Received: 20 October 2020 | Accepted: 5 January 2021
DOI: 10.1111/jfb.14667

REVIEW PAPER

JOURNAL OF FISH BIOLOGY fsbi

Physiology, endocrinology and chemical communication in aggressive behaviour of fishes

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Funding information
FDCT

Abstract

Fishes show remarkably diverse aggressive behaviour. Aggression is expressed to secure resources; adjusting aggression levels according to context is key to avoid negative consequences for fitness and survival. Nonetheless, despite its importance, the physiological basis of aggression in fishes is still poorly understood. Several reports suggest hormonal modulation of aggression, particularly by androgens, but contradictory studies have been published. Studies exploring the role of chemical communication in aggressive behaviour are also scant, and the pheromones involved remain to be unequivocally characterized. This is surprising as chemical communication is the most ancient form of information exchange and plays a variety of other roles in fishes. Furthermore, the study of chemical communication and aggression is relevant at the evolutionary, ecological and economic levels. A few pioneering studies support the hypothesis that aggressive behaviour, at least in some teleosts, is modulated by "dominance pheromones" that reflect the social status of the sender, but there is little information on the identity of the compounds involved. This review aims to provide a global view of aggressive behaviour in fishes and its underlying physiological mechanisms including the involvement of chemical communication, and discusses the potential use of dominance pheromones to improve fish welfare. Methodological considerations and future research directions are also outlined.

KEYWORDS
aggression, communication, dominance, endocrinology, pheromones, physiology

1 | AGGRESSIVE BEHAVIOUR IN FISHES

Aggression is a widespread social feature which can be defined as any behaviour associated with threats, attacks and/or defensive strategies among individuals or groups (Nelson, 2005; Siegel *et al*., 2009). Most, if not all, vertebrates express some type of aggressive behaviour, and fishes are no exception (Frommen, 2020; Magnhagen *et al*., 2008). Having radiated to virtually all aquatic habitats, fishes show remarkably diverse aggressive displays, paralleling their wide variety of social systems and modes of reproduction (Magnhagen *et al*., 2008). Nonetheless, despite its importance, the physiological basis of aggression has been poorly studied. Although most studies of aggression assume vision as the sensory channel through which opponents assess each other, recent studies have highlighted the importance of chemical communication in the establishment of dominance hierarchies in fishes (Barata *et al*., 2007; Gonçalves-de-Freitas *et al*., 2008; Keller-Costa *et al*., 2016). This review provides an overview of aggression in fishes. It explores the role of chemical communication in such behaviour, how the identification of potential dominance pheromones – chemical cues released to inform conspecifics of the high social rank of the emitter – can be relevant to fish welfare and some methodological considerations and future directions to improve studies in this field.

1.1 | Characteristics of aggressive behaviour

Aggressive behaviour is expressed to secure resources such as food, territories and/or mates (Hardy & Briffa, 2013; Magnhagen *et al*., 2008). Therefore, aggression is higher during periods of social instability or when resources become scarce (Almeida *et al*., 2014b; Grossman, 1980). For example, aggression of in-group-living species is higher during the initial phase of group formation, tending to decrease as social hierarchies stabilize (Collias, 1944). Aggression can have negative consequences, being energetically costly and potentially injurious (Haller, 1995). Dominant individuals, *i.e*., those winning more aggressive encounters against conspecifics (Oliveira *et al*., 2011), have an advantage in accessing resources, whereas subordinates have more limited access to food, territory and/or mates (Bruce & White, 1995; Koebele, 1985). Thus, aggression is intrinsically associated with life-history traits such as growth and reproduction, thereby having a direct bearing on fitness (Bruce & White, 1995; Hofmann & Fernald, 2000; Koebele, 1985; Nicieza & Metcalfe, 1999; Smith & Blumstein, 2008). Therefore, answering the question "*can we predict which individual will win an aggressive encounter?*" is relevant both at a proximate (function, mechanism) and ultimate (evolutionary) level, as it would give insights about the evolution of this conserved behaviour and a better understanding of its underlying mechanisms. The answer to this question was conceptualized by Parker (1974) under the term "Resource Holding Potential" (RHP), *i.e*., the capacity of an animal to win a dyadic encounter if one were to take place (Parker, 1974). In fishes, RHP depends on a number of variables, body size in particular, with larger animals usually being stronger and able to inflict greater damage upon their rivals (Barlow *et al*., 1986; Huntingford *et al*., 2001). Nonetheless, in one cichlid species at least, relative gonadal weight is a stronger predictor of victory than body size (Neat *et al*., 1998). It was proposed that males with larger gonads fight harder to defend their territory, possibly because the value of a territory correlates with the gonad maturity state of the individual (Neat *et al*., 1998). Evidence has also been accumulating that the outcomes of previous aggressive encounters affect RHP and thus those of subsequent interactions. The so-called "winner-loser" effect reflects the tendency of a winner or a loser, respectively, to remain so in future aggressive challenges (Hsu *et al*., 2006; Hsu & Wolf, 1999). This has now been described in several fishes, such as the three-spined sticklebacks (*Gasterosteus aculeatus*) (Bakker *et al*., 1989), mangrove killifish (*Kryptolebias marmoratus*) (Hsu *et al*., 2014), pumpkin seed sunfish (*Lepomis gibbosus*) (Chase *et al*., 1994), blue gourami (*Trichogaster trichopterus*) (Frey & Miller, 1972), paradise fish (*Macropodus opercularis*) (Francis, 1983), Siamese fighting fish (*Betta splendens*) (Wallen & Wojciechowski-Metzlar, 1985) and Mozambique tilapia (*Oreochromis mossambicus*) (Oliveira *et al*., 2009). It has been proposed that individuals that experience these effects could assess their fighting ability and consequently their fighting costs in subsequent contests (Hsu & Wolf, 1999). Others have proposed that prior winning or losing experience can affect an individual's fighting performance (Beacham, 1988), possibly mediated by androgens (Oliveira *et al*., 2009). Nonetheless, a correlation between androgen levels and aggression has not always been found (Almeida *et al*., 2014a; Smith, 1970; Weiss & Coughlin, 1979). Furthermore, in social species, dyadic aggressive interactions often occur in the presence of other conspecifics (Bertucci *et al*., 2014). During fights, non-participants can "eavesdrop" on contestants, extracting information about their intention and RHP to their advantage (Hsu *et al*., 2006). For example, zebrafish (*Danio rerio*) are more attentive towards interacting (fighting context) than towards non-interacting pairs of conspecifics (Abril-de-Abreu *et al*., 2015). Conversely, contestants can also adjust their aggressive behaviour according to the nature of the audience (Peake & McGregor, 2004). For instance, male *B. splendens* increase biting frequency in the presence of a male audience, but when females are present, they increase their tail beats and decrease bites (Doutrelant *et al*., 2001; Matos & McGregor, 2002).

1.2 | Endocrine modulation of fish aggression

The review of the role of hormones in chemical communication and aggression is important, since these compounds and their metabolites have been found to also act as potential pheromones, at least in fishes (see Section 2.1).

The organization of the neuroendocrine system in teleosts is similar to that in other vertebrates; the hypothalamus controls the activity of the anterior pituitary gland which, in turn, controls the function of several peripheral endocrine glands (Oliveira & Gonçalves, 2008). In fishes, as in other vertebrates, the pituitary gland is composed of two tissue types: the adenohypophysis and the neurohypophysis (Oliveira & Gonçalves, 2008). The adenohypophysis is the site of synthesis, storage and release into the blood stream of several hormones and is under the direct control of releasing factors produced by hypothalamic neurons and through feedback of peripheral hormones (Oliveira & Gonçalves, 2008). The neurohypophysis is an aggregate of axons with their endings storing and releasing neuropeptides synthesized in their hypothalamic cell bodies (Ball & Baker, 1969). The hypothalamic–hypophysial portal vascular system that transmits the releasing factors from the hypothalamus to the pituitary is present in higher vertebrates but considered to be generally absent in teleosts as, in this taxon, the adenohypophysis receives direct innervation from the hypothalamus (Peter *et al*., 1990). Nonetheless, a portal system or vascular contribution has been suggested (Baskaran & Sathyanesan, 1992).

Because aggression usually differs between the sexes and is generally higher in males (Huntingford & Turner, 1987), hormones of the

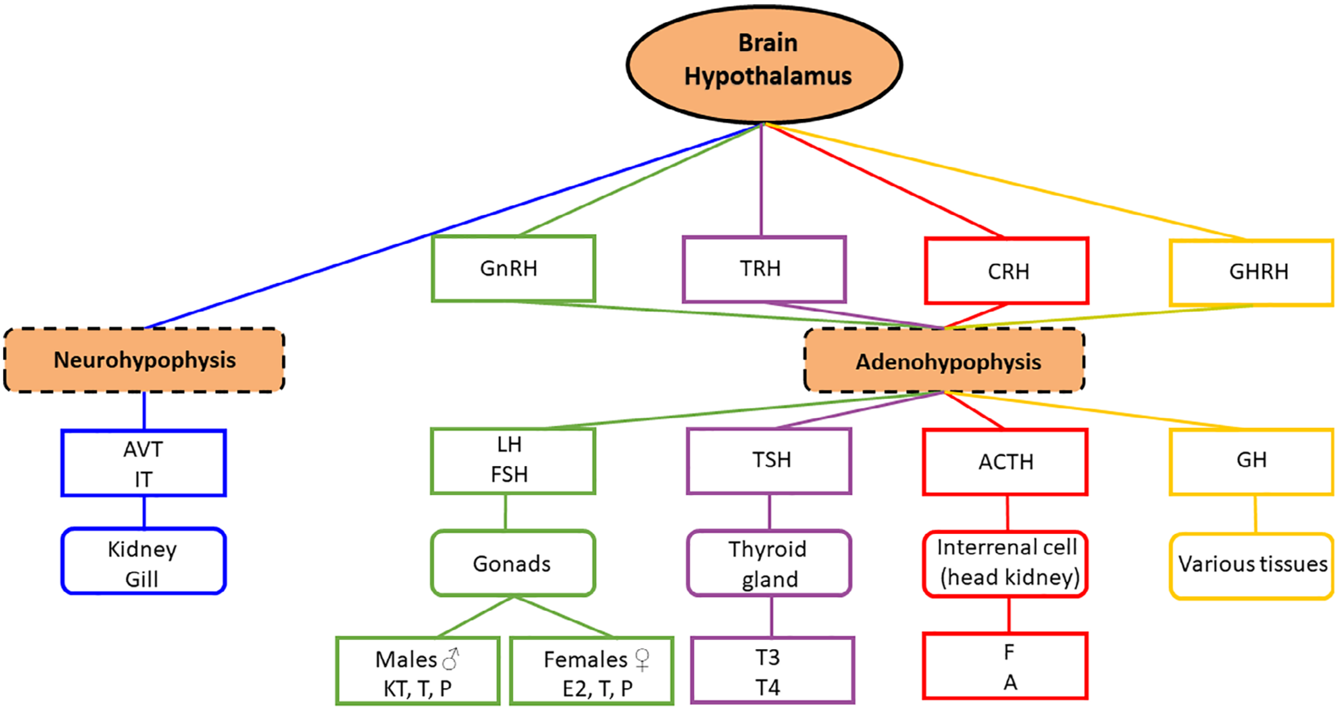

FIGURE 1 Schematic representation of the hierarchical organization of the neuroendocrine system in teleost fishes with major hypothalamic-hypophysial axis for the control of peripheral glands and tissues (each colour represents a different set of hormones related to hypothalamic–hypophysial–peripheral gland/tissues stimulation). GnRH: gonadotropin-releasing hormone; TRH: thyrotropin releasing hormone; CRH: corticotropin releasing hormone; GHRH: growth hormone-releasing hormone; LH: luteinizing hormone; FSH: follicle stimulating hormone; TSH: thyroid stimulating hormone; ACTH: adrenocorticotropic hormone; F: cortisol; A: adrenaline; GH: growth hormone; AVT: arginine–vasotocin; IT: isotocin; KT: 11-ketotestosterone; T: testosterone; P: 17,20β-dihydroxypregn-4-en-3-one; E2: 17β-estradiol; T3: triiodothyronine; T4: thyroxine. Adapted from Oliveira and Gonçalves (2008)

hypothalamus–pituitary–gonadal (HPG) axis, androgens in particular (Figure 1), have been suggested as modulators of aggression (Villars, 1983). The primary roles of androgens in male fishes are the stimulation of testes growth and maturation, the development of secondary sexual characteristics and the expression of reproductive behaviour (Borg, 1994; Patrão *et al*., 2009). Furthermore, administration of 11-ketotestosterone (11KT), the most potent androgen in fishes, can promote aggressive behaviour (Ogino *et al*., 2016). Elevated circulating 11KT levels may also reflect aggressive encounters. For example, several cichlids (*Neolamprologus pulcher*, *Lamprologus callipterus*, *Tropheus moorii*, *Pseudosimochromis curvifrons* and *O. mossambicus*) subjected to a simulated territorial intruder protocol had elevated levels of circulating 11KT and aggressively defended their territory against an intruder (Desjardins *et al*., 2005; Hirschenhauser *et al*., 2004). High levels of androgens are thought to adjust aggressive motivation in response to an agonistic social challenge, as formulated in the "challenge hypothesis" (Antunes & Oliveira, 2009; Oliveira *et al*., 2001; Wingfield *et al*., 1990). This, in turn, further increases aggression and the likelihood of winning; this could be why winners keep winning (Fernald, 1976; Oliveira *et al*., 2009). Territorial aggression may also be regulated by androgens, and aggression itself can modulate androgen levels (Desjardins *et al*., 2005). Nonetheless, high androgen levels can have long-term negative physiological consequences, such as immunosuppression (Gubbels & Jorgensen, 2018). Furthermore, cortisol and *gonadotropin-releasing hormone 1* mRNA levels (*gnrh1*) are increased after dominant status suppression (after 24 h), suggesting that individuals mount a neural defence against loss of status (Parikh *et al*., 2006). Nevertheless, alternatives to androgens as the key modulators of aggressive motivation have emerged (Oliveira *et al*., 2002; Villars, 1983). For example, castration (which dramatically reduces circulating androgen levels) fails to reduce aggression in *B. splendens* (Weiss & Coughlin, 1979), *O. mossambicus* (Almeida *et al*., 2014a) and *L. gibbosus* (Smith, 1970). This suggests that, at least in some species, androgens are not necessary to maintain high aggression.

Hormones of the hypothalamus–pituitary–interrenal (HPI) axis have also been implicated in modulation of aggression. Corticotrophin releasing factor (Crf) stimulates the release of adrenocorticotropic hormone (Acth) from the anterior pituitary gland (Carpenter *et al*., 2014), which in turn stimulates the interrenal tissue to produce cortisol, the main corticosteroid in fishes (Figure 1) (Ganga *et al*., 2006). Subordinate fishes show increased HPI activity and, in general, have higher levels of circulating cortisol (Doyon *et al*., 2003). Cortisol levels are lowered, and *crf* and *crf1 receptor* mRNA are rapidly down-regulated in ascending male *Astatotilapia burtoni*, further supporting that the HPI axis is involved in the physiological changes associated with shifts in dominance (Carpenter *et al*., 2014). In the rainbow trout (*Oncorhynchus mykiss*), administration of cortisol affects aggressive behaviour in a time-dependent way; although short-term exposure had no effect, exposure of up to 2 days led to an inhibition of aggression (Øverli *et al*., 2002).

The neuropeptides arginine-vasotocin (Avt) and isotocin (It) have also been implicated in aggressive behaviour in fishes, although their role is still unclear (reviewed in Godwin & Thompson, 2012). In *D. rerio*, AVT-related genes are associated with the expression of aggression in dominant males and females, and dominant males over-express It mRNA (Filby *et al*., 2010). Levels of It mRNA levels are higher in the brains of dominant male *G. aculeatus* defending their territory (Kleszczyńska *et al*., 2012). Dominant *D. rerio* express Avt in one to three pairs of large cells in the magnocellular preoptic area, whereas in subordinate individuals it is expressed in 7–11 pairs of small cells in the parvocellular preoptic area (Larson *et al*., 2006), indicating that the vasotocinergic system may play a role in shaping dominant–subordinate relationships. In the same species, agonistic interactions are more directly associated with changes in brain Avt than It (Teles *et al*., 2016). Avt injections in territorial male bluehead wrasse (*Thalassoma bifasciatum*) increase courtship and decrease chases (Semsar *et al*., 2001). Furthermore, Avt injections in non-territorial males increase courtship, chases and territorial behaviour, suggesting that increased levels of Avt promote the expression of territorial behaviours (Semsar *et al*., 2001). In Beaugregory damselfish (*Stegastes leucostictus*), injection of Avt also increases aggressive behaviour towards intruders in a dose-dependent manner, and injection with Manning compound (an Avt receptor antagonist) reduces such behaviour, whereas It administration has no effect (Santangelo & Bass, 2006). *A. burtoni* individuals ascending from subordinate to dominant, and treated with Manning compound, also show a reduction in aggressive behaviour (Huffman *et al*., 2015). Other studies offer contradictory evidence. For instance, *O. mykiss* receiving 200 ng Avt become subordinate, whereas a dose of 20 ng has no effect on the outcome of fights for social dominance (Backström & Winberg, 2009). In goldfish (*Carassius auratus*), Avt inhibits approach responses towards the visual stimuli of conspecifics, whereas Manning compound stimulates such responses (Thompson & Walton, 2004).

A few studies have investigated the role of metabolic hormones in aggression. Thyroxine (T_4) administration in salmonids reduces aggression (Hutchison & Iwata, 1998), whereas low and high doses of triiodothyronine (T_3) reduce and increase aggression, respectively (Godin *et al*., 2011). Growth hormone (Gh) administration, which increases metabolic demands and feeding motivation in teleosts, increases aggression in juvenile *O. mykiss*, although it does not change their social status (Jönsson *et al*., 1998). It was proposed that Gh influences aggression indirectly by increasing swimming activity and/or by inducing defence of a larger territory, thus increasing the probability of encounter between opponents. In addition, salmonids strains selected for higher growth rates have a negative cost in the generation of more aggressive behaviour (Nicieza & Metcalfe, 1999). Somatostatin (Sst) is a hypothalamic polypeptide that regulates Gh release from the pituitary gland (Brazeau *et al*., 1973). In *A. burtoni*, dominant males show reduced somatic growth and increased Sst neuron size in the preoptic area of the brain. Sst antagonists increase aggressive behaviour in a dose-dependent manner, and the potent Sst agonist octreotide decreases aggression (Hofmann & Trainor, 2006). It was proposed that Sst may reduce energetically costly processes such as somatic growth and aggressive behaviour in dominant males (Hofmann & Trainor, 2006).

A study in *D. rerio* explored gene expression linked to different levels of aggression (Filby *et al*., 2010). The authors identified several genes differentially expressed in relation to aggression; these genes belonged to seven functional pathways occurring in the hypothalamus and telencephalon, suggesting a multi-factorial control of aggression similar in several aspects to mammalian neurophysiology. A recent study in *B. splendens* explored gene expression in the brain of animals in fight context and concluded that a synchronization occurs in the opponent pairs, suggesting that this physiological phenomenon can be the basis for the behavioural synchronization (Vu *et al*., 2020).

Overall, evidence indicates a role for the endocrine system in modulating aggressive behaviour in fishes, but a clear picture of the specific function of the different hormones and potential interactions among them is far from complete. Several steroidal hormones and their derivatives can be secreted during aggressive interactions, which are then released to the water (Almeida *et al*., 2005; Barata *et al*., 2007, 2008a; Martinovic-Weigelt *et al*., 2012; Poling *et al*., 2001; Sorensen *et al*., 2005). In a similar way to some reproductive hormones, they could act as hormonal pheromones mediating aggressive interactions (Stacey & Sorensen, 2009).

1.3 | Communication and aggression

Most interactions between animals involve communication; thus, understanding this phenomenon is crucial to fully appreciate animal behaviour (Frommen, 2020). Communication can be simply defined as the act of transferring information intentionally from a sender to a receiver, eliciting a response in the latter (Bradbury & Vehrencamp, 2015). Aggressive communication in aquatic environments has been recently reviewed (Frommen, 2020); aggressive signals can be conveyed through different sensorial modalities – visual, auditory, mechanosensory, electrical and chemical, in isolation or combined multimodal communication (Butler & Maruska, 2015; Chabrolles *et al*., 2017; Frommen, 2020; Ladich & Myrberg, 2006). Visual communication has been the most widely studied form of aggressive signalling in fishes. Aggressive behaviour can be divided into threat displays, where animals increase their apparent body size, *e.g*., by erecting their fins and expanding their gill covers (Huntingford & Turner, 1987; Simpson, 1968) or by changing colour or body patterns to signal dominance (Dawkins & Guilford, 1993), and attacks, where animals overtly charge, chase or bite an opponent (Pitcher, 1993; Reebs, 2001). The frequency of these aggressive displays varies among individuals of the same species, allowing an observer to distinguish the dominant/submissive relationship among them (McDonald *et al*., 1968). It is well established that many fishes use sonorous signals in aggressive contexts, with these usually being expressed after the visual detection of an opponent and/or intruder (Ladich, 1997). Sounds can be used during agonistic encounters and may affect the outcome of contests (Ladich & Myrberg, 2006). Some fishes can produce electrical discharges, with electrical pulses in the millivolt range proposed to act as electrical signals for communication (Hopkins, 1974; Kramer, 1990; Tricas & Carlson, 2012); higher voltages may be used to evade predators or stun prey. Electroreception appeared early in vertebrate evolution (Bullock *et al*., 1983); nonetheless, it seems that it has been subsequently largely lost in teleosts (Tricas & Carlson, 2012). Among the few species that have developed the capacity to communicate by electrical signals are the glass knifefish (*Eigenmannia virescens*) (Hopkins, 1974; Hupé & Lewis, 2008); the brown ghost knifefish (*Apteronotus leptorhynchus*) (Hupé & Lewis, 2008; Zakon *et al*., 2002; Zupanc, 2002) and some mormyrids: *Petrocephalus catostoma*, *Cyphomyrus discorhynchus*, *Hippopotamyrus* sp. (Scheffel & Kramer, 2000), *Gnathonemus petersii* (Bell *et al*., 1974) and *Pollimyrus isidori* (Bratton & Kramer, 1989). Electric organ discharges can be produced during fighting contexts, and their characteristics can convey dominance and transmit information to an audience (Dunlap & Larkins-Ford, 2003; Westby, 1975). The lateral line system can be involved in agonistic interactions and has been suggested to facilitate noncontact assessment and fight behaviours as a protective mechanism against physical injury in *A. burtoni* (Butler & Maruska, 2015). The lateral line is also hypothesized to be involved in acoustic communication, as the beating of fins and tail creates a stream of water towards the opponent (Ladich & Myrberg, 2006).

The role of chemical signalling during agonistic encounters has received little attention. A few pioneering studies suggest that chemical signalling is used to transfer information during agonistic encounters, and evidence exists for a dominance pheromone(s) used by fishes to signal their social rank (Barata *et al*., 2007; Gonçalves-de-Freitas *et al*., 2008; Keller-Costa *et al*., 2016; Maruska & Fernald, 2012).

1.4 | Relevance of aggression in fish welfare

Aquaculture is one of the most rapidly evolving and technically innovative sectors of food production. It constitutes an alternative to fisheries, and the decrease in wild populations, associated with increasing demand for fish products, will drive a rapid expansion in the coming decades (Béné *et al*., 2015, 2016; Gentry *et al*., 2017; Longo *et al*., 2019). Fish welfare in aquaculture is an important issue for public perception, marketing and product acceptance, and also for the industry itself to promote efficiency, quality and quantity (Kupsala *et al*., 2013; Oka *et al*., 2012). Nonetheless, behavioural interactions occur between farmed fishes, and high stocking densities may cause chronic stress by preventing normal social behaviour (Ashley, 2007; Ejike & Schreck, 1980; Wedemeyer, 1997) leading to suppression of growth in low-ranking fish (Abbott & Dill, 1989). Nevertheless, there are exceptions; in some species, high stocking densities may lead to reduced aggression and increased growth (*e.g*., *Tilapia rendalli*) (Torrezani *et al*., 2013). Social stress and uneven sizes promote aggressive behaviour (Ashley, 2007). Aggressive interactions cause injuries to the eyes, tails and pectoral fins, which facilitates secondary infections and can lead to death (Ashley, 2007). In addition, intra-cohort cannibalism – an extreme form of aggression – because of size heterogeneity, may occur in farmed fish and lead to severe losses (Naumowicz *et al*., 2017). Aggressive behaviour also results in greater energy expenditure and higher metabolic rates, which decrease food conversion to biomass (Sloman *et al*., 2000). It is clear, therefore, that aggressive behaviour in aquaculture is of economic importance, and innovative solutions are needed to avoid compromise of welfare. Furthermore, several reports have suggested that application of pheromones may improve aquatic animal cultivation (Bardach *et al*., 1980; Barki *et al*., 2011; Wuertz, 1997) and help to control non-indigenous fish species (Kupsala *et al*., 2013; Siefkes, 2017). It has been proposed that if a certain pheromone has a desirable effect, the aquaculture producers can supplement the holding water with artificially synthetized pheromone (Wuertz, 1997). Thus, it is important to explore pheromones related to aggressive behaviour, as this behaviour compromises these activities, and improve welfare (Ashley, 2007; Naumowicz *et al*., 2017; Sloman *et al*., 2000; Wuertz, 1997).

A major market that has been neglected is the production of ornamental fish. It is estimated that this trade involves up to 1.5 billion individuals per year, with mortality reaching 73% because of stressors that affect their welfare similar to aquaculture (Huntingford *et al*., 2006). Nonetheless, to improve welfare by expanding the space of animal rearing would constitute an economic impact to producers. In addition, after the fish arrive at peoples' home as pets, aggression continues to be a problem, mainly because the animals are often confined in small aquaria (Oldfield, 2011). Ornamental species often require larger aquaria and complex habitats, which allow more natural behaviour, thereby improving welfare through reduced aggression (Oldfield, 2011). Reduction of stock density is effective in the reduction of aggression in some ornamental species, such as swordtails (*Xiphophorus helleri*) (Magellan *et al*., 2012), angelfish (*Pterophyllum scalare*) and tiger barbs (*Puntigrus tetrazona*) (Stevens *et al*., 2017). The use of pheromones could constitute an improvement in this market not only to increase profitability but also, equally importantly, to improve the quality of life for the fish produced.

D. rerio is one of the most used vertebrate species in biological research (Lawrence, 2007), and the welfare of such experimental animals is therefore an important consideration (Toni *et al*., 2019). Recently, environmental enrichment to maximize the well-being of *D. rerio* used for experimental purposes was explored (Woodward *et al*., 2019). Curiously, this attempt led to increased aggression, as individuals would become territorial over objects placed in the tanks (Woodward *et al*., 2019). The authors concluded that when considering environmental enrichment of a certain species, its natural behaviour should be taken into consideration (Woodward *et al*., 2019).

In this context, the discovery of a pheromone released during dominance contests that modulates behaviour by reducing aggression would be a promising tool to promote welfare. Nonetheless, such a pheromone has yet to be unequivocally identified in fishes. Thus, a better understanding of factors, including chemical communication, regulating social interactions is most pertinent from both scientific and practical viewpoints.

2 | CHEMICAL COMMUNICATION MOLECULES

2.1 | Pheromones and cues

In chemical communication the message is transferred *via* the release and detection of chemical cues and/or pheromones (Scott-Phillips, 2008). Chemical cues can be defined as any stimuli capable of triggering a chemo-sensory response in an animal (Sorensen & Wisenden, 2015), whereas pheromones are chemical cues released by one individual that cause innate behavioural and/or physiological responses in conspecifics (Kekan *et al*., 2017). Pheromones are categorized as "signals" that evolved to alter the behaviour of other organisms and are effective because the receiver's response has also evolved (Smith & Harper, 2003). Chemical cues transmit information unidirectionally to the receiver and provide no advantage to the sender; conversely, pheromones are used to communicate, which means that there is feedback from the receiver to the sender, and both may benefit (Laidre & Johnstone, 2013; Sorensen & Stacey, 1999). It has been proposed that chemical cues might have been the evolutionary basis for pheromones, by an evolutionary process referred to as ritualization (Smith & Harper, 2003; Wyatt, 2014). Pheromonal systems have evolved specifically for communication and are defined according to the biological response that they induce (Sorensen *et al*., 2010). Accordingly, pheromones that elicit immediate behavioural responses are classified as "releaser" pheromones, whereas those causing physiological effects, which may later also drive behavioural change, are classified as "primer" pheromones (Sorensen & Wisenden, 2015). As functional definitions, nonetheless, these terms are not mutually exclusive (Sorensen *et al*., 2010). Hormonal metabolites that drive sexual arousal are classic examples of releaser pheromones, whereas primer pheromones are exemplified by preovulatory compounds produced by females that induce endocrine changes in male conspecifics leading to increases in milt production (Sorensen & Wisenden, 2015). Some pheromones derive from, and can be confused with, hormones – hormonal pheromones (Stacey, 2011); nonetheless, hormones are a class of signalling molecules that are produced in internal glands and transported by the circulatory system to regulate physiology and behaviour of the producer individual itself (Karlson & Lüscher, 1959).

Fish pheromones include: dominance pheromones (important for the establishment and maintenance of social hierarchies); kin recognition and aggregation pheromones, (important to avoid predation and also facilitate migratory orientation); and reproductive pheromones, which are important for mate-choice and reproductive behaviour (Sorensen & Wisenden, 2015).

Examples of chemical cues in fishes are kairomones, odorants originating from other species such as predators or prey, *e.g*., post-ingestion cues released from the predator's diet (Sorensen & Wisenden, 2015).

In fishes, chemical stimuli known to be excreted and/or to induce behavioural and physiological responses in conspecifics include amino acids (and their derivatives), bile acids, gonadal steroids (and their conjugates) and prostaglandins (Hara, 1994; Sorensen *et al*., 2010). Pheromones may be single compounds or – more often – multicomponent mixtures and thus a distinction of pheromones and pheromonal components/constituents is important (Sorensen *et al*., 2010). Slight variation in the mix may reflect the individual's physiological state, including status within a hierarchy, and affect the response in conspecifics (Sorensen & Wisenden, 2015).

2.2 | Secretion, transmission and reception

2.2.1 | Secretion

The study of pheromone production is common in mammals and insects, but scarce in fishes. Pheromones in insects and mammals are often secreted by a variety of specialized glands, which can be internal or external (Wyatt, 2014). Most studies in fishes deal with reproductive pheromones and show that these are mostly produced by the gonads (testes and ovaries) (Hurk & Resink, 1992). In the male peacock blenny (*Salaria pavo*), pheromones involved in sexual attraction of females are secreted by an anal gland located on the anal fin-rays (Laumen *et al*., 1974; Serrano *et al*., 2008b). The testicular glands, anal glands and/or the blind pouches (paired evaginations of the spermatic ducts) may be sites of pheromone production (Serrano *et al*., 2008a). In the black goby (*Gobius niger*), these attractants appear to be synthesized in the mesorchial gland, which is a part of the testis (Colombo *et al*., 1980; Colombo & Burighel, 1974). Such structural specialization for sex pheromone production also occurs in the seminal vesicles in African catfish (*Clarias gariepinus*) (Resink *et al*., 1989). Females also emit sex pheromones to attract males, and the compounds have been found to be produced in the ovaries (Crow & Liley, 1979). Migratory pheromones in salmonids may be produced in the liver and secreted into the bile (Selset & Doving, 1980). In the sea lamprey (*Petromyzon marinus*), larval bile acid pheromones are synthesized in the liver, stored in the gallbladder and secreted into the intestine *via* the bile duct (Buchinger *et al*., 2015), whereas adult males release them through the gills (Siefkes *et al*., 2003).

2.2.2 | Transmission

Transmission is the course taken by pheromones from release until it reaches the receiver. Pheromones released to the water are transported through turbulence and variable flows, and animals may use natural or self-generated water currents to amplify the effectiveness of pheromone transmission (Chung-Davidson *et al*., 2010). During transmission, pheromone action may be compromised by other dissolved chemicals, which can bind pheromones or inhibit receptors, *e.g*., humic acids (Hubbard *et al*., 2002), or disrupt the function or cause degeneration of olfactory sensory neurons (OSN), *e.g*., heavy metals (Tierney *et al*., 2010). Pheromones may be released to the environment through the gills, or *via* the urine, skin mucus, faeces, semen and ovarian fluids (Almeida *et al*., 2005; Bayani *et al*., 2017; Brown *et al*., 1995; Døving *et al*., 1980; Félix *et al*., 2013; Giaquinto *et al*., 2015; Giaquinto & Hara, 2008; Hubbard *et al*., 2003; Lecchini *et al*., 2018; Marui & Caprio, 1992; Rosenthal *et al*., 2011; Saraiva *et al*., 2017; Scott *et al*., 2019; Stacey & Sorensen, 2009). In *O. mossambicus*, *C. auratus* and *S. salar*, the urine is an important vehicle for pheromone release (Almeida *et al*., 2005; Appelt & Sorensen, 1999, 2007; Barata *et al*., 2007, 2008a). The frequency of urination of male *O. mossambicus* depends on the social context; dominant males store more urine than subordinate males, and the pheromone concentration is higher (Keller-Costa *et al*., 2012, 2014). The size of urinary bladder and its musculature thickness is directly proportional to social status (Keller-Costa *et al*., 2012).

2.2.3 | Reception

Most terrestrial vertebrates possess two distinct chemosensory organs: the main olfactory epithelium (OE) and the vomeronasal organ. Nonetheless, teleosts lack both the vomeronasal organ and accessory olfactory bulb (OB) (Mombaerts, 2004a). Instead, they possess a single pseudostratified OE on each side of the head, generally organized in a multilamellar olfactory rosette (Figure 2), and their odorant receptors are expressed in the OE with information relayed to the central nervous system by cranial nerve 1, the olfactory nerve (Hashiguchi *et al*., 2008; Sorensen & Wisenden, 2015). The olfactory rosettes are located inside the nasal cavities, which are usually composed of two inlet nostrils, through which the water enters, and two outlet nostrils located posteriorly (Kermen *et al*., 2013); cichlids are the notable exception in that they only have a single nostril per side (Escobar-Camacho & Carleton, 2015). The olfactory rosettes are organized into lamellae, the size and number of which increase throughout development and stabilize at maturity (Olivares & Schmachtenberg, 2019). The shape of the rosettes, the number and morphology of lamellae are highly variable from species to species (Hara & Zielinski, 2006). The OE lies between the inlet and outlet nostrils and contains up to five distinct classes of olfactory receptor neurons (ORNs): ciliated, microvillus, crypt cells, pear and kappe neurons (Figure 3), with the last three being thought to be specific to teleosts. Nonetheless, pear and kappe neurons have so far only been identified in *D. rerio* (Ahuja *et al*., 2014; Hansen & Eckart, 1998; Hansen & Finger, 2000; Miyasaka *et al*., 2014). At the basal level of the OE, basal cells are capable of regeneration in case of epithelium damage (Iqbal & Byrd-Jacobs, 2010). The OE is exposed to mixtures

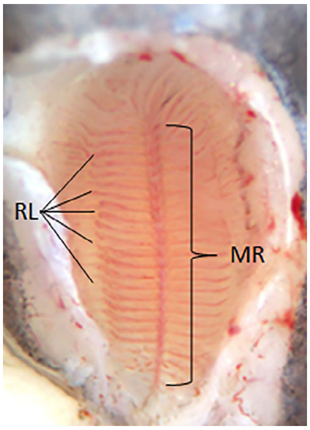

FIGURE 2 The olfactory rosette of the European eel (*Anguilla anguilla* L.). The olfactory rosette is composed of a narrow elongated median raphe (MR) in the middle that extends longitudinally from one extremity to another. Numerous radial lamellae (RL) are arranged around the MR and attached to the membrane of the olfactory chamber

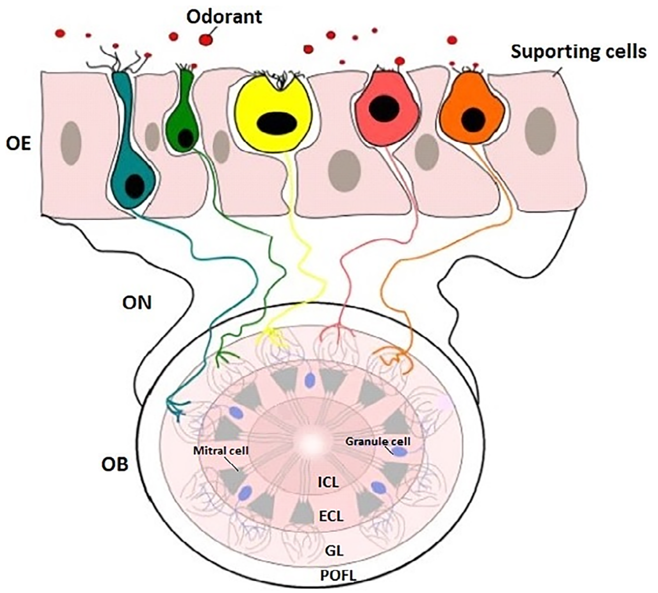

FIGURE 3 Schematic representation of the organization of the olfactory bulb. The five types of olfactory receptor neurons (ORNs) described in teleosts and their respective laminar position are represented with different colours (blue, green, yellow, pink and orange). The odorant molecules (red circles) are detected in the olfactory epithelium (OE) by the five different types of sensory neurons. The soma of the ORNs are located at different depths in the OE and each has specific characteristics: ciliated neurons (blue) that are the most basal ORNs have round cell bodies and thin dendrites that terminate in clusters of cilia on the epithelial surface; the microvillous neurons (green) that are also known to have round soma, but thicker dendrites with bundles of microvilli on their apical surface; the crypt neurons (yellow) that have globular-shaped and exhibit both microvilli and cilia on their apical surface and are located more apically than ciliated and microvillous neurons; the kappe neurons (pink) are in pear-shaped form with an apical appendage resembling a cap (German: *Kappe*), and these neurons do not have cilia and are the ORNs type located more apically and, finally, the pear neurons (orange) that are also located apically, are pear-shaped and possess short apical dendrites. The ORNs project their axons, *via* the olfactory nerve (ON), to different glomeruli located in the olfactory bulb (OB). The OB is composed of four different layers: POFL: primary olfactory fibre layer; GL: glomerular layer; ECL: external cell layer; ICL: internal cell layer. The axons of the olfactory neurons establish contact with the dendrites of the mitral cells in each glomerulus (adapted from Ahuja *et al*., 2014; Kermen *et al*., 2013)

of different substances dissolved in the water, and the capacity to discriminate between different odorants is important for animals to navigate and take decisions (Chung-Davidson *et al*., 2010). Detection of odorants requires their binding to odorant receptors which, in vertebrates, are members of the G-protein-coupled receptor superfamily, in the membrane of ORNs in the OE (Buck & Axel, 1991; Fleischer *et al*., 2009; Sorensen & Wisenden, 2015; Spehr & Munger, 2009). Odorant receptors are highly diverse and can be grouped into olfactory receptors (ORs), trace amine-associated receptors (TAARs) and type I and II vomeronasal receptors (V1Rs and V2Rs) (Alioto & Ngai, 2005; Fleischer *et al*., 2009; Mombaerts, 2004a). It has been proposed that ciliated cells express ORs, whereas microvillous and crypt cells express V1Rs and V2Rs (Oka *et al*., 2012; Yoshihara, 2009). TAARs are expressed in sparse ORNs (Hussain *et al*., 2009).

Some studies have given insights into the ORNs and their interaction with pheromones. For example, in *O. mykiss*, ciliated ORN have a generalist response to a wide range of odorants, among them pheromones and amino acids, whereas microvillous ORNs are specific for amino acid detection (Sato & Suzuki, 2001). In the channel catfish (*Ictalurus punctatus*), amino acids are detected by both ciliated and microvillous ORNs, and bile salts by ciliated ORNs (Hansen *et al*., 2003). In the crucian carp (*Carassius carassius*), detection of alarm cues occurs in ciliated ORs (Døving & Lastein, 2009; Hamdani & Døving, 2002) as with some sex pheromones (Lastein *et al*., 2006). A spatial coding of the olfactory input occurs in the OB, because each ORN expressing a particular OR sends its axon to the same glomeruli (*e.g*., amino acids induce activity in the glomeruli of the lateral bulb; bile salts induce the medial part and the posterior part is induced by alarm cues (Lastein *et al*., 2006). This "olfactory coding" that stipulates that the OB is organized into subregions ("glomeruli") to process certain classes of odorant has been extensively studied in *D. rerio*, another cyprinid (Ahuja *et al*., 2013; Friedrich & Korsching, 1998; Sato *et al*., 2005). Crypt ORNs have been suggested to be involved in sex pheromone detection (Kermen *et al*., 2013). These ORNs have a seasonal variation in *C. carassius*; during winter few crypt ORS are dispersed in the OE; throughout spring the majority are located deep in the OE not yet exposed to the environment but during summer, the spawning season, they appear at the surface of the OE (Hamdani *et al*., 2008). Furthermore, in mature *O. mykiss* crypt ORS are larger than those of juveniles and locate preferentially the apical surface of the OE (Bazáes & Schmachtenberg, 2012). Nevertheless, crypt ORNs detect odorants, such as amino acids and bile salts, other than sex pheromones (Schmachtenberg, 2006; Vielma *et al*., 2008). Nonetheless, in mature *O. mykiss*, a preference exists for gonadal extracts and hormones from the opposite sex, supporting the involvement of these ORNs in reproductive chemical communication in fishes (Bazáes & Schmachtenberg, 2012). The recently identified pear ORNs may be involved in the detection of food-derived odorants (VanHook, 2017); nonetheless, studies correlating these ORNs and the kappe ORNs with pheromone detection have not yet been carried out.

The processing of odours in vertebrates occurs in the OB, a brain structure organized in four layers that receives input from the ORNs axons *via* the olfactory nerves (Figure 3) (Kermen *et al*., 2013). The primary olfactory fibre layer, the most external layer, is composed of axons of the ORNs, the dendrites of which extend into the following inner layer, the glomerular layer, where ORNs form glutamatergic synapses with the dendrites of the mitral cells, which have their somas located in a deeper layer, the external cell layer (Braubach *et al*., 2012; Hara & Zielinski, 2006; Vassar *et al*., 1994). The granule cells are located in the external cell layer that, in *D. rerio*, are GABAergic cells without axons and make dendro-dendritic synaptic connections with principal cells (Kermen *et al*., 2013). In the internal cell layer, the deepest layer of the OB, the axons of the mitral cells are located, which connect to telencephalon and diencephalon brain areas as targets to further process olfactory input, where it is integrated with other information to mediate appropriate output responses (Kermen *et al*., 2013; Miyasaka *et al*., 2014).

Studies in mammals initially suggested that ORNs express a single OR (Chess *et al*., 1994; Serizawa *et al*., 2004). Nonetheless, this " one receptor–one neuron" theory has been revised (Mombaerts, 2004b; Tan *et al*., 2015), in that an ORN initially express several ORs, but epigenetic regulation occurs during development leading to expression of a single OR per ORN (Tan *et al*., 2015). Thus, this specificity of one OR per ORN and its projection to a specific glomerulus are key events for the organization and function of the olfactory system and result in the production of a topographic odour map in the brain (Sato *et al*., 2007). Nonetheless, it appears that the "one receptor–one neuron" may have an exception in *D. rerio* (Sato *et al*., 2007). In this species, multiple ORs exist in an ORNs subpopulation and may represent a specific way to integrate information from multiple odours (Sato *et al*., 2007).

Studies focusing on whether olfactory processing in higher-order brain centre is influenced by an animal's physiological condition are scarce. Nonetheless, a recent study in *A. burtoni* using local field potential recordings from the ventral telencephalon of dominant and subordinate males revealed that the social rank and reproductive state influence the neuronal response properties (Nikonov & Maruska, 2019). More specifically, dominant males had a high percentage of neurons that responded to several odour types, which may indicate that males in reproductive and territory defending conditions exhibit a differential sensitivity (Nikonov & Maruska, 2019).

2.3 | Chemical identity of fish aggression pheromones

Table 1 summarizes studies linking pheromones to dominance and aggression. One of the first studies to suggest that aggressive behaviour is modulated by pheromones was conducted in *B. splendens*, showing that they secrete substances that reduce aggression in conspecifics, and that these substances are secreted by either one or both combatants in response to prolonged fighting stress (Colyer & Jenkins, 1976). In bullhead catfish (*Ictalurus nebulosus*), individuals detect the body odours of conspecifics, and these compounds play a role in signalling dominance and territorial relationships and evoke increased aggression towards chemical "strangers" (Bryant & Atema, 1987).

TABLE 1 Summary of studies suggesting that fishes use chemical communication in an aggressive context

Species	Identity	Transmission	Behaviour elicited/function	Reference
Etta splendens	n.i. Pheromone	n.i.	Reduces aggressiveness in conspecifics	(Colyer & Jenkins, 1976)
Ictalurus nebulosus	n.i. Pheromone	n.i.	Signals dominance and increases aggression towards strangers	(Bryant & Atema, 1987)
Gasterosteus aculeatus	n.i. Chemical cue	n.i.	Promotes aggression from males and gravid females	(Waas & Colgan, 1992)
Carassius auratus	Androstenedione (pré-ovulatory pheromone)	n.i.	Courtship and aggressive behaviour	(Poling *et al*., 2001)
Gobius niger	n.i Sexual pheromone.	Sperm	Attracts females and induces aggressive displays in males	(Locatello *et al*., 2002)
Oreochromis mossambicus	n.i. Pheromone	Urine	Signals social status to male rivals	(Almeida *et al*., 2005)
Danio rerio	n.i. Pheromone	n.i	Suppress other females' reproduction according to their social rank	(Gerlach, 2006)
Oreochromis mossambicus	n.i. Pheromone	Urine	Signals dominance and modulate aggression in rivals contributing to social stability	(Barata *et al*., 2007)
Oreochromis mossambicus	Pheromone aminosterol-like	Urine	Signals of dominance, thereby influencing female spawning	(Barata *et al*., 2008a)
Oreochromis niloticus	n.i. Pheromone or chemical cue	n.i.	Water renewal increases aggression and leads to social instability	(Gonçalves-de-Freitas *et al*., 2008)
Pimephales promelas	n.i. pheromone (bile acids and/or volatile amines)	Urine	Signals dominance	(Martinovic-Weigelt *et al*., 2012)
Oreochromis mossambicus	Multicomponent pheromone	Urine	Lowers aggression when added to a tank containing a male fighting its mirror image	(Keller-Costa *et al*., 2016)
Neolamprologus pulcher	n.i. Pheromone	Urine	Communicate the aggressive propensity	(Bayani *et al*., 2017)
Oreochromis mossambicus	n.i.	Urine	Signals social dominance and fighting ability to avoid energetic costs and/or risk of injury in fights. Exposure to urine leads to 11KT response of subordinate males suggesting chemical eavesdropping	(Saraiva *et al*., 2017)
Porichthys notatus	n.i. Pheromone	Sperm	Dominant males suggest that accessory glands may play a role in parental care and chemical signalling	(Miller *et al*., 2019)
Cichlasoma paranaense	n.i. Pheromone/chemical cue	n.i.	Water renewal reduces aggression	(Gauy *et al*., 2019)

Note. n.i., non-identified.

Female *D. rerio* release pheromones to suppress reproduction by other females, and the extent of this inhibition depends on social rank, which in turn is related to aggressive interactions (Gerlach, 2006). The identification of these compound(s) was not pursued, but it could be a sex pheromone that influences both reproductive and aggressive behaviour.

C. auratus is the best-studied fish species for reproductive pheromones (Stacey & Sorensen, 2009). Males respond to pre-ovulatory female pheromone components, and the responses include courtship and aggressive behaviour (Poling *et al*., 2001). Androstenedione (AD) is released by females at the end of vitellogenesis, eliciting aggressive behaviour in mature males (Poling *et al*., 2001). Sexually active males also release considerable amounts of this steroid (50 ng h^{-1}), which suppresses female responsiveness to pheromones (Sorensen *et al*., 2005). The olfactory system is highly sensitive to AD; because AD is released by both sexes, discrimination of the sex of the donor may be based on the bouquet of C_{19} and C_{21} steroids released and detected, which is different between males and females; during sexual arousal in males, the ratio of C_{19} to C_{21} steroids was 50:1, markedly different from that (1:7) in females (Sorensen *et al*., 2005).

Territorial male fathead minnows (*Pimephales promelas*) use urinary cues to signal dominance Martinovic-Weigelt *et al*., 2012). Reproduction in this species depends on the male's ability to acquire and defend a high-quality nesting territory, and to attract a female to his nest. Dominant males use aggression to visually and physically suppress subordinates to deter them from their territory and females (Unger, 1983). Based on their different concentrations in urine from dominant and subordinate males, bile acids and volatile amines were suggested as the active components (Martinovic-Weigelt *et al*., 2012).

In *N. pulcher*, urine is also the vehicle of chemical signals to communicate aggressive propensity and appropriate agonistic responses are dependent on chemical information (Bayani *et al*., 2017). In the cichlids *O. mossambicus* and *N. pulcher*, male aggression levels and urination frequency during fights depend on the social rank of the opponents; dominant males urinate more often, and the urinary emissions act as a signal before the physical contact to inform the opponent of their social status or, perhaps, RHP (Barata *et al*., 2007; Bayani *et al*., 2017).

Some males use an alternative reproductive strategy – sneaking – to gain fertilization without investing in territorial defence (Taborsky, 1994). Sneakers are usually smaller and behave like females to access the territory without being confronted by the dominant male, and ultimately fertilize a proportion of the ova (Taborsky, 1994). Sneaking is an interesting strategy from the chemical communication point of view as sneakers must either be "pheromonally silent" (Locatello *et al*., 2002; Miller *et al*., 2019) or mimic females in odour as well as looks. One example is the *G. niger*, wherein parental males release a sex pheromone produced in the mesorchial gland that attracts females and induces aggressive displays in other males (Locatello *et al*., 2002). Nonetheless, sneakers have undeveloped mesorchial glands; it has been hypothesized that they are "pheromonally silent" so as not to be detected by the other males, thus facilitating fertilization of eggs by avoiding aggressive encounters with other males (Locatello *et al*., 2002). A similar strategy is found in the plainfin midshipman (*Porichthys notatus*). In this species, the dominant male accessory glands may play a role not only in parental care but also in pheromonal signalling. Again, sneakers have smaller accessory glands (Miller *et al*., 2019). In *S. pavo*, male sneakers lack both the anal gland and the accessory testicular organs, suggesting that this renders them chemically undetectable by conspecifics (Barata *et al*., 2008b).

Studies in *O. niloticus* found that aggression of subordinates, but not dominant fish, was higher when their water was renewed compared with not renewed (Gonçalves-de-Freitas *et al*., 2008). Nonetheless, in another cichlid *Cichlasoma paranaense*, 50% water replacement led to a reduction in aggression, suggesting the existence of species specificity in the aggressive response to chemical stimuli in the social environment (Gauy *et al*., 2019).

Studies in *O. mossambicus* have addressed the identity of putative dominance pheromones. Dominant male *O. mossambicus* release urine pulses to communicate their status during agonistic interactions with rival males and in the presence of pre-ovulatory females (Almeida *et al*., 2005; Barata *et al*., 2007, 2008a). Two steroid glucuronates, 5β-pregnane-3α,17,20β-triol-3-glucuronate (20β-P-3-G) and its 20α-epimer (20α-P-3-G), were identified in male urine (Keller-Costa *et al*., 2014, 2016). The urinary concentration of these steroid glucuronates correlates positively with the donor's social rank, and both have high olfactory potency. Although the two steroid glucuronates are sufficient to prime the female endocrine system to accelerate oocyte maturation, alone they had no clear effect on male behaviour (Hubbard *et al*., 2014; Keller-Costa *et al*., 2014, 2016). Although dominant male urine lowers aggression in males fighting their own mirror image, urine fractionation and reconstitution in combination with mirror assays showed that the dominance pheromone is likely to be a mixture (Keller-Costa *et al*., 2016). It was hypothesized that male tilapia signalling of social dominance and fighting ability *via* pheromonal communication may be an adaptive mechanism to avoid energic costs and/or risk of injury in fights (Saraiva *et al*., 2017).

Some of the studies discussed here suggest a possible overlap between reproductive and dominance pheromones. This is not unlikely considering that aggressive behaviours can be triggered in several contexts, reproduction being one of them. Most likely, the complexity of some behaviours implies the release of a mixture of compounds, different components of which may acquire more or less importance in different contexts. During reproduction, some might affect male–male rivalry to increase the chances of accessing a sexual partner and others might play a direct role in attracting and promoting spawning of the partners. In this study, the authors use "dominance pheromone" to refer to odorants released to show an individual's – usually male – rank within a social hierarchy. One function of a dominance pheromone would be to reduce aggression in rivals, thus reducing the risk of injury and maintaining a stable social order. Clearly, however, many of the components in such a pheromone may also be used by females in their mate-choice.

Studies on the use of chemicals cues in aggressive contexts in fishes are scarce. Some crustaceans, however, are good models and this topic was already reviewed (Chung-Davidson *et al*., 2010). For example, some crustaceans that lose a fight learn to associate unique cues with the winner (Chung-Davidson *et al*., 2010). Among the scant extant fish literature, a behavioural study in *G. aculeatus* showed that aggression is elicited by both visual and chemical stimuli released by conspecifics (Waas & Colgan, 1992). Odorants from displaying males were detected by non-territorial males and gravid females, and both attempted to bite or bump in the direction of a water source from a displaying male (Waas & Colgan, 1992). The authors proposed that these cues were associated with different rates of physical activity (Waas & Colgan, 1992). Sexual ornaments (odorants that advertise mate quality) are further evidence of chemical cues used in aggressive behaviour; these compounds are bifunctional, both attracting sexual partners and inducing aggressive behaviour from rivals (Sorensen & Wisenden, 2015).

3 | METHODOLOGICAL CONSIDERATIONS AND FUTURE DIRECTIONS

The identification of dominance pheromones requires the compound(s) to be isolated from tissues or body fluids and demonstration that is capable of eliciting dominance behaviour. This requires an inter-disciplinary approach including behavioural, physiological and chemical methods. An important component of the isolation procedure is to have standardized behavioural and physiological assays to test the extracts, fractions and isolates (Barata *et al*., 2008a; Breithaupt & Thiel, 2011; Sorensen *et al*., 2010).

The methodologies to measure aggressive behaviour, such as live encounters, video playbacks, mirrors and robots, have been a subject of much discussion (Balzarini *et al*., 2014; D'Eath, 1998; Huntingford, 1980; Patricelli, 2010; Ramos & Gonçalves, 2019; Romano *et al*., 2017). This may be because of intrinsic characteristics of the methodology and species-specific responses. In *B. splendens*, responses to the mirror assay were similar to responses to a live conspecific and provided less variability (Ramos & Gonçalves, 2019). Nonetheless, another study revealed that the cleaner wrasse (*Labroides dimidiatusa*) may recognize its mirror image as itself (Kohda *et al*., 2018). Studies also reported differences between mirror and live assay at the behaviour, endocrine and transcriptomic levels (Balzarini *et al*., 2014; Desjardins & Fernald, 2010; Oliveira *et al*., 2005). A study exploring the mirror assay, live conspecific, video assay and model replicas to test for aggression in *D. rerio* revealed significant differences between the assays, concluding that the specific research goals should be considered when selecting the appropriate stimulus to trigger aggression (Way *et al*., 2015).

From the few studies that attempted to identify dominance pheromones, these seem at least in some cases to be a mix of compounds (Section 2.3). This makes the identification of the individual components more complex, as each separate component may not have a measurable effect.

Another confounding factor is that communication can be multimodal (see Section 1.3) and to fully understand a behaviour is important to consider the different sensory channels involved in communication of aggressive behaviour. Few studies have been performed combining chemical senses with other sensorial modalities. For instance, the cichlid *Neolamprologus pulcher* shows similar behaviour when using vision or olfaction (Fischer *et al*., 2017); and in the *G. aculeatus* kin recognition, visual and olfactory cues combined are involved (Mehlis *et al*., 2008).

Another aspect that would benefit standardization is the measurement of aggression. There is currently wide variation in how aggression is measured in fishes, from single behaviours to compound indexes (Budaev, 2010; Félix *et al*., 2013; Teles & Oliveira, 2016). Ideally, there should be consistency in methodology, too, but difficulties may arise because of variation in aggressive displays across species (Noleto-Filho *et al*., 2019). Behaviour is usually recorded on video. Video-taping allows multiple viewings for precise and detailed measurement of aggressive behaviours; furthermore, they can be analysed "blind" in that the scorer may be unaware of the treatment. Studies using different species have followed this approach (Barata *et al*., 2007; Dunlap & Larkins-Ford, 2003; Giaquinto & Volpato, 1998; Oliveira *et al*., 2011). Numerous displays are used by researchers to evaluate the fish's agonistic behaviour and can be quantified in terms of frequency and duration. Some examples are: time spent with the gill covers extended, proximity to the opponent, tail beats, attempted bites, swimming, flight and nipping (Giaquinto & Volpato, 1998; McGregor *et al*., 2001). Video-taping and counting the aggressive displays also enable researchers to identify the winner, the loser and provide rankings. Some behaviours may be species- and sex-specific; in male *B. splendens*, gill flaring is the initial aggressive display towards both males and females but after prolonged exposure to intruders, there is a switch to fin-spreading (Forsatkar *et al*., 2016). Change of colour patterns in cichlids can also be viewed as a species-specific feature; an example is the oscar (*Astronotus ocellatus*) that, when defeated, changes from olive-green to brown/black (Beeching, 1995). It is now possible to extract information on aggressive displays using purpose-designed software, which improves data analysis compared to unaided human observation (Way *et al*., 2016). Progress in artificial intelligence for automatic detection of behavioural patterns has emerged as a new tool. Because analysis of animal behaviour is time-consuming and can be biased by the observer, studies using this technology show progress in this field (Han *et al*., 2018; Yang *et al*., 2020).

Usually, studies exploring aggressive behaviour use ethograms and quantify the number of aggressive responses; and there is a separation of "high" and "low" intensity displays, based on the energetic cost (Noleto-Filho *et al*., 2017, 2019). Quantifying aggressive behaviour by behavioural units is a common practice; nonetheless, this may generate a bias when pooling variables that are shown in different temporal patterns (Noleto-Filho *et al*., 2017). The use of a Bayesian Hierarchical Linear Model (BHLM) was suggested to overcome this; it provided a clear description of the changes even when patterns were tenuous (Noleto-Filho *et al*., 2017, 2019).

4 | FINAL REMARKS

Understanding the underlying physiological mechanisms of aggression is of great interest at several levels, yet our knowledge is far from complete. Chemical communication is predominant in many fishes but, although some pheromones and other chemical cues associated with reproduction, migration and alarm have been characterized, those associated with modulation of aggression remain to be identified. Nevertheless, the few studies so far provide clear evidence that a modulation of aggression by chemical cues exists in fishes. The combination of behavioural, physiological and analytical chemical approaches together with the right choice of model species is likely to advance our understanding of the role(s) of chemical communication in aggression over the coming years, and potentially use these compounds as tools to improve fish welfare.

ACKNOWLEDGEMENTS

This study was supported by the Portuguese Science and Technology Foundation (FCT) through project UIDB/04326/2020 and fellowship SFRH/BD/143872/2019 to MCS, and by the Macao Science and Technology Development Fund (FDCT) through project 093/2017/A2.

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How to cite this article: da Silva MC, Canário AVM, Hubbard PC, Gonçalves DMF. Physiology, endocrinology and chemical communication in aggressive behaviour of fishes. *J Fish Biol*. 2021;98:1217–1233. https://doi.org/10.1111/jfb.14667