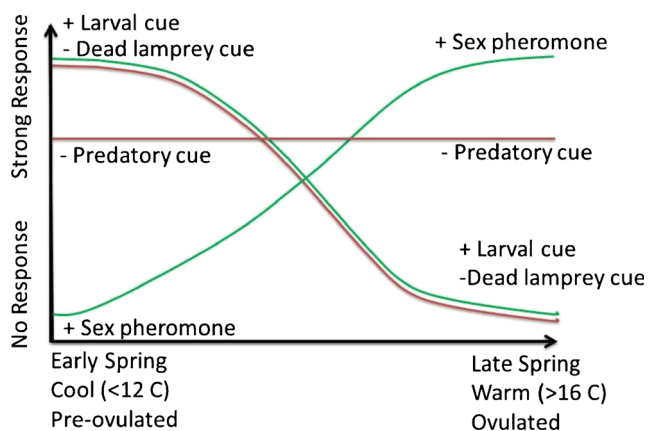
migratory nuisance species, they only have been seriously considered for the sea lamprey, which we review below.

**Short-Range Re-Direction** The possibility of redirecting the movement of adult migratory sea lamprey on a short-range (i.e., within stream) scale has been explored with modest, but intriguing, success. This possibility is especially appealing because sea lamprey control already deploys stream traps. Further, many sea lamprey-producing streams in the Great Lakes Basin are dendritic, meaning that blocking sea lamprey from entering small tributaries of the mainstream could be simple, inexpensive, and make subsequent pesticide application easier. Finally, a range of cues is already available in some form. Both migratory and sex pheromones have been partially identified and synthesized, and alarm cues can be collected from dead sea lamprey (Wagner et al. 2011). Additionally, a potential predatory odor comprised of polyamines is commercially available (Imre et al. 2014).

Integration of multiple semiochemicals that induce opposing responses (attract and repel) may be especially effective for redirecting migration following the push-pull approach (Fig. 5). As described above, initial experiments using a crude (whole) extract migratory pheromone found that upstream migrating sea lamprey could be attracted to one side of a stream, but that responses to point sources of larval odor were not robust when completing sources of larval odor were present (Wagner et al. 2009). Increasing the application of larval odor to 10-fold above the concentration of the background odor only resulted in 13 % of sea lamprey redirecting their movement to that side of the stream (Wagner et al. 2009). Although this result is not surprising, because the migratory pheromone system presumably is used to facilitate stream localization from the ocean on a large-scale with little background odor, it is a serious issue for applications within individual streams which may contain populations of native lamprey species that release the same larval odor (Fine et al. 2004). To overcome these problems, applications of larval odor within streams could conceivably be paired with applications of alarm and/or predator cues. Adult sea lamprey might be drawn to trapping sites or streams that lack spawning habitat. This possibility has yet to be explored for the migratory pheromone but has been examined for the sea lamprey sex pheromone and is described below.

Sex pheromones also have been examined as short-range re-directing agents for sea lamprey in streams. This is an important possibility because as female sea lamprey mature, responses to larval cues and damage-released alarm cues appear to diminish while responses to sex pheromone increase (Bals and Wagner 2012; Bjerselius et al. 2000; Brant et al. 2015; Fig. 5). Mature male sea lamprey do not seem to stop responding to alarm cue, and it is not clear whether sexually mature sea lamprey also stop responding to predator cue. In any case, larval cues and alarm cues are likely less useful for





**Fig. 5** Female sea lamprey are attracted to cues released by larval lampreys (+Larval cue; Bjerselius et al. 2000) and repelled by damage released alarm cues (– dead lamprey cue; Bals and Wagner 2012) early during the spring migration when water temperatures are cool and they are pre-ovulated. As the spring progresses and water temperatures warm, females become ovulated and no longer respond to larval (Brant et al. 2015) and alarm cues (Bals and Wagner 2012). Instead, ovulated females are attracted toward sex pheromone released by spermated males (Brant et al. 2015; Johnson et al. 2009; Li et al. 2002). Pre-ovulatory females are repelled by predatory cues (Imre et al. 2014), but it is not known if aversion to predatory cues are maintained through ovulation. In this figure, we speculate that responses to predator cues are maintained through ovulation because avoiding predators while spawning would yield fitness benefits. Taken together, early in the spring, push-pull approaches using alarm (–), predator (–), and larval (+) cues may be effective, but generally become less potent as the spring progresses. Late in the spring, push-pull approaches using predator (–) cues and sex pheromone (+) may be effective

control when sea lamprey are spawning. Further, as mentioned above, initial studies using the pheromone component 3kPZS alone showed only modest increases in trap catch (0–30 %; Johnson et al. 2013, 2015a, 2015b). As a means to increase trap catch further, application of the sea lamprey sex pheromone might be paired with alarm and predator cues in push-pull scenarios. A recent study by Hume et al. (2015) showed that when an extract of the alarm cue was added to the side of the river opposite of a trap, the extract caused sea lamprey to move to the other side of the river and encounter the trap sooner than when not present. However, the simultaneous addition of 3kPZS to the trap did not enhance attraction and neither treatment had any effect on trap capture rates. This may have been because nominal capture rates already were low but this must be tested. Taken together, the integration of larval cues, sex pheromones, alarm cues, and predator cues in push-pull configurations seems to offer strong promise, but this field is still in its infancy and new research on cue identity, function and application (and whether it might be considered a pheromone) is urgently needed.

**Long-Distance Re-Direction** Presumably, the primary function of the sea lamprey migratory pheromone is to guide sea lamprey into suitable spawning streams from the open ocean

and lakes. Because various species of larval lamprey share the same spawning and nursery habitats, they seem to use the same cues including the migratory pheromone (Buchinger et al. 2013; Fine et al. 2004). This creates not only challenges (as noted above) for the use of a synthesized cue, because it must compete with this background, but also opportunity, because native (desirable) lamprey species naturally produce it. Hypothetically, larval native species of lamprey could be stocked and managed above extant lamprey barriers and dams (which sea lamprey migrating from the lakes cannot reach) in Great Lakes streams. In this case, the odor of native lampreys should attract long-distance migrating adult sea lamprey and where adult sea lamprey could then either be captured, or in those downstream locations lacking spawning habitat, fail to reproduce (Sorensen and Vrieze 2003). This could be both simple and inexpensive, and does not require special permitting. Analyses of extant adult sea lamprey capture records at dozens of trap locations and barrier sites, and their relationship to larval densities located upstream, suggest that adult sea lamprey are already selecting certain streams in the Great Lakes as a result of control efforts that remove larval lamprey and thus the pheromone (Sorensen and Vrieze 2003). This scenario might be actively managed to address this phenomenon and perhaps to help restore native lampreys in the upper reaches of watersheds.

### Lessons that Studies of Nuisance Fish Semiochemicals May Have for Valued Fish

Most fishes that have become a nuisance or invasive, do so because of ecological factors (degraded or simplified habitat, lack of predators, etc.) that promote their abundance, not because they are atypical of fish. This is highlighted by the fact while many of these fishes are invasive in their new habitats, they often are endangered in their native systems. For example, the sea lamprey now is threatened or endangered in much of Europe, as is the wild common carp (Vilizzi 2012). Most cyprinid minnows appear to use hormonal pheromones and their complexes much like common carp do (Stacey 2015), while native lampreys appear to use biliary steroids in manners similar to the sea lamprey. Notably, much of the work on common carp is based on earlier work on its close relative, the goldfish, *Carassius auratus*, which also can be invasive in some locations (Stacey and Sorensen 2009; Stacey 2015). While little work has as yet been performed to extend findings on the molecular biology, physiology, behavior, and chemical ecology of the semiochemicals used by nuisance species to their close and valued relatives, it would be reasonable to focus on these approaches to gain insight into the basic science of chemical ecology, and hence its application.

Fish semiochemicals and pheromones may be used in controlling pest species, but also may be useful in restoring valued fish species (Sorensen 2015a). For example, semiochemicals are used by native lamprey species whose populations are threatened in the North American Pacific Northwest and much of Europe (Sorensen et al. 2005). The Pacific lamprey, *Lampertra tridentata*, a culturally valued fish species (Close et al. 2002), has been extirpated from some of its historical range in the Columbian River Basin due to dam construction. Here, larval cues could be used to direct lampreys to fish ladders or to tributaries with no dams (Yun et al. 2011). Sex pheromones also could be used to direct mature Pacific lampreys to highly productive spawning riffles and to synchronize spawning activity. European eels, *Anguilla anguilla*, also might be guided around dam using migratory pheromones (Briand et al. 2002). Predatory odors have already been proposed to aid in the stocking of native Pacific salmon by exposing young fish in hatcheries to predators and their associated stimuli (odors) before releasing them so that these stocked fish respond to predators later as adults (Berejikian et al. 1999). Further, various products including semiochemicals also are now being proposed for use in embryonic imprinting programs for hatchery-raised salmon (Dittman et al. 2015). Finally, endangered cypriniform minnows appears to use hormonal pheromones that are similar to those of the carps (Stacey 2015), and pheromones might be considered for use in their possible restoration.

Pheromones also may be used in fish propagation in aquaculture to synchronize spawning of broodstock and increase milt quality and quantity (Hubbard 2015). Many economically valuable salmonid species are cultured for fish restoration or for human consumption. Studies show that Atlantic salmon (*Salmo salar*) (Waring et al. 1996), brown trout (Olsen et al. 2001), and rainbow trout (*Oncorhynchus mykiss*) (Vermeirssen et al. 1997) release priming pheromones that synchronize spawning and increase milt production in males. These pheromones likely resemble some of those used by invasive lake trout (especially the nonreproductive signals; Stacey 2015). If identified, priming pheromones may be a cost-effective, natural method of synchronizing spawning and improving milt production and quality without handling or transferring fish. Pheromones influence major life history events in fishes and may become useful additions to the tool box of fisheries. The possible uses of pheromones to achieve management goals are as diverse as the goals themselves. More research also must be focused on fish pheromones to advance the use of this potentially potent and environmentally benign method of managing wild and captive fisheries.

## Summary and Future Directions

Semiochemicals, and pheromones in particular, appear to have considerable, largely unrealized potential for use in invasive and pest fish control. Although the field is young and the science is very challenging, many options exist for using semiochemicals. The need is great as the number of nuisance species increases, and few new tools emerge for working in large bodies of public water. Use of pheromones for monitoring, trapping, disruption, and redirection as part of IPM schemes appears promising as they are environmentally safe and can be species- and location-specific. Monitoring identified pheromonal components using mass spectrometry could provide new, valuable information to compliment eDNA monitoring. Likewise, application of pheromonally-enhanced sterilized Judas fish can precede using existing information for the carps. Pheromone-assisted trapping, especially using push-pull schemes, seem promising for the migratory and well-studied sea lamprey. Certain types of diversion schemes that use natural sources of semiochemicals also could proceed using natural cues released by stocked fish to complement nascent IPM schemes. Ultimately, however, as with insects, synthesized complete pheromones will be needed for control. While addition of synthesized pheromone may present regulatory complications, only synthesized odorants can presently be produced in quantities practical for large-scale use while being fully quantifiable. This represents a considerable challenge because laboratory and field studies conducted to date suggest that fish pheromones are complex multi-component mixtures (Sorensen and Baker 2015). Identification and eventual production of these multi-component signals, which must be extracted from waters, will be more difficult than for many insect semiochemicals that can be isolated from glands (Fine and Sorensen 2008). However, the effort seems worthwhile given the progress we have made in identifying many of these pheromones' key components, the inspiring example of how research on insects has eventually proven fruitful, and the almost complete lack of tools to control invasive fishes. Basic questions of pheromone identity, chemistry, and function need to be addressed. Further, field tests show that for pheromones to be useful, large quantities of them must be available at reasonable cost and high quality because they must compete with natural cues in open waters. Detailed bioassay-guided fractionation in field settings are needed. One interim solution may be to develop analogues (i.e., simpler versions of pheromone structures that could be easily and inexpensively synthesized) which might then be deployed in lieu of natural cues but in greater quantities (Burns et al. 2011). Another possibility is to explore using natural cues either isolated en masse from the fish themselves or as stimulated by implants containing pheromone

precursors (ex. F prostaglandin-implanted carp). Identifying and applying semiochemicals from different taxa of fish present different challenges and will have different solutions. Likely more and better options will become apparent as this young and exciting field matures.

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