Please cite the Published Version

Frommen, JG (2019) Aggressive communication in aquatic environments. Functional Ecology, 34 (2). pp. 364-380. ISSN 0269-8463

DOI: https://doi.org/10.1111/1365-2435.13482

Publisher: John Wiley & Sons Ltd on behalf of British Ecological Society

Version: Published Version

Received: 13 January 2019 | Accepted: 18 October 2019

DOI: 10.1111/1365-2435.13482

SENSORY ECOLOGY AND COGNITION IN SOCIAL DECISIONS

Functional Ecology BRITISH ECOLOGICAL SOCIETY

Aggressive communication in aquatic environments

Joachim G. Frommen[1,2]

[1]Division of Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland

[2]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK

Correspondence
Joachim G. Frommen
Email: j.frommen@mmu.ac.uk

Funding information
Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 31003A_166470; University of Bern; Brown

Handling Editor: Charles Fox

Abstract

1. Aggressive interactions are ubiquitous among animals. They are either directed towards heterospecifics, like predators or competitors, or conspecifics. During intraspecific encounters, aggression often serves to establish hierarchies within the social group. Thus, in order to understand the mechanisms mediating social organization, it is important to comprehend the escalation and avoidance of aggressive behaviour.
2. Overt aggressive interactions are costly not only in terms of increased risk of injury or death, but also due to opportunity costs and energy expenditure. In order to reduce these costs, animals are expected to communicate their strength and aggressive motivation prior to fights. For this purpose, they use different means of communication in various sensory modalities, that is visual, acoustic, chemical, mechanosensory and electric cues. These different modalities can convey different or similar information, underlining the importance of understanding the multimodal communication of aggression.
3. Thus far, most studies on signalling during aggressive encounters have focussed on visual or acoustic cues, most likely as these are the two modalities predominantly used by humans. However, depending on the species' ecology, visual or acoustic cues might play a minor role for many species. Especially in aquatic systems, visual communication is often hampered due to high levels of turbidity or limited light conditions. Here, alternative modalities such as chemical, mechanical or electrical cues are expected to play a prominent role.
4. In this review, I provide an overview of different modalities used during aggressive communication in aquatic organisms. I highlight the importance of studying the role of multimodal communication during aggressive encounters in general and discuss the importance of understanding aquatic communication in the light of conservation and animal welfare issues.

KEYWORDS

acoustic cues, aggression, chemical cues, contest theory, electric cues, mechanosensory cues, multimodal communication, visual cues

---

1 | INTRODUCTION

Most interactions between individuals involve some form of communication. Animals communicate when coordinating cooperative behaviours, choosing a mating partner, raising their offspring or avoiding predators. Understanding animal communication is thus crucial to understand animal behaviour in general. Consequently, animal communication has become a central topic in behavioural research within the last decades, witnessed by the publication of considerable numbers of scientific studies and textbooks focussing on different facets of this fascinating topic, ranging from the physiological foundations to the evolutionary consequences of animal communication (e.g., Bradbury & Vehrencamp, 1998; Maynard Smith & Harper, 2003; Stevens, 2013). Given the ubiquitous importance of animal communication in multifarious fields of research, it is not astonishing that there exists a huge variety of different definitions of terms. Box 1 provides an overview of how I use different terms in the following review. The modality in which animals communicate strongly depends on the environment in which communication takes place (Endler, 1992). Furthermore, communication might be based on multiple signals, either in the same or different modality. Aquatic habitats differ drastically in their physical settings from terrestrial ones, often requiring communication to take place in different modalities. In this review, I will provide an overview of the different modalities used to communicate during aggressive encounters in aquatic environments, underlining the importance of multimodal communication, especially in complex social systems. I will further outline implications of such communication in respect to ethics, welfare and conservation. Finally, I highlight how understanding multimodal communication in a broad range of animal taxa will allow us to plan and conduct more meaningful animal experiments.

BOX 1 Terms and definitions

Animal communication is a central topic in behavioural research. Given this importance, it is not astonishing that there exists a huge variety of different definition of terms (see for example Bradbury & Vehrencamp, 1998 for a summary).

In this review, I use the term *communication* as the intentional transfer of information between a sender and a receiver that elicits a response by the receiver (Bradbury & Vehrencamp, 1998). This response might be behavioural, morphological or physiological, and has positive fitness effects for both the receiver and the sender (cf. ‘true communication’ in Bradbury & Vehrencamp, 1998, pp. 2–3). Such intended transfer of information always occurs via *signals*. To fully comprehend animal communication, it is important to understand how the signal produced by the sender and the perceptual system of the receiver is matched to each other. In the current review, I mainly focus on the production of aggressive signals using various modalities and how they are influenced by the environment. Detailed reviews on the sensory ecology of aquatic organisms underlying communication can be found for example in Atema, Fay, Popper, and Tavolga (1988), Collin and Marshall (2003) and Gill (2019).

Like *communication*, the term *signal* has also been used in different ways. In this review, I apply a slightly modified definition of Maynard-Smith and Harper (2003): A signal can be any act or structure that has the potential to change the phenotype of another organism, which benefits the sender and which is effective because the receiver has evolved an adequate response. Note that such act or structure might be exploited by third parties like competitors or predators. In such case, there is no beneficial effect for the sender, and the emitted stimuli function as mere cues, not signals. The same act or structure might therefore serve as a signal in communication on the one hand, and as a cue in an eavesdropping event on the other (Bradbury & Vehrencamp, 1998). For an in-depth discussion of the different terms, I refer the reader to much more detailed textbooks (e.g., Bradbury & Vehrencamp, 1998; Breithaupt & Thiel, 2010; Maynard Smith & Harper, 2003; Stevens, 2013).

Following Hand (1986), I will use the term *aggression* broadly as ‘actual attacks, threats of attack or encroachments’. I call signals which suggest that an attack may occur aggressive (Drews, 1993).

2 | COMMUNICATING FIGHTING ABILITIES AND MOTIVATION

Aggressive interactions are ubiquitous throughout the animal kingdom. Animals may fight over resources like food, mating partners or high-quality territories (Hardy & Briffa, 2013). In gregarious animals, access to such resources is often facilitated by a high social rank, which is obtained and maintained through aggression. Aggressive encounters can be resolved either by overt fights or through the assessment of own or the opponent's fighting abilities (i.e., the *resource-holding potential* [RHP]) and aggressive motivation (Arnott & Elwood, 2009), followed by the surrender of one of the contestants. The advantage of direct physical fights is that opponents can compare their RHP and motivation directly, making cheating impossible. On the other hand, fights usually comprise significant costs like the risk of injury and death, missed opportunities to forage, mate or care for the offspring or the attraction of competitors or predators. Thus, animals should keep such overt fights as short as possible or avoid them entirely. Here, the decision to join or withdraw from a fight might either be purely based on assessment of own abilities, or it might include information gathered from the opponent (Arnott & Elwood, 2009; Elwood & Arnott, 2012). In the latter case, the individuals might base their decision only on the assessment opponent, or on mutual assessment, where the information gathered from the opponent is compared with own abilities (Elwood

& Arnott, 2012). Contestants might communicate their RHP and their motivation to invest in aggressive encounters by using a wide range of threat signals (Bakker, 1986; Breithaupt & Thiel, 2010; Hardy & Briffa, 2013). Still, only if these signals are honest, both partners benefit from such communication by avoiding costly conflicts (Maynard Smith & Harper, 2003; van Staaden, Searcy, & Hanlon, 2011). Signals informing about its bearer's RHP are often static and change only slowly (Setchell & Wickings, 2005; Tibbetts & Dale, 2004). They include, for example, visual or acoustic signals that inform about it bearers body size and cannot be faked (Arnott & Elwood, 2009; Brantley & Bass, 1994; Briffa, 2015; Elwood & Arnott, 2012). In contrast, signals informing about its bearer's aggressive motivation can be adjusted depending on the situation (Barlow, 2000). Such motivational signals have been frequently debated, as they are assumed to be unreliable and should therefore not be evolutionary stable. Still, honest signalling can be possible when the expression of the signal is costly. Indeed, recent models show that honest and deceitful signals can coexist (see Briffa, 2015 and citations therein). Finally, the communication of RHP and aggressive motivation is not the only way to avoid severe aggressive encounters. Individuals of low aggressive potential might instead signal submission (Schenkel, 1967). For example, many fish species signal their submission by showing submissive gestures or positions or by presenting submissive colour patterns, which often end a fight immediately (Barlow, 2000; Gibson, 1968; O'Connor, Metcalfe, & Taylor, 1999).

3 | COMMUNICATION IN AQUATIC ENVIRONMENTS

Animals use a fascinating variety of modalities to communicate, including visual, acoustic, chemical, mechanosensory and electric cues. The choice of the respective modality strongly depends on the environmental conditions perceived by the sender and the receiver. Such environmental conditions might change drastically within a short time frame. For example, while visual signals are a good way to communicate during a bright and clear day, they are of very limited use under foggy conditions or during the night. Similarly, olfactory information might be difficult to be conveyed against the wind or might dispense quickly. Besides such short-term variability, environments also differ on a large scale. For example, aquatic environments differ drastically from terrestrial environments in their suitability to transfer information (Pitcher, 1993). While visual cues can be a very fast and highly reliable source of information in clear and shallow waters, they are of much less value under turbid conditions. Furthermore, light conditions change drastically with increasing depth of a water body, with long wavelengths of the light spectrum (i.e., red) being scattered and absorbed within the first metres, while shorter wavelengths (i.e., blue and violet) penetrating up to 60m and beyond. Acoustic cues are transmitted about four times faster in water than in air and carry information over longer distances. Still, the direction of acoustic signals is difficult to assess, leading to the evolution of special organs enabling recognition of directionality of a sound source in several species (e.g., Aroyan, 2001). Chemical cues might dispense quickly in water, making them sub-optimal for long-term markings, but ideal for short-term communication. Vibrational and mechanosensory might be transferred via direct contact between the sender and receiver. Furthermore, aquatic organisms frequently produce changes in water pressure, which can be perceived by the receiver, often using special organs, like the lateral line (Bleckmann & Zelick, 2009; Butler & Maruska, 2015). Finally, communication by the production of weakly electric fields has been demonstrated mainly in aquatic species. To avoid unintended attraction of predators or heterospecific competitors, communication might involve ‘private channels’ using cues that other species are not able to perceive. Sound outside the hearing range, colours outside the visual range (e.g., UV or fluorescent coloration) or electric cues are classic examples. Such private channel communication might result in an arms race where predators or competitors evolve mechanisms to detect these signals (ter Hofstede & Ratcliffe, 2016).

Communication signals are often composed of a combination of several cues, either using the same or different modalities. Different cues might elicit or enhance the same response in an opponent (Partan & Marler, 1999). Sending such redundant information might on the one hand be beneficial in situations where signal transfer is unsecure due to environmental disturbances. By sending the same information, either in the same or different modality, receivers are more likely to realize the signal (Partan & Marler, 1999). For example, in situations where visual communication is temporarily hampered by variation in turbidity, acoustic cues might transport comparable information in another modality. On the other hand, redundant multimodal cues might underline the strength of signal, leading to an increased response of the receiver. In both scenarios, multimodal signals will lead to an increase in the accuracy of the receiver response (Hebets & Papaj, 2005). Further, different components of a signal might also be used in non-redundancy and provide an increase in information content. Such multiple components might transfer independent information, for example about the sender's size and motivation. These components might overrule each other when elicited at the time or modulate the response to the other. Finally, both signal components combined might lead to the emergence of a reaction that both components alone would not elicit (see Partan & Marler, 2005 for a detailed discussion). While such multimodal communication appears to be highly beneficial on the first view, communicating using multimodal signals also comes with costs, including energetic costs of producing, perceiving and integrating such diverse cues as well as an increased attraction of predators or competitors (Partan & Marler, 2005). Thus, the necessity to evolve multimodal communication signals is again strongly dependent on the ecological settings.

4 | SINGLE AND MULTIMODAL COMMUNICATION OF AGGRESSIVE PROPENSITY

Given such multifarious ways to communicate, it is not surprising that signals employed during aggressive encounters are transferred using the same broad range of modalities. Still, despite decades of research on communication of aggression in aquatic systems, the majority of studies have focussed on visual cues; most likely because these are predominantly used in human communication (Levinson & Holler, 2014) and easy to measure. However, as outlined above, visual modalities might play a minor role in aquatic systems depending on the ecology of the respective species. Indeed, already Baglioni (1910) described not only visual but also mechanosensory and olfactory perception in different fish and cephalopod species. In the following, I shall introduce briefly the different modalities aquatic organisms use in their communication, thereby highlighting the scope for future studies.

5 | VISUAL CUES

Aquatic animals show a fascinating diversity of morphological phenotypes, many of them being strikingly colourful, which can play a crucial role in intraspecific communication. Vision is an important modality as shown by the widespread ability to perceive light and colours in aquatic organisms. Most fish species, cephalopods and many crustaceans show highly derived photoreceptors, allowing them to see various colours, including the UV range (Cronin, 2006; Douglas & Djamgoz, 2012; Marshall & Oberwinkler, 1999). While modern teleosts possess four spectral classes of cones (Bowmaker, 2008), some mantis shrimp have up to 20 functional colour receptors allowing them to perceive wavelengths of light ranging from deep ultraviolet to far-red (Cronin, Bok, Marshall, & Caldwell, 2014) as well as polarized light (Thoen, How, Chiou, & Marshall, 2014). Still, the usefulness of visual cues in communication strongly depends on the environment (Endler, 1992). For example, high turbidity might temporarily or continuously reduce visibility. Furthermore, depending on the depth within a water body, certain wavelengths are removed, making communication via colour signals more difficult. The colour red, for example, is completely removed at a depth of 10 m. Depending on biotic and abiotic conditions the aphotic zone, where less than 1% of sunlight penetrates, begins around 200m of depth (Jerlov, 1968). Here, visual communication can only be achieved by the production of light signals. Nonetheless, even under optimal light conditions the distance in which visual information can be received seldom exceeds 30 metres, making visual cues unfeasible for communication over longer distances.

5.1 | Communication by morphological cues

Morphological features are constant cues and often serve to transfer visually information about body size, which usually correlates well with strength and RHP (Arnott & Elwood, 2009). Classical examples include fin displays in many fishes (Brantley & Bass, 1994; Gibson, 1968; Taborsky, 1984). Here, the opponents spread the unpaired fins (i.e., dorsal, anal and caudal fin) (Balzarini, Taborsky, Wanner, Koch, & Frommen, 2014). Such fin spreads may transfer information about a fish's size and health status (Bakker & Mundwiler, 1999). They are often accompanied by the lifting of the opercula lids (Abrahams, Robb, & Hare, 2005; Frances & Hinde, 1968), which makes the head appear bigger (Balzarini, Taborsky, Villa, & Frommen, 2017). Such opercula spreads reduce a signaller's ability to breath and are thus costly (Abrahams et al., 2005). In the Siamese fighting fish (*Betta splendens*), for example, opercula displays serve as an acute response to a territory intrusion, while fin spreading is a chronic response, probably due to the lower energetic costs of such displays (Forsatkar, Nematollahi, & Brown, 2017). The intensity of opercula displays is a good predictor for the outcome of subsequent fights, indicating that they are honest signals for the signaller's RHP (Evans, 1985). Fin displays might be short and are often followed by a submissive signal of the smaller opponent. However, they might escalate into long-lasting, energetically costly displays, where opponents present their lateral sides towards each other, usually in an anti-parallel manner (Arnott, Ashton, & Elwood, 2011). Such lateral displays might be further reinforced by pushing water towards each other using the caudal fin (see mechanosensory communication). The amount of moved water is here thought to be used as a further proxy of the signaller's body size and strength. Presenting morphological features to communicate strength is also common in many crustaceans (Mazel, Cronin, Caldwell, & Marshall, 2004). Different crab species, for example, wave their enlarged chelipeds towards each other before engaging in costly overt fights (Arnott & Elwood, 2010; Callander, Kahn, Maricic, Jennions, & Backwell, 2013; Jachowski, 1974).

5.2 | Communication by colour

In contrast to morphological features, colour signals can either be stable over time or change quickly within seconds. Similar to morphological signals, long-lasting colour patterns might transfer information about the signaller's body size (Balzarini et al., 2017), RHP (Moretz, 2005) or health status (Milinski & Bakker, 1990). Flexible signals in contrast might change rapidly depending in the bearer's motivational state. Contestants might signal their aggressive propensity by showing aggressive colour patterns, which can be accompanied by threat displays involving morphological cues. However, if they withdraw before aggression escalates or lose the fight such colour patterns might change drastically, signalling the submissive status of its bearer. Such fast colour changes are known for many fish species (Beeching, 1995; Dawkins & Guilford, 1993; O'Connor et al., 1999), but also for example in cephalopods (Scheel, Godfrey-Smith, & Lawrence, 2016). Mourning cuttlefish (*Sepia plangon*), for example, deceive rivals by displaying male courtship colour patterns to receptive females on one side of the body and simultaneously displaying female patterns on the other (Brown, Garwood, & Williamson, 2012).

5.2.1 | Private communication channels and aggression

While striking colour patterns can be highly suitable to communicate RHP and aggressive propensity, they bear at the same time the risk of attracting predators. Several aquatic animals therefore use colour patterns that cannot be assessed by their predators. Such 'hidden' or 'private' communication channels might employ ultraviolet colour vision (Cummings, Rosenthal, & Ryan, 2003; Losey et al., 1999; Marshall & Oberwinkler, 1999; Modarressie, Rick, & Bakker, 2013; Siebeck, 2004). Male three-spined stickleback (*Gasterosteus aculeatus*), for example, show distinctive UV-colour patterns (Hiermes, Rick, Mehlis, & Bakker, 2016; Rick, Modarressie, & Bakker, 2004) that not only play a role during mate choice (Boulcott, Walton, & Braithwaite, 2005; Rick & Bakker, 2008a; Rick, Modarressie, & Bakker, 2006), but are also incorporated in aggressive encounters (Rick & Bakker, 2008b). Furthermore, some aquatic animals like cuttlefish or different stomatopods possess polarization vision (Marshall, Cronin, Shashar, & Land, 1999; Shashar, Rutledge, & Cronin, 1996). This makes polarized light a further candidate for a private communication channel (Marshall et al., 2019). However, our knowledge about the function of polarized light in animal communication is currently limited to few species and a limited range of contexts (i.e., mate and habitat choice or comouflage, see Marshall et al., 2019 for a review), making communication using polarized light a promising topic for future studies. It is important to notice that private communication channels only work if predators do not possess comparable sensory capabilities. Therefore, the concept has been challenged as being overly anthropocentric by some authors (see for example Stevens & Cuthill, 2007 for a critical review).

5.2.2 | Biofluorescence and bioluminescence

Under dim light conditions, the emission of light bears the potential to transfer information. Such light emission might be achieved by the absorption of light by fluorescent proteins and the subsequent emission of light at a lower energy level (Biofluorescence) or by the production of light based on chemical processes (Bioluminescence).

Biofluorescence depends on the presence of external sources of light. It is therefore only found in the photic zone, where there is enough light left that can be absorbed (Sparks et al., 2014). It is important in cephalopods (Mäthger & Denton, 2001), sharks (Gruber et al., 2016) and several families of bony fishes (Sparks et al., 2014). Potential functions include camouflage, foraging and communication (Michiels et al., 2008). The best evidence for the role of biofluorescence in aggressive communication comes from mantis shrimp. Male *Lysiosquillina glabriuscula*, for example, threaten their opponents by raising the head and thorax, spreading the striking appendages and other maxillipeds, and laterally extending the prominent, oval antennal scales. Such displays are accentuated by colour patterns emitted both in the visual and UV spectrum (Cronin et al., 2014; Franklin, Marshall, & Lewis, 2016). Fluorescent coloration contributes to signal brightness and visibility of yellow spots, particularly at greater depths. The emitted wavelengths transmit well through seawater, so the signal is visible at distances at which communication occurs (Mazel et al., 2004).

Other animals emit light as the result of chemical reactions. Such bioluminescence has been described in many marine taxa that either live in the constant darkness of the deep sea or that are nocturnal (see Haddock, Moline, & Case, 2010 for a review). This includes many jellyfishes, crustaceans, cephalopods, sharks and teleost fishes (Haddock et al., 2010; Widder, 2010). Bioluminescence plays a role in diverse contexts such as foraging (Claes et al., 2014) or finding and attracting mating partners (Birk, Blicher, & Garm, 2018; Herring, 2007; Morin, 1986), but also during social interactions (Morin et al., 1975). However, as the behaviour of nocturnal or deep-sea species is notoriously difficult to study, we know little about the role of bioluminescence in aggressive signalling.

6 | ACOUSTIC CUES

Water is a highly suitable medium to conduct sound waves. Sound propagates about four times faster in water than in air and can transmit information over much longer distances (Hawkins, 1993; Tsuchiya, Naoi, Futa, & Kikuchi, 2004). However, considerable energy expenditure is needed to produce sound loud enough to propagate over large distances. Furthermore, the production of long sound waves requires a large resonating body. Consequently, the use of sound in long-distance underwater communication is reported solely for large animals, like cetaceans (Janik, 2009). Sounds produced by many whale species have the potential to travel over several thousand kilometres (Tsuchiya et al., 2004). They are known to play a crucial role in finding mating partners (Croll et al., 2002), organizing social groups (Clapham, 1996; Payne & Webb, 1971) or hunting (Panova, Belikov, Agafonov, & Bel'kovich, 2012).

While the occurrence of such long-distance acoustic communication is limited to members of few taxonomic groups, sound plays a much more prominent role in short distance communication in many aquatic species, including fishes, amphibians, crustaceans or cephalopods. Indeed, fishes are the vertebrate group that show the most diverse systems to generate sound (Ladich & Fine, 2006). They produce sound either by vibrating their swim bladder using intrinsic or extrinsic drumming muscles or by vibrating the pectoral girdle, rubbing of the enlarged pectoral spine in a groove of the shoulder girdle, plucking of enlarged fin tendons or by moving neck vertebrae and pharyngeal structures (see Ladich & Fine, 2006 for a detailed review of different mechanisms). Furthermore, several fish species are known to produce different sounds depending on the context. Male plainfin midshipman (*Porichthys notatus*), for example, produce three different types of sound that are termed *hums*, *grunts* and *growls* (McIver, Marchaterre, Rice, & Bass, 2014). Hums are long-lasting monotone sounds that are produced at night by contracting swim bladder muscles in order to attract females (Ibara, Penny, Ebeling, van Dykhuizen, & Caillet, 1983). Grunts are short sounds that are produced during agonistic encounters and serve as a threat signal (Brantley & Bass, 1994). Finally, growls are more complex than grunts and are emitted solely during agonistic encounters (McIver et al., 2014). Male plainfin midshipman occur in two different morphs, dominants and sneakers. While the much larger dominant males use the full acoustic repertoire to attract females and to show dominance, sneaker males do not develop morphological features that allow them to produce humming sounds and only seldom produce low amplitude, short duration grunts (Brantley & Bass, 1994).

Acoustic communication during agonistic encounters is not restricted to fishes. For example, vocalization has been described during both intra- and intersexual aggressive encounters in several cetacean species (Connor & Smolker, 1996; Graham & Noonan, 2010; Nakahara, 2002; Sayigh, 2014), though the exact function of calls is often challenging to determine as much aggressive behaviour occurs at depths where direct visual observations are difficult (Graham & Noonan, 2010; Sayigh, 2014). Finally, most amphibians emit encounter-, fighting or release calls during intrasexual agonistic interactions (Wells & Schwartz, 2007). These might be emitted under water, especially in fully aquatic species like members of the Pipidae (Ringeis, Krumscheid, Bishop, Vries, & Elepfandt, 2017; Weygoldt, 1976). Here, sound production is highly adapted to an aquatic lifestyle, with the structure and function of the larynx being completely different from those of other frogs. Sounds are produced without moving an air column and therefore without externally visible movements of vocal sacs (see Irisarri, Vences, San Mauro, Glaw, & Zardoya, 2011 for a detailed description of sound production). Pipid frog's repertoire of agonistic calls can be large. Male clawed frogs (*Xenopus laevis*), for example, produce six different calls that not only attract females but also function in intrasexual aggressive communication (Tobias et al., 2004). Here, they are used to suppress subordinate males and thus have a crucial function in building up dominance hierarchies (Tobias, Corke, Korsh, Yin, & Kelley, 2010).

7 | CHEMICAL CUES

In contrast to terrestrial environments, long-lasting territorial scent marks are absent in aquatic habitats. This might be due to the high solubility of chemical cues in water causing any scent marks to be diluted by water movements within short times. Furthermore, the ubiquitous bacteria in aquatic environments might rapidly degrade any scent mark. However, chemical cues play an important role during short-term interactions. For example, chemical cues are used during mate choice (Mehlis, Bakker, & Frommen, 2008; Reusch, Häberli, Aeschlimann, & Milinski, 2001) and social decisions (Kullmann, Thünken, Baldauf, Bakker, & Frommen, 2008; Raveh, Langen, Bakker, Josephs, & Frommen, 2019). Furthermore, they play an important role in assessing predatory threats and in informing others about these (Ferrari, Wisenden, & Chivers, 2010; von Frisch, 1938; Hettyey et al., 2015; Kullmann et al., 2008). Chemical communication of aggression in aquatic systems is thus far best understood in crustaceans (Breithaupt & Thiel, 2010). Indeed, chemical signalling is the most prevalent form of communication in this taxonomic group (Thiel & Breithaupt, 2010). Crayfishes and lobsters, for example, communicate by urinary signals (Breithaupt & Eger, 2002; Shabani, Kamio, & Derby, 2009). Competing American lobsters (*Homarus americanus*) shoot jets of urine towards each other. Urine is excreted through two nephropores located on the anterior ventral face of the base of the second antenna (Bushmann & Atema, 1996). These nephropores are connected to small rosette glands, which release their products into the urine (Atema, 1995). The urine is then released under high pressure into the gill current, which transports it forward towards the opponent (Bushmann & Atema, 1996). Such urine jets might carry information over distances of above one metre (Atema, 1985). The perception of an opponent's urine reduces the duration and aggression of male fights, especially when a subordinate individual repeatedly faces a dominant opponent (Karavanich & Atema, 1998). Therefore, urine might not only carry information about the senders RHP or aggressive propensity (Breithaupt & Eger, 2002), but also serve in individual recognition (Karavanich & Atema, 1998). Communication via urine appears thus to be crucial to establish stable dominance hierarchies in crustaceans (Katoh, Johnson, & Breithaupt, 2008; Shabani et al., 2009). Similar effects have been shown in several African cichlid species (see Keller-Costa, Canario, & Hubbard, 2015 for a review). Different tilapia species, for example, use chemical cues to signal dominance and to mediate aggressive encounters (Barata, Hubbard, Almeida, Miranda, & Canario, 2007; Giaquinto & Volpato, 1997). Furthermore, in juvenile Nile tilapia (*Oreochromis niloticus*) the exchange of chemical cues informs about the sender's motivation and about individual identity (Giaquinto & Volpato, 1997). Chemical cues excreted via the urine also play an important role in mediating aggression in the cooperatively breeding cichlid *Neolamprologus pulcher* (Bayani, Taborsky, & Frommen, 2017). In this species, members of both sexes change their urination patterns during agonistic encounters. Blocking olfactory contact between contestants lead to an increase in fight intensity and to a higher rate of overt aggressive attacks (Bayani et al., 2017). As larger individuals excreted larger amounts of urine, chemical cues might be a reliable proxy of the opponent's body size, which might be beneficial especially under turbid conditions. Furthermore, an aggression-mediated increase in urination frequency was accompanied by an increased amount of conjugated 11-ketotestosterone in the water (Hirschenhauser, Canario, Ros, Taborsky, & Oliveira, 2008; Hirschenhauser, Taborsky, Oliveira, Canario, & Oliveira, 2004). Thus, urine might not only transfer information about the contestants RHP, but also about the opponents' motivational state (Hirschenhauser et al., 2008).

8 | ELECTRIC CUES

The ability to produce or receive electric fields has evolved in several taxonomic groups. The reception of electric fields has been shown in terrestrial and aquatic species alike, including various invertebrates (Clarke, Whitney, Sutton, & Robert, 2013; Greggers et al., 2013; Morley & Robert, 2018), monotremes (Gregory, Iggo, McIntyre, & Proske, 1989; Scheich, Langner, Tidemann, Coles, & Guppy, 1986), lampreys (Bodznick & Northcutt, 1981), sharks and rays (Kalmijn, 1966), teleost fishes (Bullock, Hopkins, & Fay, 2006) and dolphins

(Czech-Damal et al., 2012). In these species, the reception of the electric field plays a role in navigation and foraging (Clarke et al., 2013; Peters & Bretschneider, 1972), and might further be used as communication channel in a social or sexual context (Kramer, 1996; Werneyer & Kramer, 2005). In contrast, the production of electric fields has been demonstrated predominantly in aquatic species (but see Greggers et al., 2013; Ishay, Goldstein, Rosenzweig, Kalicharan, & Jongebloed, 1997). In fishes, electric field production evolved several times independently, including rays, catfishes, knifefishes and elephantfishes. These species are able to produce electric fields by using modified muscle cells or endings of spinal motor nerves (Kramer, 1996). Here, the production of strong and weak electric fields can be differentiated. The production of strong electrical fields is usually used as a defensive mechanism as for example in the famous electric eel (*Electrophorus electricus*) (Keynes & Martins-Ferreira, 1953; Williamson, 1775) or in various catfishes (Howes, 1985). These species commonly lack the ability to receive such electric cues, making electric communication impossible. In contrast to such strong fields, some freshwater fishes possess the ability to produce and receive weakly electric cues, enabling the possibility of electric communication. Such electric communication has been demonstrated in different South American knifefishes and African elephantfishes (Kramer, 1996). These species are mainly nocturnal and usually live in highly turbid water, where visual communication is impossible, creating the need for alternative ways to communicate. Accordingly, they use weak electric fields in various contexts, like orientation (Schumacher, von der Emde, & Burt de Perera, 2017), foraging (von der Emde & Bleckmann, 1998) and during reproduction (Werneyer & Kramer, 2005). Importantly, such electric cues play a role in aggressive signalling. For example, studies on different South American ghost knifefish species have shown that both sexes produce an array of different electric signals that they modulate during agonistic encounters (Tallarovic & Zakon, 2002). While some of these cues play a role in signalling dominance (Hupe & Lewis, 2008; Triefenbach & Zakon, 2008), others are used in signalling submission (Zubizarreta, Stoddard, & Silva, 2015). Similar patterns have been shown in several African mormyrids (Gebhardt, Alt, & von der Emde, 2012; Kramer & Bauer, 1976).

9 | MECHANOSENSORY CUES

9.1 | Mechanosensory communication with contact

Information about an individual's RHP or aggressive propensity might be exchange via mechanosensory cues. For example, some crayfish species wave their antennae as part of a visual threat signal. Such waving is sometimes followed by antennae tapping, during which the constants quickly touch the anterior region of the contestant with their antennae (Tierney, Godleski, & Massanari, 2000). Such brief contacts mediate agonistic encounters. In the rusty crayfish (*Orconetes rusticus*), the decision to engage in fights with an opponent was influenced by prior antennal contact. Here, individuals with ablated antennae were less likely to show overt aggressive behaviours, but showed more aggressive displays not involving body contact (Smith & Dunham, 1996). While such brief antennal contact in crustaceans most likely does not have the potential to harm the opponent, mechanosensory communication of aggressiveness in other species is difficult to discern from overt aggressive interactions. Contests of hermit crabs, for example, involve a behaviour called *shell rapping*, during which the attacking individual brings its shell rapidly and repeatedly into contact with the opponent's shell. Such shell rapping might transfer information about the attackers RHP and motivation. It might furthermore reduce the opponent's ability to obtain an optimal grip on its shell (Briffa & Elwood, 2000). Rock mantis shrimp (*Neogonodactylus bredini*) use potentially deadly telson strikes to engage into ritualized attacks, a behaviour termed *telson sparring* (Green & Patek, 2015). Here, the individual performing higher amounts of ritualized strikes usually wins the contest. Such telson sparring fulfils the prerequisite of mutual assessment models proposed by contest theory (Green & Patek, 2018).

Mechanosensory cues play finally an important role in affiliative and submissive behaviours, for example in fishes (Hamilton, Heg, & Bender, 2005; Tanaka et al., 2015). Subordinates of the cooperatively breeding cichlid *Neolamprologus pulcher*, for example, regularly touch the body flank of dominant individuals with their mouth. Such bumping behaviour does not induce aggressive reactions of the receiver and is interpreted as a way to affirm the subordinate state of the signaller (Hamilton et al., 2005).

9.2 | Mechanosensory communication without contact

Aquatic animals face constant hydrodynamic stimuli, like water displacements and pressure fluctuations. These can be caused by abiotic factors like currents or tidal swell, but also by movements of con- and heterospecifics. Petromyzont agnathans, fishes, and larval and some adult amphibians are able to perceive such water movements or pressure changes via their lateral line (see Northcutt, 1989 for a review). This sensory system is built of structures that consists of a hair cell epithelium and a cupula that connects the ciliary bundles of the hair cells with the water surrounding the fish (termed neuromasts, Bleckmann & Zelick, 2009). Depending on the species, the number of such neuromasts differs greatly. They can be distributed over the head, trunk and tail fin (Bleckmann & Zelick, 2009). In many fishes, the neuromasts are further embedded in lateral line canals that are open to the environment through a series of pores (Bleckmann & Zelick, 2009). Fishes use their lateral line system for orientation (Montgomery, Baker, & Carton, 1997) and localization of stationary objects (Goulet et al., 2008), when foraging for food (Schwalbe, Bassett, & Webb, 2012) or when forming synchronized schools (Greenwood, Wark, Yoshida, & Peichel, 2013; Partridge & Pitcher, 1980). The lateral line system is furthermore hypothesized to play a crucial role in the mutual assessment of an opponents' strength (Enquist, Leimar, Ljungberg, Mallner, & Segerdahl, 1990).

Indeed, many fish often swish water at one another during lateral displays (Barlow, 2000). A recent study on Burton's mouthbrooder (*Astatotilapia burtoni*) showed that these fish use mechanosensory information perceived by their lateral line to avoid overt aggressive encounters during territorial interactions (Butler & Maruska, 2015). While the lateral line system of vertebrates is most likely of monophyletic origin (Northcutt, 1989), Budelmann and Bleckmann (1988) described a lateral line like organ also in two cephalopod species, which were able to recognize water movement with their epidermal head-lines. Whether this organ is used for aggressive communication as well is hitherto not known. Such convergently evolved perceptual abilities underline the importance of perceiving pressure changes in aquatic environments and may indicate a potential role for using water movement and pressure changes also in the communication of distantly related taxa.

10 | MULTIMODAL COMMUNICATION

Most studies on communication, and especially on aggressive communication, focus on information transfer in a single modality. This is unfortunate, as information is usually transferred via multiple signals, either in the same or in different modalities (Hebets & Papaj, 2005). Such different signals are processed in concert by the receiver, corroborating or modulating each other (Partan & Marler, 2005). The importance of such multimodal communication was already stressed by Darwin (1872) and gained attention from behavioural ecologists ever since (Hebets & Papaj, 2005; Partan & Marler, 2005; Rowe, 1999). Indeed, it is difficult to imagine examples, where the communication of aggressive propensity takes place only in a single modality. In many fishes, for example visual threat displays are accompanied by acoustic or olfactory signals (e.g., Bayani et al., 2017; Brantley & Bass, 1994; Chabrolles et al., 2017). Similar patterns are also found in agonistic interactions of many crustaceans (Breithaupt & Eger, 2002; Hebets & Rundus, 2011; Katoh et al., 2008). Rock mantis shrimp, for example, communicate their RHP and aggressive motivation by using chemical cues and performing threat displays showing a coloured patch, that reflects UV light. These different signals appear to work in non-redundancy and transfer different information: The UV reflectance and/or luminance of the colour patch appears to amplify the threat displays of the male, whereas chemical cues indicate size and identity (Franklin et al., 2016). While evidence for such multimodal communication during aggressive encounters is thus far limited to a small number of aquatic and terrestrial species (e.g., Ballentine, Searcy, & Nowicki, 2008; Green & Patek, 2015; Stuart-Fox, Firth, Moussalli, & Whiting, 2006), there is no reason to assume that this phenomenon is not widespread. Thus, understanding the interplay of multiple signals is crucial in order to understand animal contests in general. For example, one reason for the low number of studies demonstrating the role of mutual assessment during agonistic encounters (Arnott & Elwood, 2009; Elwood & Arnott, 2012) might be that the signals are multimodal but researchers only study one modality, using that as a proxy for RHP (e.g., visual cues of body size). Yet, the contestants may be mutually assessing each other using different cues (e.g., olfactory or acoustic) (see Arnott & Elwood, 2009 for a comparable argument). Still, studies elucidating the use of multimodal signals might be complex and technically demanding. As a first step, it would be important to gain information on the potential modalities that are part of the signal. Therefore, single modalities might be tested in isolation first (Chabrolles et al., 2017). Once knowledge about the importance of single modalities is established different signals might be tested in combination in order to obtain the complete picture (Chabrolles et al., 2017). Broadening the taxonomic scope of multimodal communication during aggressive encounters will be an important challenge for future research.

11 | COMMUNICATION IN COMPLEX SOCIAL SYSTEMS

Aggressive communication is expected to be most derived in highly complex animal societies (Freeberg, Dunbar, & Ord, 2012; Leighton, 2017; Pika, 2017; Pollard & Blumstein, 2012), although this assumption might be partly explained by an overrepresentation of studies on such social systems in the literature (Pika, 2017). Complex social systems usually possess a clear hierarchical structure. Low ranked individuals that aim at improving their hierarchy position might do so by challenging higher ranked group members, which in turn must defend their position constantly. However, constant escalating fights are detrimental for each group member. Thus, aggressive and submissive communication should be highly pronounced and include the broadest repertoire of signals. Such complex communication is expected to include several modalities and a broad range of displays differing in meaning and intensity. Cooperatively breeding species are great examples for socially complex groups. Thus far, the best studied cooperative breeding fish is the East African cichlid *Neolamprologus pulcher* (see Taborsky, 2016; Wong & Balshine, 2011 for reviews). In this species, social groups consist of a dominant breeding pair and up to 25 subordinate helpers (Bergmüller, Heg, Peer, & Taborsky, 2005; Groenewoud et al., 2016), which form a strictly size-based hierarchy (Balshine et al., 2001; Heg, Brouwer, Bachar, & Taborsky, 2005; Reddon et al., 2011). Aggressive interactions take place between all individuals, though they are most pronounced between individuals of similar hierarchy position (Ligocki et al., 2015). Agonistic encounters within a group are usually solved by a broad array of aggressive signals using different modalities. Visual signals might consist of different components, which can be shown either alone or in combination (Balzarini et al., 2014; Sopinka et al., 2009; Taborsky, 1984). These components differ in intensity and meaning, ranging from mildly aggressive fin flicks to long-lasting and energetically costly displays (Grantner & Taborsky, 1998). Such threat signals are accentuated by black colour patterns on the gill covers of both males and females. The intensity of these black stripes is a honest signal for an individual's aggressive motivation (Balzarini et al., 2017). Furthermore, visual displays are accompanied by olfactory cues, which are transferred via the urine and which contain information about the signaller's size, sex and motivational state (Bayani, 2016; Bayani et al., 2017; Hirschenhauser et al., 2008). Subordinate individuals answer such threat displays using several submissive and affiliative displays, including visual and mechanosensory cues (Balzarini et al., 2014; Sopinka et al., 2009; Taborsky, 1984). Similar patterns have been described in other cooperatively breeding fishes (Heg & Bachar, 2006; Tanaka et al., 2015), indicating that complex aggressive signalling is common in highly social fishes.

12 | HUMAN IMPACT ON AGGRESSIVE COMMUNICATION

In recent years, many aquatic habitats have faced drastic human-induced changes, including altered visibility due to algal blooms caused by eutrophication and soil import (van der Sluijs et al., 2011), increased noise levels by boat engines and other sources (Kunc, McLaughlin, & Schmidt, 2016; Williams et al., 2015), increased ocean acidification caused by the uptake of additional carbon dioxide (Caldeira & Wickett, 2003; Munday et al., 2009), and pharmaceutical (Puckowski et al., 2016) and chemical pollution (Lürling & Scheffer, 2007). These changes are known to impair species recognition (Seehausen, vanAlphen, & Witte, 1997), homing behaviour (Munday et al., 2009), mating preferences (Tuomainen & Candolin, 2011) and social behaviour (Fischer & Frommen, 2013; Williams et al., 2015) in many aquatic species. A major cause for these impairments is the disruption of one or more communication modalities.

An increase in turbidity, for example, potentially hampers the visual assessment of the opponent's RHP or motivation. Consequently, opponents will have to invest more time and energy in their signalling behaviour as well as in their attempts to receive the signals from the opponent. Juvenile brown trout (*Salmo trutta*), for example, showed exaggerated aggressive visual signals under turbid conditions (Eaton & Sloman, 2011). Furthermore, when opponent's assessment is unsuccessful, turbid conditions might lead to more or longer aggressive encounters. This assumption is supported by a study on the African cichlid *Pseudocrenilabrus multicolour*, where males performed more aggressive behaviours when tested under turbid conditions (Gray, McDonnell, Cinquemani, & Chapman, 2012).

Underwater noise pollution is considered as one of the most hazardous forms of anthropogenically driven environmental change (World Health Organization, 2011). Noise pollution has been shown to impair organisms on all levels, from individuals to ecosystems (Kunc et al., 2016), including agonistic encounters. In *N. pulcher*, for example, sound produced by boat engines altered the amount of aggressive and submissive displays shown by dominant and subordinate group members (Bruintjes & Radford, 2013). In the red-mouthed goby (*Gobius cruentatus*), a species where males acoustically communicate during territorial fights (Sebastianutto, Picciulin, Costantini, Rocca, & Ferrero, 2008), male territory holders were more likely to lose their territory to an intruder when fights took place while boat noise was present (Sebastianutto, Picciulin, Costantini, & Ferrero, 2011).

Within the last decades, aquatic systems faced drastic increases in chemicals released into the environment. These include herbicides, hormones, licit and illicit drugs and pharmaceuticals, some of which have endocrine disrupting function (Gavrilescu, Demnerová, Aamand, Agathoss, & Fava, 2015; Petrie, Barden, & Kasprzyk-Hordern, 2015). Such chemical compounds have been shown to alter chemoreception and information transfer (Lürling & Scheffer, 2007) and to impair species recognition, mating behaviour, foraging abilities and social interactions in several fishes and crustaceans (Olsén, 2011; Scott & Sloman, 2004). Also, aggressive interactions are influenced by such chemical pollution (Shinn, Santos, Lek, & Grenouillet, 2015). In the crayfish *Orconectus rusticus*, for example, the exposure to non-lethal levels of the herbicide metolachlor made individuals being less likely to initiate fights with untreated control individuals and lowered their chance to win aggressive encounters (Cook & Moore, 2008). Male guppies (*Poecilia reticulata*) that were exposed to an androgenic steroid (17 beta-trenbolone) used to promote growth in beef cattle showed more aggressive behaviours towards rival males and performed less courting behaviour and more sneak mating attempts (Tomkins et al., 2017). Both studies highlight that chemical pollutants bear the potential to interfere with the natural agonistic behaviours of aquatic species. Furthermore, increased atmospheric CO2 levels lead to ocean acidification and increases in water temperature, and both have been shown to influence animal behaviour and communication (Briffa, de la Haye, & Munday, 2012; Cattano, Claudet, Domenici, & Milazzo, 2018; Clements & Hunt, 2015; Rosa, Rummer, & Munday, 2017). However, thus far, knowledge on the influence of increasing CO2 levels on aggressive behaviour is scarce.

Animals might react to such changed environments in mutually non-exclusive ways: species that use different modalities during communication might adjust their signalling to the changed conditions, potentially lowering the importance of some of these signals while increasing the importance of others (Dunlop, Cato, & Noad, 2010). However, little is known about such adjustments during aggressive interactions thus far. Furthermore, animals might change their assessment strategy. For example, in situations where a reliable assessment of the opponent becomes impossible, they may switch to a self-assessment strategy instead. Currently, our knowledge about the impact of human activities on aquatic communication is limited to few taxonomic groups. For example, most information about the impact of anthropogenic noise on behaviour of aquatic animals come from vertebrates (Morley, Jones, & Radford, 2014). Investigating the multifarious ways that aquatic animals of different taxonomic groups communicate with each other will therefore allow us to better predict how their social behaviour is influenced by human activities. Such knowledge is necessary to inform animal conservation decisions (Delhey & Peters, 2017).

13 | PRACTICAL AND WELFARE ASPECTS

Humans heavily depend on aquatic organisms in multiple ways. For example, fishes, molluscs and crustaceans provide important sources of proteins in human nutrition and are therefore kept in aquacultures world-wide (Ashley, 2007; Håstein, Scarfe, & Lund, 2005; Vidal et al., 2014). In addition, aquatic animals are among the most commonly used laboratory animals (Vidal et al., 2014). World-wide, the number of fishes used in animal research reach comparable numbers to rodents (Sneddon, 2011), and their popularity is continuously rising (McKinnon, Kitano, & Aubin-Horth, 2019). Finally, there are millions of shrimp, molluscs and fishes bred and caught for the pet market each year (Håstein et al., 2005; King, 2019). Trading and keeping these enormous amounts of individuals puts a strong ethical obligation on humans to provide them with adequate living conditions that reduce suffering and discomfort (Huntingford et al., 2006; Iwama, 2007).

Many of the species living in human custody show elaborate social behaviours, like the shoal living zebrafish (*Danio rerio*) and three-spined stickleback, many social cichlids or the highly aggressive Siamese fighting fish. This includes highly derived communication during aggressive encounters (Balzarini et al., 2014; Pleeging & Moons, 2017; Rick & Bakker, 2008b). Understanding aggressive communication is therefore a crucial step to minimize agonistic interactions in such species. Acknowledging aggression in animals that live in groups in limited space is a first step. However, the link between fish density and aggressive interactions is complex and species-dependent. While high stocking densities lead to an increased amount of agonistic interactions and higher stress levels in some species, the opposite effect was shown in others (Ashley, 2007). Consequently, means to reduce aggression are supposed to be species-dependent and include, for example, the enrichment of the environment, the use of appropriate background and substrate colours, the feeding of aggression-reducing feeding supplements or means to support the fast establishment of clear dominance hierarchies (Ashley, 2007; Kistler, Hegglin, Würbel, & König, 2011; Williams, Readman, & Owen, 2009). Further, recognizing aggressive threats before escalation and identifying the source of aggressions may reduce costs of potentially losing injured animals and increase animal well-being. A recent study on angelfish (*Pterophyllum scalare*), for example, showed that fluctuations in water chemistry caused by regular water changes lead to an increase in aggression, especially when large amounts of water were exchanged. This was most likely caused by the disruption of chemical communication due to changed water chemistry. Changing only a small volume of water at a time was in turn found to be a good solution to prevent exaggerated aggressive interactions in these fish, leading to a reduction of detrimental effects on fish welfare (Gauy, Boscolo, & Gonçalves-de-Freitas, 2018).

Understanding aggressive communication should not only be motivated for ethical reasons but is also required to produce high-quality food resources and obtain reproducible scientific results. For example, many studies in behavioural ecology, ecotoxicology, genetics and neurobiology include measuring the aggressive potential of a given test animal. Here, mirror tests are a standard testing procedure. During such tests, an individual is presented with its mirror image and its reaction is scored. This reaction usually includes not only overt attacks, but also several visual aggressive displays (Balzarini et al., 2014). Generally, it is assumed that displays shown towards a mirror are a good proxy for an individual's aggressive potential. However, the assumption that such mirror tests reliably reflect the true aggressive propensity of an individual have recently been challenged on several grounds: neurobiological studies showed that a mirror images elicit different patterns of gene expression than a live conspecific in the brains of Burton's mouthbrooder (*Astatotilapia burtoni*) (Desjardins & Fernald, 2010) and zebrafish (Oliveira et al., 2016). Furthermore, recent studies on different cichlid fishes (e.g., three sympatric lamprologine cichlid species from Lake Tanganyika (*N. pulcher*, *Lepidiolamprologus elongatus*, *Telmatochromis vittatus*); two African riverine cichlids (*A. burtoni*, *Pelvicachromis pulcher*) and South American convict cichlids (*Amatitlania nigrofasciata*) revealed that mirror images elicit meaningful responses only in some of them, but not in others (Balzarini et al., 2014; Desjardins & Fernald, 2010; Elwood, Stoilova, McDonnell, Earley, & Arnott, 2014; Scherer, Buck, & Schuett, 2016). Thinking about the ways different fish species communicate during aggressive encounters will help explain such contrasting results. There are two potential reasons why mirror images failed in some of these species. First, one of the most common threat signals shown by many fishes are lateral threat displays. These usually involve the two contestants aligning side by side in an anti-parallel manner, which is not possible when displaying towards a mirror image (Arnott et al., 2011). Indeed, *N. pulcher*, in which mirror images were shown to be a good proxy, relies strongly on frontal displays, where orientation can only be frontally to the opponent (Balzarini et al., 2017, 2014). Second, aggressive communication might occur via a multimodal signal, including visual cues combined with acoustic, chemical, electric or mechanosensory information (Bayani et al., 2017; Chabrolles et al., 2017). When presented with a mirror image alone, the focal individual might thus react in an artificial way, as it finds it impossible to draw meaningful information from its simulated opponent. Comparable arguments need also to be considered when creating virtual stimuli using computer animations (see Chouinard-Thuly et al., 2017 for review). Incorporating knowledge of the multifarious ways in which animals communicated into such standard tests will eventually allow us to develop more reliable ways to measure animal behaviour in general.

14 | SUMMARY AND FUTURE DIRECTIONS

Aquatic organisms use a fascinating range of different sensory modalities in order to communicate their RHP and aggressive propensity. Furthermore, information might be transferred by combining several cues into multimodal signals. Understanding these signals is crucial to understand an individual's social behaviour. Still, thus far most of our knowledge of communication during aggressive encounters in aquatic animals focus on one modality, with a strong bias towards cues easily accessible and measurable for the human observer. This shortcoming prevents us from fully understanding how aquatic animals, which possess different sensory abilities to humans, communicate. Furthermore, the vast amount of studies has been conducted on species coming from a limited taxonomic range, mainly marine mammals, fishes and crustaceans. This limited knowledge is unfortunate as it prevents us from gaining an overarching understanding of aggressive communications in aquatic environments. Such in-depth understanding will be crucial not only in the light of ethics and animal welfare, but also to obtain reliable scientific results. Thus, the aim of future studies should be to apply broader sensory as well as taxonomic approaches, aiming at understanding complex multimodal signals in order to deepen our knowledge on aquatic animal's aggressive communication.

ACKNOWLEDGEMENTS

During manuscript preparation, I greatly benefitted from discussions with Leif Engqvist, Dario Josi, Manon Schweinfurth, Michael Taborsky and the participants of the lecture series in Ecology and Evolution of the University of Bern. Manon Schweinfurth, Culum Brown and three anonymous referees provided helpful comments on earlier drafts of the manuscript. I am grateful to the editors of the special feature on 'Sensory ecology and cognition in social decisions' for inviting me to write this review. My work was funded by a grant of the SNSF (31003A_166470).

DATA AVAILABILITY STATEMENT

There are no data to archive.

ORCID

Joachim G. Frommen https://orcid.org/0000-0002-1752-6944

REFERENCES

Abrahams, M. V., Robb, T. L., & Hare, J. F. (2005). Effect of hypoxia on opercular displays: Evidence for an honest signal? *Animal Behaviour*, *70*, 427–432. https://doi.org/10.1016/j.anbehav.2004.12.007

Arnott, G., Ashton, C., & Elwood, R. W. (2011). Lateralization of lateral displays in convict cichlids. *Biology Letters*, *7*, 683–685. https://doi.org/10.1098/rsbl.2011.0328

Arnott, G., & Elwood, R. W. (2009). Assessment of fighting ability in animal contests. *Animal Behaviour*, *77*, 991–1004. https://doi.org/10.1016/j.anbehav.2009.02.010

Arnott, G., & Elwood, R. W. (2010). Signal residuals and hermit crab displays: Flaunt it if you have it!. *Animal Behaviour*, *79*, 137–143. https://doi.org/10.1016/j.anbehav.2009.10.011

Aroyan, J. L. (2001). Three-dimensional modeling of hearing in *Delphinus delphis*. *Journal of the Acoustical Society of America*, *110*, 3305–3318.

Ashley, P. J. (2007). Fish welfare: Current issues in aquaculture. *Applied Animal Behaviour Science*, *104*, 199–235. https://doi.org/10.1016/j.applanim.2006.09.001

Atema, J. (1985). Receiver psychology and the evolution of multicomponent signals. *Symposia of the Society for Experimental Biology*, *39*, 387–423.

Atema, J. (1995). Chemical signals in the marine environment - dispersal, detection, and temporal signal analyses. *Proceedings of the National Academy of Sciences of the United States of America*, *92*, 62–66.

Atema, J., Fay, R. R., Popper, A. N., & Tavolga, W. N. (1988). *Sensory biology of aquatic animals*. New York, NY: Springer.

Baglioni, S. (1910). Zur Kenntnis der Leistungen einiger Sinnesorgane (Gesichtssinn, Tastsinn und Geruchssinn) und des Zentralnervensystems der Zephalopoden und Fische. *Zeitschrift Für Biologie*, *53*, 255–286.

Bakker, T. C. M. (1986). Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.) - a behaviour-genetic study. *Behaviour*, *98*, 1–144. https://doi.org/10.1163/156853986X00937

Bakker, T. C. M., & Mundwiler, B. (1999). Pectoral fin size in a fish species with paternal care: A condition-dependent sexual trait revealing infection status. *Freshwater Biology*, *41*, 543–551. https://doi.org/10.1046/j.1365-2427.1999.00403.x

Ballentine, B., Searcy, W. A., & Nowicki, S. (2008). Reliable aggressive signalling in swamp sparrows. *Animal Behaviour*, *75*, 693–703. https://doi.org/10.1016/j.anbehav.2007.07.025

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M., & Werner, N. (2001). Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology*, *50*, 134–140. https://doi.org/10.1007/s002650100343

Balzarini, V., Taborsky, M., Villa, F., & Frommen, J. G. (2017). Computer animations of color markings reveal the function of visual threat signals in *Neolamprologus pulcher*. *Current Zoology*, *63*, 45–54.

Balzarini, V., Taborsky, M., Wanner, S., Koch, F., & Frommen, J. G. (2014). Mirror, mirror on the wall: The predictive value of mirror tests for measuring aggression in fish. *Behavioral Ecology and Sociobiology*, *68*, 871–878. https://doi.org/10.1007/s00265-014-1698-7

Barata, E. N., Hubbard, P. C., Almeida, O. G., Miranda, A., & Canario, A. V. M. (2007). Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). *BMC Biology*, *5*, 54. https://doi.org/10.1186/1741-7007-5-54

Barlow, G. W. (2000). *The cichlid fishes: Nature's grand experiment in evolution*. Cambridge, MA: Perseus Publishing.

Bayani, D.-M. (2016). *Olfactory communication in the cichlid* Neolamprologus pulcher (Master thesis). University of Bern.

Bayani, D.-M., Taborsky, M., & Frommen, J. G. (2017). To pee or not to pee: Urine signals mediate aggressive interactions in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behavioral Ecology and Sociobiology*, *71*, 37. https://doi.org/10.1007/s00265-016-2260-6

Beeching, S. C. (1995). Color pattern and inhibition of aggression in the cichlid fish *Astronotus ocellatus*. *Journal of Fish Biology*, *47*, 50–58.

Bergmüller, R., Heg, D., Peer, K., & Taborsky, M. (2005). Extended safe havens and between-group dispersal of helpers in a cooperatively breeding cichlid. *Behaviour*, *142*, 1643–1667. https://doi.org/10.1163/156853905774831800

Birk, M. H., Blicher, M. E., & Garm, A. (2018). Deep-sea starfish from the Arctic have well-developed eyes in the dark. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1872), 20172743. https://doi.org/10.1098/rspb.2017.2743

Bleckmann, H., & Zelick, R. (2009). Lateral line system of fish. *Integrative Zoology*, *4*, 13–25.

Bodznick, D., & Northcutt, R. (1981). Electroreception in lampreys: Evidence that the earliest vertebrates were electroreceptive. *Science*, *212*, 465–467. https://doi.org/10.1126/science.7209544

Boulcott, P. D., Walton, K., & Braithwaite, V. A. (2005). The role of ultraviolet wavelengths in the mate-choice decisions of female three-spined sticklebacks. *Journal of Experimental Biology*, *208*, 1453–1458. https://doi.org/10.1242/jeb.01569

Bowmaker, J. K. (2008). Evolution of vertebrate visual pigments. *Vision Research*, *48*, 2022–2041. https://doi.org/10.1016/j.visres.2008.03.025

Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication*. Sunderland, UK: Sinauer.

Brantley, R. K., & Bass, A. H. (1994). Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae). *Ethology*, *96*, 213–232. https://doi.org/10.1111/j.1439-0310.1994.tb01011.x

Breithaupt, T., & Eger, P. (2002). Urine makes the difference - chemical communication in fighting crayfish made visible. *Journal of Experimental Biology*, *205*, 1221–1231.

Breithaupt, T., & Thiel, M. (2010). *Chemical communication in crustaceans*. New York, NY: Springer.

Briffa, M. (2015). Agonistic signals: Integrating analysis of functions and mechanisms. In D. J. Irschick, M. Briffa, & J. Podos (Eds.), *Animal signaling and function* (pp. 141–173). Hoboken, NJ: John Wiley & Sons.

Briffa, M., de la Haye, K., & Munday, P. L. (2012). High CO_2 and marine animal behaviour: Potential mechanisms and ecological consequences. *Marine Pollution Bulletin*, *64*, 1519–1528. https://doi.org/10.1016/j.marpolbul.2012.05.032

Briffa, M., & Elwood, R. W. (2000). The power of shell rapping influences rates of eviction in hermit crabs. *Behavioral Ecology*, *11*, 288–293. https://doi.org/10.1093/beheco/11.3.288

Brown, C., Garwood, M. P., & Williamson, J. E. (2012). It pays to cheat: Tactical deception in a cephalopod social signalling system. *Biology Letters*, *8*, rsbl20120435. https://doi.org/10.1098/rsbl.2012.0435

Bruintjes, R., & Radford, A. N. (2013). Context-dependent impacts of anthropogenic noise on individual and social behaviour in a cooperatively breeding fish. *Animal Behaviour*, *85*, 1343–1349.

Budelmann, B. U., & Bleckmann, H. (1988). A lateral line analog in cephalopods - water-waves generate microphonic potentials in the epidermal head lines of *Sepia* and *Lolliguncula*. *Journal of Comparative Physiology A*, *164*, 1–5.

Bullock, T. H., Hopkins, C. D., & Fay, R. R. (2006). *Electroreception*. New York, NY: Springer.

Bushmann, P. J., & Atema, J. (1996). Nephropore rosette glands of the lobster *Homarus americanus*: Possible sources of urine pheromones. *Journal of Crustacean Biology*, *16*, 221–231. https://doi.org/10.2307/1548878

Butler, J. M., & Maruska, K. P. (2015). The mechanosensory lateral line is used to assess opponents and mediate aggressive behaviors during territorial interactions in an African cichlid fish. *Journal of Experimental Biology*, *218*, 3284–3294. https://doi.org/10.1242/jeb.125948

Caldeira, K., & Wickett, M. E. (2003). Oceanography: Anthropogenic carbon and ocean pH. *Nature*, *425*, 365. https://doi.org/10.1038/425365a

Callander, S., Kahn, A. T., Maricic, T., Jennions, M. D., & Backwell, P. R. (2013). Weapons or mating signals? Claw shape and mate choice in a fiddler crab. *Behavioral Ecology and Sociobiology*, *67*, 1163–1167. https://doi.org/10.1007/s00265-013-1541-6

Cattano, C., Claudet, J., Domenici, P., & Milazzo, M. (2018). Living in a high CO2 world: A global meta-analysis shows multiple trait-mediated fish responses to ocean acidification. *Ecological Monographs*, *88*, 320–335.

Chabrolles, L., Ammar, I. B., Fernandez, M. S., Boyer, N., Attia, J., Fonseca, P. J., … Beauchaud, M. (2017). Appraisal of unimodal cues during agonistic interactions in *Maylandia zebra*. *PeerJ*, *5*, e3643.

Chouinard-Thuly, L., Gierszewski, S., Rosenthal, G. G., Reader, S. M., Rieucau, G., Woo, K. L., … Witte, K. (2017). Technical and conceptual considerations for using animated stimuli in studies of animal behavior. *Current Zoology*, *63*, 5–19. https://doi.org/10.1093/cz/zow104

Claes, J. M., Partridge, J. C., Hart, N. S., Garza-Gisholt, E., Ho, H. C., Mallefet, J., & Collin, S. P. (2014). Photon hunting in the twilight zone: Visual features of mesopelagic bioluminescent sharks. *PLoS ONE*, *9*, 8. https://doi.org/10.1371/journal.pone.0104213

Clapham, P. J. (1996). The social and reproductive biology of Humpback Whales: An ecological perspective. *Mammal Review*, *26*, 27–49. https://doi.org/10.1111/j.1365-2907.1996.tb00145.x

Clarke, D., Whitney, H., Sutton, G., & Robert, D. (2013). Detection and learning of floral electric fields by bumblebees. *Science*, *340*, 66–69. https://doi.org/10.1126/science.1230883

Clements, J. C., & Hunt, H. L. (2015). Marine animal behaviour in a high CO_2 ocean. *Marine Ecology Progress Series*, *536*, 259–279. https://doi.org/10.3354/meps11426

Collin, S. P., & Marshall, N. J. (2003). *Sensory processing in aquatic environments*. New York, NY: Springer.

Connor, R. C., & Smolker, R. A. (1996). 'Pop' goes the dolphin: A vocalization male bottlenose dolphins produce during consortships. *Behaviour*, *133*, 643–662.

Cook, M. E., & Moore, P. A. (2008). The effects of the herbicide metolachlor on agonistic behavior in the crayfish, *Orconectes rusticus*. *Archives of Environmental Contamination and Toxicology*, *55*, 94–102. https://doi.org/10.1007/s00244-007-9088-z

Croll, D. A., Clark, C. W., Acevedo, A., Tershy, B., Flores, S., Gedamke, J., & Urban, J. (2002). Only male fin whales sing loud songs. *Nature*, *417*, 809–809. https://doi.org/10.1038/417809a

Cronin, T. (2006). Invertebrate vision in water. In E. Warrant, & D.-E. Nilsson (Eds.), *Invertebrate Vision* (pp. 211–249). Cambridge, UK: Cambridge University Press.

Cronin, T. W., Bok, M. J., Marshall, N. J., & Caldwell, R. L. (2014). Filtering and polychromatic vision in mantis shrimps: Themes in visible and ultraviolet vision. *Philosophical Transactions of the Royal Society B*, *369*, 20130032. https://doi.org/10.1098/rstb.2013.0032

Cummings, M. E., Rosenthal, G. G., & Ryan, M. J. (2003). A private ultraviolet channel in visual communication. *Proceedings of the Royal Society of London B: Biological Sciences*, *270*, 897–904. https://doi.org/10.1098/rspb.2003.2334

Czech-Damal, N. U., Liebschner, A., Miersch, L., Klauer, G., Hanke, F. D., Marshall, C., … Hanke, W. (2012). Electroreception in the Guiana dolphin (*Sotalia guianensis*). *Proceedings of the Royal Society of London B: Biological Sciences*, *279*, 663–668.

Darwin, C. (1872). *The expression of the emotions in man and animals*. London, UK: John Murray.

Dawkins, M. S., & Guilford, T. (1993). Color and pattern in relation to sexual and aggressive behavior in the bluehead wrasse *Thalassoma bifasciatum*. *Behavioural Processes*, *30*, 245–251.

Delhey, K., & Peters, A. (2017). Conservation implications of anthropogenic impacts on visual communication and camouflage. *Conservation Biology*, *31*, 30–39. https://doi.org/10.1111/cobi.12834

Desjardins, J. K., & Fernald, R. D. (2010). What do fish make of mirror images? *Biology Letters*, *6*, 744–747. https://doi.org/10.1098/rsbl.2010.0247

Douglas, R., & Djamgoz, M. (2012). *The visual system of fish*. Dordrecht, The Netherlands: Springer.

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour*, *125*, 283–313. https://doi.org/10.1163/156853993X00290

Dunlop, R. A., Cato, D. H., & Noad, M. J. (2010). Your attention please: Increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*). *Proceedings of the Royal Society of London B: Biological Sciences*, *277*, 2521–2529.

Eaton, L., & Sloman, K. A. (2011). Subordinate brown trout exaggerate social signalling in turbid conditions. *Animal Behaviour*, *81*, 603–608. https://doi.org/10.1016/j.anbehav.2010.12.005

Elwood, R. W., & Arnott, G. (2012). Understanding how animals fight with Lloyd Morgan's canon. *Animal Behaviour*, *84*, 1095–1102. https://doi.org/10.1016/j.anbehav.2012.08.035

Elwood, R. W., Stoilova, V., McDonnell, A., Earley, R. L., & Arnott, G. (2014). Do mirrors reflect reality in agonistic encounters? A test of mutual cooperation in displays. *Animal Behaviour*, *97*, 63–67. https://doi.org/10.1016/j.anbehav.2014.07.028

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist*, *139*, S125–S153. https://doi.org/10.1086/285308

Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y., & Segerdahl, N. (1990). A test of the sequential assessment game: Fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, *40*, 1–14. https://doi.org/10.1016/S0003-3472(05)80660-8

Evans, C. S. (1985). Display vigour and subsequent fight performance in the siamese fighting fish, *Betta splendens*. *Behavioural Processes*, *11*, 113–121. https://doi.org/10.1016/0376-6357(85)90053-1

Ferrari, M. C. O., Wisenden, B. D., & Chivers, D. P. (2010). Chemical ecology of predator-prey interactions in aquatic ecosystems: A review and prospectus. *Canadian Journal of Zoology*, *88*, 698–724.

Fischer, S., & Frommen, J. G. (2013). Eutrophication alters social preferences in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, *67*, 293–299. https://doi.org/10.1007/s00265-012-1449-6

Forsatkar, M. N., Nematollahi, M. A., & Brown, C. (2017). Male Siamese fighting fish use gill flaring as the first display towards territorial intruders. *Journal of Ethology*, *35*, 51–59. https://doi.org/10.1007/s10164-016-0489-1

Frances, L. C., & Hinde, R. A. (1968). The habituation and recovery of aggressive display in *Betta splendens*. *Behaviour*, *30*, 96–106.

Franklin, A. M., Marshall, N. J., & Lewis, S. M. (2016). Multimodal signals: Ultraviolet reflectance and chemical cues in stomatopod agonistic encounters. *Royal Society Open Science*, *3*, 8. https://doi.org/10.1098/rsos.160329

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 1785–1801. https://doi.org/10.1098/rstb.2011.0213

Gauy, A. C. D. S., Boscolo, C. N. P., & Gonçalves-de-Freitas, E. (2018). Less water renewal reduces effects on social aggression of the cichlid *Pterophyllum scalare*. *Applied Animal Behaviour Science*, *198*, 121–126. https://doi.org/10.1016/j.applanim.2017.10.003

Gavrilescu, M., Demnerová, K., Aamand, J., Agathoss, S., & Fava, F. (2015). Emerging pollutants in the environment: Present and future challenges in biomonitoring, ecological risks and bioremediation. *New Biotechnology*, *32*, 147–156. https://doi.org/10.1016/j.nbt.2014.01.001

Gebhardt, K., Alt, W., & von der Emde, G. (2012). Electric discharge patterns in group-living weakly electric fish, *Mormyrus rume* (Mormyridae, Teleostei). *Behaviour*, *149*, 623–644. https://doi.org/10.1163/156853912X649911

Giaquinto, P. C., & Volpato, G. L. (1997). Chemical communication, aggression, and conspecific recognition in the fish Nile tilapia. *Physiology & Behavior*, *62*, 1333–1338. https://doi.org/10.1016/S0031-9384(97)00347-8

Gibson, R. N. (1968). Agonistic behaviour of juvenil *Blennius pholis* (Teleostei). *Behaviour*, *30*, 192–200.

Gill, A. B. (2019). The sensory ecology of fishes. *Journal of Fish Biology*, *95*, 3–4.

Goulet, J., Engelmann, J., Chagnaud, B. P., Franosch, J.-M.-P., Suttner, M. D., & van Hemmen, J. L. (2008). Object localization through the lateral line system of fish: Theory and experiment. *Journal of Comparative Physiology A*, *194*, 1–17. https://doi.org/10.1007/s00359-007-0275-1

Graham, M. A., & Noonan, M. (2010). Call types and acoustic features associated with aggressive chase in the killer whale (*Orcinus orca*). *Aquatic Mammals*, *36*, 9–18.

Grantner, A., & Taborsky, M. (1998). The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, *168*, 427–433. https://doi.org/10.1007/s003600050162

Gray, S. M., McDonnell, L. H., Cinquemani, F. G., & Chapman, L. J. (2012). As clear as mud: Turbidity induces behavioral changes in the African cichlid *Pseudocrenilabrus multicolor*. *Current Zoology*, *58*, 146–157.

Green, P., & Patek, S. (2015). Contests with deadly weapons: Telson sparring in mantis shrimp (Stomatopoda). *Biology Letters*, *11*, 20150558. https://doi.org/10.1098/rsbl.2015.0558

Green, P., & Patek, S. (2018) Mutual assessment during ritualized fighting in mantis shrimp (Stomatopoda). *Proceedings of the Royal Society B: Biological Sciences*, *285*, 20172542. https://doi.org/10.1098/rspb.2017.2542

Greenwood, A. K., Wark, A. R., Yoshida, K., & Peichel, C. L. (2013). Genetic and neural modularity underlie the evolution of schooling behavior in threespine sticklebacks. *Current Biology*, *23*, 1884–1888. https://doi.org/10.1016/j.cub.2013.07.058

Greggers, U., Koch, G., Schmidt, V., Dürr, A., Floriou-Servou, A., Piepenbrock, D., … Menzel, R. (2013) Reception and learning of electric fields in bees. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20130528.

Gregory, J. E., Iggo, A., McIntyre, A. K., & Proske, U. (1989). Responses of electroreceptors in the snout of the echidna. *Journal of Physiology*, *414*, 521–538. https://doi.org/10.1113/jphysiol.1989.sp017701

Groenewoud, F., Frommen, J. G., Josi, D., Tanaka, H., Jungwirth, A., & Taborsky, M. (2016). Predation risk drives social complexity in cooperative breeders. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 4104–4109. https://doi.org/10.1073/pnas.1524178113

Gruber, D. F., Loew, E. R., Deheyn, D. D., Akkaynak, D., Gaffney, J. P., Smith, W. L., … Sparks, J. S. (2016). Biofluorescence in catsharks (Scyliorhinidae): Fundamental description and relevance for elasmobranch visual ecology. *Scientific Reports*, *6*, 24751. https://doi.org/10.1038/srep24751

Haddock, S. H. D., Moline, M. A., & Case, J. F. (2010). Bioluminescence in the sea. *Annual Review of Marine Science*, *2*, 443–493. https://doi.org/10.1146/annurev-marine-120308-081028

Hamilton, I. M., Heg, D., & Bender, N. (2005). Size differences within a dominance hierarchy influence conflict and help in a cooperatively breeding cichlid. *Behaviour*, *142*, 1591–1613. https://doi.org/10.1163/156853905774831846

Hand, J. L. (1986). Resolution of social conflicts: Dominance, egalitarianism, spheres of dominance, and game theory. *Quarterly Review of Biology*, *61*, 201–220. https://doi.org/10.1086/414899

Hardy, I. C. W., & Briffa, M. (2013). *Animal contests*. Cambridge, UK: Cambridge University Press.

Håstein, T., Scarfe, A. D., & Lund, V. L. (2005). Science-based assessment of welfare: Aquatic animals. *Revue Scientifique Et Technique-Office International Des Epizooties*, *24*, 529–547.

Hawkins, A. D. (1993). Underwater sound and fish behaviour. In T. J. Pitcher (Ed.), *The behaviour of teleost fishes* (pp. 129–170). London, UK: Chapman & Hall.

Hebets, E. A., & Papaj, D. R. (2005). Complex signal function: Developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, *57*, 197–214. https://doi.org/10.1007/s00265-004-0865-7

Hebets, E. A., & Rundus, A. (2011). Chemical communication in a multimodal context. In T. Breithaupt, & M. Thiel (Eds.), *Chemical communication in crustaceans* (pp. 335–354). New York, NY: Springer.

Heg, D., & Bachar, Z. (2006). Cooperative breeding in the lake Tanganyika cichlid *Julidochromis ornatus*. *Environmental Biology of Fishes*, *76*, 265–281. https://doi.org/10.1007/s10641-006-9032-5

Heg, D., Brouwer, L., Bachar, Z., & Taborsky, M. (2005). Large group size yields group stability in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Behaviour*, *142*, 1615–1641. https://doi.org/10.1163/156853905774831891

Herring, P. J. (2007). Sex with the lights on? A review of bioluminescent sexual dimorphism in the sea. *Journal of the Marine Biological Association of the United Kingdom*, *87*, 829–842.

Hettyey, A., Tóth, Z., Thonhauser, K. E., Frommen, J. G., Penn, D. J., & Van Buskirk, J. (2015). The relative importance of prey-borne and predator-borne chemical cues for inducible antipredator responses in tadpoles. *Oecologia*, *179*, 699–710. https://doi.org/10.1007/s00442-015-3382-7

Hiermes, M., Rick, I. P., Mehlis, M., & Bakker, T. C. M. (2016). The dynamics of color signals in male threespine sticklebacks *Gasterosteus aculeatus*. *Current Zoology*, *62*, 23–31.

Hirschenhauser, K., Canario, A. V. M., Ros, A. F. H., Taborsky, M., & Oliveira, R. F. (2008). Social context may affect urinary excretion of 11-ketotestosterone in African cichlids. *Behaviour*, *145*, 1367–1388. https://doi.org/10.1163/156853908785765935

Hirschenhauser, K., Taborsky, M., Oliveira, T., Canario, A. V. M., & Oliveira, R. F. (2004). A test of the 'challenge hypothesis' in cichlid fish: Simulated partner and territory intruder experiments. *Animal Behaviour*, *68*, 741–750. https://doi.org/10.1016/j.anbehav.2003.12.015

Howes, G. J. (1985). The phylogenetic relationships of the electric catfish family Malapteruridae (Teleostei: Siluroidei). *Journal of Natural History*, *19*, 37–67. https://doi.org/10.1080/00222938500770031

Huntingford, F. A., Adams, C., Braithwaite, V., Kadri, S., Pottinger, T., Sandøe, P., & Turnbull, J. (2006). Current issues in fish welfare. *Journal of Fish Biology*, *68*, 332–372. https://doi.org/10.1111/j.0022-1112.2006.001046.x

Hupe, G. J., & Lewis, J. E. (2008). Electrocommunication signals in free swimming brown ghost knifefish, *Apteronotus leptorhynchus*. *Journal of Experimental Biology*, *211*, 1657–1667. https://doi.org/10.1242/jeb.013516

Ibara, R. M., Penny, L. T., Ebeling, A. W., van Dykhuizen, G., & Caillet, G. (1983). The mating call of the plainfin midshipman fish, *Porichthys notatus*. In D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, & J. A. Ward (Eds.), Predators and prey in fishes. Dordrecht, The Netherlands: Springer.

Irisarri, I., Vences, M., San Mauro, D., Glaw, F., & Zardoya, R. (2011). Reversal to air-driven sound production revealed by a molecular phylogeny of tongueless frogs, family Pipidae. *BMC Evolutionary Biology*, *11*, 114. https://doi.org/10.1186/1471-2148-11-114

Ishay, J. S., Goldstein, O., Rosenzweig, E., Kalicharan, D., & Jongebloed, W. L. (1997). Hornets yellow cuticle microstructure: A photovoltaic system. *Physiological Chemistry and Physics and Medical Nmr*, *29*, 71–93.

Iwama, G. K. (2007). The welfare of fish. *Diseases of Aquatic Organisms*, *75*, 155–158. https://doi.org/10.3354/dao075155

Jachowski, R. L. (1974). Agonistic behaviour of the blue crab, *Callinectus sapidus* Rathbun. *Behaviour*, *50*, 232–253.

Janik, V. M. (2009). Acoustic communication in delphinids. *Advances in the Study of Behavior*, *40*, 123–157.

Jerlov, N. G. (1968). *Optical oceanography*. Amsterdam, The Netherlands: Elsevier.

Kalmijn, A. J. (1966). Electro-perception in sharks and rays. *Nature*, *212*, 1232–1233.

Karavanich, C., & Atema, J. (1998). Olfactory recognition of urine signals in dominance fights between male lobster, *Homarus americanus*. *Behaviour*, *135*, 719–730. https://doi.org/10.1163/156853998792640440

Katoh, E., Johnson, M., & Breithaupt, T. (2008). Fighting behaviour and the role of urinary signals in dominance assessment of Norway lobsters, *Nephrops norvegicus*. *Behaviour*, *145*, 1447–1464. https://doi.org/10.1163/156853908785765917

Keller-Costa, T., Canario, A. V. M., & Hubbard, P. C. (2015). Chemical communication in cichlids: A mini-review. *General and Comparative Endocrinology*, *221*, 64–74. https://doi.org/10.1016/j.ygcen.2015.01.001

Keynes, R. D., & Martins-Ferreira, H. (1953). Membrane potentials in the electroplates of the electric eel. *Journal of Physiology*, *119*, 315–351. https://doi.org/10.1113/jphysiol.1953.sp004849

King, T. A. (2019). Wild caught ornamental fish: A perspective from the UK ornamental aquatic industry on the sustainability of aquatic organisms and livelihoods. *Journal of Fish Biology*, *94*, 925–936.

Kistler, C., Hegglin, D., Würbel, H., & König, B. (2011). Preference for structured environment in zebrafish (*Danio rerio*) and checker barbs (*Puntius oligolepis*). *Applied Animal Behaviour Science*, *135*, 318–327. https://doi.org/10.1016/j.applanim.2011.10.014

Kramer, B. (1996). *Electroreception and communication in fishes*. Stuttgart, Germany: Gustav Fischer.

Kramer, B., & Bauer, R. (1976). Agonistic behavior and electric signalling in a mormyrid fish, *Gnathonemus petersii*. *Behavioral Ecology and Sociobiology*, *1*, 45–61.

Kullmann, H., Thünken, T., Baldauf, S. A., Bakker, T. C. M., & Frommen, J. G. (2008). Fish odour triggers conspecific attraction behaviour in an aquatic invertebrate. *Biology Letters*, *4*, 458–460. https://doi.org/10.1098/rsbl.2008.0246

Kunc, H. P., McLaughlin, K. E., & Schmidt, R. (2016). Aquatic noise pollution: Implications for individuals, populations, and ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20160839. https://doi.org/10.1098/rspb.2016.0839.

Ladich, F., & Fine, M. L. (2006). Sound-generating mechanisms in fishes: A unique diversity in vertebrates. In F. Ladich, S. P. Collin, P. Moller, & B. Kapoor (Eds.), *Communication in fishes* (pp. 3–43). Enfield, NH: Science Publishers.

Leighton, G. M. (2017). Cooperative breeding influences the number and type of vocalizations in avian lineages. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171508. https://doi.org/10.1098/rspb.2017.1508

Levinson, S. C., & Holler, J. (2014). The origin of human multi-modal communication. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*, 20130302. https://doi.org/10.1098/rstb.2013.0302

Ligocki, I. Y., Reddon, A. R., Hellmann, J. K., O'Connor, C. M., Marsh-Rollo, S., Balshine, S., & Hamilton, I. M. (2015). Social status influences responses to unfamiliar conspecifics in a cooperatively breeding fish. *Behaviour*, *152*, 1822–1840. https://doi.org/10.1163/1568539X-00003306

Losey, G. S., Cronin, T. W., Goldsmith, T. H., Hyde, D., Marshall, N. J., & McFarland, W. N. (1999). The UV visual world of fishes: A review. *Journal of Fish Biology*, *54*, 921–943. https://doi.org/10.1111/j.1095-8649.1999.tb00848.x

Lürling, M., & Scheffer, M. (2007). Info-disruption: Pollution and the transfer of chemical information between organisms. *Trends in Ecology and Evolution*, *22*, 374–379. https://doi.org/10.1016/j.tree.2007.04.002

Marshall, J., Cronin, T. W., Shashar, N., & Land, M. (1999). Behavioural evidence for polarisation vision in stomatopods reveals a potential channel for communication. *Current Biology*, *9*, 755–758. https://doi.org/10.1016/S0960-9822(99)80336-4

Marshall, J., & Oberwinkler, J. (1999). The colourful world of the mantis shrimp. *Nature*, *401*, 873–874. https://doi.org/10.1038/44751

Marshall, N. J., Powell, S. B., Cronin, T. W., Caldwell, R. L., Johnsen, S., Gruev, V., … How, M. J. (2019). Polarisation signals: A new currency for communication. *Journal of Experimental Biology*, *222*, jeb134213. https://doi.org/10.1242/jeb.134213

Mäthger, L., & Denton, E. (2001). Reflective properties of iridophores and fluorescent 'eyespots' in the loliginid squid *Alloteuthis subulata* and *Loligo vulgaris*. *Journal of Experimental Biology*, *204*, 2103–2118.

Maynard Smith, J., & Harper, D. (2003). *Animal signals*. Oxford, UK: Oxford University Press.

Mazel, C., Cronin, T., Caldwell, R., & Marshall, N. (2004). Fluorescent enhancement of signaling in a mantis shrimp. *Science*, *303*, 51–51. https://doi.org/10.1126/science.1089803

McIver, E. L., Marchaterre, M. A., Rice, A. N., & Bass, A. H. (2014). Novel underwater soundscape: Acoustic repertoire of plainfin midshipman fish. *The Journal of Experimental Biology*, *217*, 2377–2389. https://doi.org/10.1242/jeb.102772

McKinnon, J., Kitano, J., & Aubin-Horth, N. (2019). *Gasterosteus*, *Anolis*, *Mus* and more: The changing roles of vertebrate models in evolution and behaviour. *Ecolutionary Ecology Research*, *20*, 1–25.

Mehlis, M., Bakker, T. C. M., & Frommen, J. G. (2008). Smells like sib spirit: Kin recognition in three-spined sticklebacks (*Gasterosteus aculeatus*) is mediated by olfactory cues. *Animal Cognition*, *11*, 643–650. https://doi.org/10.1007/s10071-008-0154-3

Michiels, N. K., Anthes, N., Hart, N. S., Herler, J., Meixner, A. J., Schleifenbaum, F., … Wucherer, M. F. (2008). Red fluorescence in reef fish: A novel signalling mechanism? *BMC Ecology*, *8*, 16. https://doi.org/10.1186/1472-6785-8-16

Milinski, M., & Bakker, T. C. M. (1990). Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature*, *344*, 330–333. https://doi.org/10.1038/344330a0

Modarressie, R., Rick, I. P., & Bakker, T. C. M. (2013). Ultraviolet reflection enhances the risk of predation in a vertebrate. *Current Zoology*, *59*, 151–159. https://doi.org/10.1093/czoolo/59.2.151

Montgomery, J. C., Baker, C. F., & Carton, A. G. (1997). The lateral line can mediate rheotaxis in fish. *Nature*, *389*, 960. https://doi.org/10.1038/40135

Moretz, J. (2005). Aggression and fighting ability are correlated in the swordtail fish *Xiphophorus cortezi*: The advantage of being barless. *Behavioral Ecology and Sociobiology*, *59*, 51–57. https://doi.org/10.1007/s00265-005-0008-9

Morin, J. G. (1986). Fireflies of the sea - luminescent signaling in marine ostracode crustaceans. *Florida Entomologist*, *69*, 105–121.

Morin, J. G., Harrington, A., Nealson, K., Krieger, N., Baldwin, T. O., & Hastings, J. W. (1975). Light for all reasons - versatility in behavioral repertoire of flashlight fish. *Science*, *190*, 74–76.

Morley, E. L., Jones, G., & Radford, A. N. (2014). The importance of invertebrates when considering the impacts of anthropogenic noise. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132683. https://doi.org/10.1098/rspb.2013.2683

Morley, E. L., & Robert, D. (2018). Electric fields elicit ballooning in spiders. *Current Biology*, *28*, 2324–2330. https://doi.org/10.1016/j.cub.2018.05.057

Munday, P. L., Dixson, D. L., Donelson, J. M., Jones, G. P., Pratchett, M. S., Devitsina, G. V., & Doving, K. B. (2009). Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 1848–1852. https://doi.org/10.1073/pnas.0809996106

Nakahara, F. (2002). Social functions of cetacean acoustic communication. *Fisheries Science*, *68*, 298–301. https://doi.org/10.2331/fishsci.68.sup1_298

Northcutt, R. G. (1989). The phylogenetic distribution and innervation of craniate mechanoreceptive lateral lines. In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line: Neurobiology and evolution* (pp. 17–78). New York, NY: Springer.

O'Connor, K. I., Metcalfe, N. B., & Taylor, A. C. (1999). Does darkening signal submission in territorial contests between juvenile Atlantic salmon, Salmo salar? *Animal Behaviour*, *58*, 1269–1276. https://doi.org/10.1006/anbe.1999.1260

Oliveira, R. F., Simoes, J. M., Teles, M. C., Oliveira, C. R., Becker, J. D., & Lopes, J. S. (2016). Assessment of fight outcome is needed to activate socially driven transcriptional changes in the zebrafish brain. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, E654–E661. https://doi.org/10.1073/pnas.1514292113

Olsén, K. H. (2011). Effects of pollutants on olfactory mediated behaviors in fish and crustaceans. In T. Breithaupt, & M. Thiel (Eds.), *Chemical communication in crustaceans* (pp. 507–529). New York: Springer.

Panova, E. M., Belikov, R. A., Agafonov, A. V., & Bel'kovich, V. M. (2012). The relationship between the behavioral activity and the underwater vocalization of the beluga whale (*Delphinapterus leucas*). *Oceanology*, *52*, 79–87. https://doi.org/10.1134/S000143701201016X

Partan, S., & Marler, P. (1999). Communication goes multimodal. *Science*, *283*, 1272–1273.

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *American Naturalist*, *166*, 231–245. https://doi.org/10.1086/431246

Partridge, B. L., & Pitcher, T. J. (1980). The sensory basis of fish schools: Relative roles of lateral line and vision. *Journal of Comparative Physiology*, *135*, 315–325. https://doi.org/10.1007/BF00657647

Payne, R., & Webb, D. (1971). Orientation by means of long range acoustic signalling in baleen whales. *Annals of the New York Academy of Sciences*, *188*, 110–141.

Peters, R., & Bretschneider, F. (1972). Electric phenomena in the habitat of the catfish *Ictalurus nebulosus* LeS. *Journal of Comparative Physiology*, *81*, 345–362. https://doi.org/10.1007/BF00697755

Petrie, B., Barden, R., & Kasprzyk-Hordern, B. (2015). A review on emerging contaminants in wastewaters and the environment: Current knowledge, understudied areas and recommendations for future monitoring. *Water Research*, *72*, 3–27. https://doi.org/10.1016/j.watres.2014.08.053

Pika, S. (2017). Unpeeling the layers of communicative complexity. *Animal Cognition*, *134*, 223–227.

Pitcher, T. J. (1993). *The behaviour of teleost fishes*. London, UK: Chapman & Hall.

Pleeging, C., & Moons, C. (2017). Potential welfare issues of the Siamese fighting fish (*Betta splendens*) at the retailer and in the hobbyist aquarium. *Vlaams Diergeneeskundig Tijdschrift*, *2017*, 86.

Pollard, K. A., & Blumstein, D. T. (2012). Evolving communicative complexity: Insights from rodents and beyond. *Philosophical Transactions of the Royal Society B*, *367*, 1869–1878. https://doi.org/10.1098/rstb.2011.0221

Puckowski, A., Mioduszewska, K., Lukaszewicz, P., Borecka, M., Caban, M., Maszkowska, J., & Stepnowski, P. (2016). Bioaccumulation and analytics of pharmaceutical residues in the environment: A review. *Journal of Pharmaceutical and Biomedical Analysis*, *127*, 232–255. https://doi.org/10.1016/j.jpba.2016.02.049

Raveh, S., Langen, K., Bakker, T. C. M., Josephs, C., & Frommen, J. G. (2019). Oddity, predation risk and social decisions in aquatic invertebrates. *Ethology*, *125*, 106–113. https://doi.org/10.1111/eth.12835

Reddon, A. R., Voisin, M. R., Menon, N., Marsh-Rollo, S. E., Wong, M. Y., & Balshine, S. (2011). Rules of engagement for resource contests in a social fish. *Animal Behaviour*, *82*, 93–99. https://doi.org/10.1016/j.anbehav.2011.04.003

Reusch, T. B. H., Häberli, M. A., Aeschlimann, P. B., & Milinski, M. (2001). Female sticklebacks count alleles in a strategy of sexual selection explaining MHC polymorphism. *Nature*, *414*, 300–302. https://doi.org/10.1038/35104547

Rick, I. P., & Bakker, T. C. M. (2008a). Color signaling in conspicuous red sticklebacks: Do ultraviolet signals surpass others? *BMC Evolutionary Biology*, *8*, 189. https://doi.org/10.1186/1471-2148-8-189

Rick, I. P., & Bakker, T. C. M. (2008b). Males do not see only red: UV wavelengths and male territorial aggression in the three-spined stickleback (*Gasterosteus aculeatus*). *Naturwissenschaften*, *95*, 631–638. https://doi.org/10.1007/s00114-008-0365-0

Rick, I. P., Modarressie, R., & Bakker, T. C. M. (2004). Male three-spined sticklebacks reflect in ultraviolet light. *Behaviour*, *141*, 1531–1541. https://doi.org/10.1163/1568539042948222

Rick, I. P., Modarressie, R., & Bakker, T. C. M. (2006). UV wavelengths affect female mate choice in three-spined sticklebacks. *Animal Behaviour*, *71*, 307–313. https://doi.org/10.1016/j.anbehav.2005.03.039

Ringeis, A., Krumscheid, B., Bishop, P. J., de Vries, C., & Elepfandt, A. (2017). Acoustic communication and reproductive behaviour in the aquatic frog *Xenopus laevis* (Pipidae), a field study. *African Journal of Herpetology*, *66*, 122–146.

Rosa, R., Rummer, J. L., & Munday, P. L. (2017). Biological responses of sharks to ocean acidification. *Biology Letters*, 13. https://doi.org/10.1098/rsbl.2016.0796

Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, *58*, 921–931. https://doi.org/10.1006/anbe.1999.1242

Sayigh, L. S. (2014). Cetacean acoustic communication. In G. Witzany (Ed.), *Biocommunication of animals* (pp. 275–297). Dordrecht, The Netherlands: Springer.

Scheel, D., Godfrey-Smith, P., & Lawrence, M. (2016). Signal use by octopuses in agonistic interactions. *Current Biology*, *26*, 377–382. https://doi.org/10.1016/j.cub.2015.12.033

Scheich, H., Langner, G., Tidemann, C., Coles, R. B., & Guppy, A. (1986). Electroreception and electrolocation in platypus. *Nature*, *319*, 401. https://doi.org/10.1038/319401a0

Schenkel, R. (1967). Submission - Its features and function in wolf and dog. *American Zoologist*, *7*, 319–320.

Scherer, U., Buck, M., & Schuett, W. (2016). Lateralisation in agonistic encounters: Do mirror tests reflect aggressive behaviour? A study on a West African cichlid. *Journal of Fish Biology*, *89*, 1866–1872. https://doi.org/10.1111/jfb.13069

Schumacher, S., von der Emde, G., & Burt de Perera, T. (2017). Sensory influence on navigation in the weakly electric fish *Gnathonemus petersii*. *Animal Behaviour*, *132*, 1–12. https://doi.org/10.1016/j.anbehav.2017.07.016

Schwalbe, M. A., Bassett, D. K., & Webb, J. F. (2012). Feeding in the dark: Lateral-line-mediated prey detection in the peacock cichlid *Aulonocara stuartgranti*. *Journal of Experimental Biology*, *215*, 2060–2071.

Scott, G. R., & Sloman, K. A. (2004). The effects of environmental pollutants on complex fish behaviour: Integrating behavioural and physiological indicators of toxicity. *Aquatic Toxicology*, *68*, 369–392. https://doi.org/10.1016/j.aquatox.2004.03.016

Sebastianutto, L., Picciulin, M., Costantini, M., & Ferrero, E. A. (2011). How boat noise affects an ecologically crucial behaviour: The case of territoriality in *Gobius cruentatus* (Gobiidae). *Environmental Biology of Fishes*, *92*, 207–215. https://doi.org/10.1007/s10641-011-9834-y

Sebastianutto, L., Picciulin, M., Costantini, M., Rocca, M., & Ferrero, E. A. (2008). Four type of sounds for one winner: Vocalizations during territorial behavior in the red-mouthed goby *Gobius cruentatus* (Pisces Gobiidae). *Acta Ethologica*, *11*, 115–121. https://doi.org/10.1007/s10211-008-0048-z

Seehausen, O., vanAlphen, J. J. M., & Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, *277*, 1808–1811. https://doi.org/10.1126/science.277.5333.1808

Setchell, J. M., & Wickings, E. J. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology*, *111*, 25–50. https://doi.org/10.1111/j.1439-0310.2004.01054.x

Shabani, S., Kamio, M., & Derby, C. D. (2009). Spiny lobsters use urine-borne olfactory signaling and physical aggressive behaviors to influence social status of conspecifics. *Journal of Experimental Biology*, *212*, 2464–2474. https://doi.org/10.1242/jeb.026492

Shashar, N., Rutledge, P., & Cronin, T. (1996). Polarization vision in cuttlefish in a concealed communication channel? *Journal of Experimental Biology*, *199*, 2077–2084.

Shinn, C., Santos, M. M., Lek, S., & Grenouillet, G. (2015). Behavioral response of juvenile rainbow trout exposed to an herbicide mixture. *Ecotoxicology and Environmental Safety*, *112*, 15–21. https://doi.org/10.1016/j.ecoenv.2014.10.013

Siebeck, U. E. (2004). Communication in coral reef fish: The role of ultraviolet colour patterns in damselfish territorial behaviour. *Animal Behaviour*, *68*, 273–282. https://doi.org/10.1016/j.anbehav.2003.11.010

Smith, M. R., & Dunham, D. W. (1996). Antennae mediate agonistic physical contact in the crayfish *Orconectes rusticus* (Girard, 1852) (Decapoda, Cambaridae). *Crustaceana*, *69*, 668–674. https://doi.org/10.1163/156854096X00673

Sneddon, L. U. (2011). Cognition and welfare. In C. Brown, K. Laland, & J.Krause, (Eds.), *Fish cognition and behavior*. Chichester, UK: Wiley-Blackwell.

Sopinka, N. M., Fitzpatrick, J. L., Desjardins, J. K., Stiver, K. A., Marsh-Rollo, S. E., & Balshine, S. (2009). Liver size reveals social status in the African cichlid *Neolamprologus pulcher*. *Journal of Fish Biology*, *75*, 1–16.

Sparks, J. S., Schelly, R. C., Smith, W. L., Davis, M. P., Tchernov, D., Pieribone, V. A., & Gruber, D. F. (2014). The covert world of fish biofluorescence: A phylogenetically widespread and phenotypically variable phenomenon. *PLoS ONE*, *9*, e83259. https://doi.org/10.1371/journal.pone.0083259

Stevens, M. (2013). *Sensory ecology, behaviour, and evolution* (1st ed.). Oxford, UK: Oxford University Press.

Stevens, M., & Cuthill, I. C. (2007). Hidden messages: Are ultraviolet signals a special channel in avian communication? *BioScience*, *57*, 501–507. https://doi.org/10.1641/B570607

Stuart-Fox, D. M., Firth, D., Moussalli, A., & Whiting, M. J. (2006). Multiple signals in chameleon contests: Designing and analysing animal contests as a tournament. *Animal Behaviour*, *71*, 1263–1271. https://doi.org/10.1016/j.anbehav.2005.07.028

Taborsky, M. (1984). Broodcare helpers in the cichlid *Lamprologus brichardi* - their costs and benefits. *Animal Behaviour*, *32*, 1236–1252.

Taborsky, M. (2016). Cichlid fishes: A model for the integrative study of social behavior. In W. D. Koenig, & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution, and behavior* (pp. 272–293). Cambridge, UK: Cambridge University Press.

Tallarovic, S. K., & Zakon, H. H. (2002). Electrocommunication signals in female brown ghost electric knifefish, *Apteronotus leptorhynchus*. *Journal of Comparative Physiology*, *188*, 649–657. https://doi.org/10.1007/s00359-002-0344-4

Tanaka, H., Heg, D., Takeshima, H., Takeyama, T., Awata, S., Nishida, M., & Kohda, M. (2015). Group composition, relatedness, and dispersal in the cooperatively breeding cichlid *Neolamprologus obscurus*. *Behavioral Ecology and Sociobiology*, *69*, 169–181. https://doi.org/10.1007/s00265-014-1830-8

ter Hofstede, H. M., & Ratcliffe, J. M. (2016). Evolutionary escalation: The bat–moth arms race. *Journal of Experimental Biology*, *219*, 1589–1602. https://doi.org/10.1242/jeb.086686

Thiel, M., & Breithaupt, T. (2010). Chemical communication in crustaceans: Research challenges for the twenty-first century. In T. Breithaupt & M. Thiel (Eds.), *Chemical communication in crustaceans* (pp. 3–22). New York, NY: Springer.

Thoen, H. H., How, M. J., Chiou, T.-H., & Marshall, J. (2014). A different form of color vision in mantis shrimp. *Science*, *343*, 411–413. https://doi.org/10.1126/science.1245824

Tibbetts, E. A., & Dale, J. (2004). A socially enforced signal of quality in a paper wasp. *Nature*, *432*, 218–222. https://doi.org/10.1038/nature02949

Tierney, A. J., Godleski, M. S., & Massanari, J. R. (2000). Comparative analysis of agonistic behavior in four crayfish species. *Journal of Crustacean Biology*, *20*, 54–66. https://doi.org/10.1163/20021975-99990016

Tobias, M. L., Barnard, C., O'Hagan, R., Horng, S. H., Rand, M., & Kelley, D. B. (2004). Vocal communication between male *Xenopus laevis*. *Animal Behaviour*, *67*, 353–365. https://doi.org/10.1016/j.anbehav.2003.03.016

Tobias, M. L., Corke, A., Korsh, J., Yin, D., & Kelley, D. B. (2010). Vocal competition in male *Xenopus laevis* frogs. *Behavioral Ecology and Sociobiology*, *64*, 1791–1803. https://doi.org/10.1007/s00265-010-0991-3

Tomkins, P., Saaristo, M., Bertram, M. G., Tomkins, R. B., Allinson, M., & Wong, B. B. M. (2017). The agricultural contaminant 17 beta-trenbolone disrupts male-male competition in the guppy (*Poecilia reticulata*). *Chemosphere*, *187*, 286–293.

Triefenbach, F. A., & Zakon, H. H. (2008). Changes in signalling during agonistic interactions between male weakly electric knifefish, *Apteronotus leptorhynchus*. *Animal Behaviour*, *75*, 1263–1272. https://doi.org/10.1016/j.anbehav.2007.09.027

Tsuchiya, T., Naoi, J., Futa, K., & Kikuchi, T. (2004). Difference in simulated low-frequency sound propagation in the various species of baleen whale. *Japanese Journal of Applied Physics*, *43*, 3193–3196. https://doi.org/10.1143/JJAP.43.3193

Tuomainen, U., & Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, *86*, 640–657. https://doi.org/10.1111/j.1469-185X.2010.00164.x

van der Sluijs, I., Gray, S. M., Amorim, M. C. P., Barber, I., Candolin, U., Hendry, A. P., … Wong, B. B. M. (2011). Communication in troubled waters: Responses of fish communication systems to changing environments. *Evolutionary Ecology*, *25*, 623–640. https://doi.org/10.1007/s10682-010-9450-x

van Staaden, M. J., Searcy, W. A., & Hanlon, R. T. (2011). Signaling aggression. In R. Huber, D. L. Bannasch, P. Brennan, & K. Frishman (Eds.), *Aggression* (pp. 23–49). San Diego, CA: Elsevier Academic Press Inc.

Vidal, E. A. G., Villanueva, R., Andrade, J. P., Gleadall, I. G., Iglesias, J., Koueta, N., … Wood, J. (2014). Cephalopod culture: Current status of main biological models and research priorities. In E. A. G. Vidal (Ed.), *Advances in cephalopod science: Biology, ecology, cultivation and fisheries* (pp. 1–98). Amsterdam: Elsevier.

von der Emde, G., & Bleckmann, H. (1998). Finding food: Senses involved in foraging for insect larvae in the electric fish *Gnathonemus petersii*. *Journal of Experimental Biology*, *201*, 969–980.

von Frisch, K. (1938). Zur Psychologie des Fisch-Schwarmes. *Naturwissenschaften*, *26*, 601–606. https://doi.org/10.1007/BF01590598

Wells, K. D., & Schwartz, J. J. (2007). The behavioral ecology of anuran communication. In P. M. Narins, A. S. Feng, R. R. Fay, & A. N. Popper (Eds.), *Hearing and sound communication in amphibians* (pp. 44–86). New York, NY: Springer.

Werneyer, M., & Kramer, B. (2005). Electric signalling and reproductive behaviour in a mormyrid fish, the bulldog *Marcusenius macrolepidotus* (South African form). *Journal of Ethology*, *23*, 113–125. https://doi.org/10.1007/s10164-004-0136-0

Weygoldt, P. (1976). Beobachtungen zur Biologie und Ethologie von *Pipa* (*Hemipipa*) *carvalhoi* Mir. RiB. 1937. (Anura, Pipidae). *Zeitschrift für Tierpsychologie*, *40*, 80–99.

Widder, E. A. (2010). Bioluminescence in the ocean: Origins of biological, chemical, and ecological diversity. *Science*, *328*, 704–708. https://doi.org/10.1126/science.1174269

Williams, R., Wright, A. J., Ashe, E., Blight, L. K., Bruintjes, R., Canessa, R., … Wale, M. A. (2015). Impacts of anthropogenic noise on marine life: Publication patterns, new discoveries, and future directions in research and management. *Ocean & Coastal Management*, *115*, 17–24. https://doi.org/10.1016/j.ocecoaman.2015.05.021

Williams, T. D., Readman, G. D., & Owen, S. F. (2009). Key issues concerning environmental enrichment for laboratory-held fish species. *Laboratory Animals*, *43*, 107–120. https://doi.org/10.1258/la.2007.007023

Williamson, H. (1775). Experiments and observations on the gymnotus electricus, or electric eel. *Philosophical Transactions*, *65*, 94–101.

Wong, M., & Balshine, S. (2011). The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*. *Biological Reviews*, *86*, 511–530. https://doi.org/10.1111/j.1469-185X.2010.00158.x

World Health Organization, W.H (2011). *Burden of disease from environmental noise: Quantification of healthy life years lost in Europe*. Copenhagen: World Health Organization, Regional Office for Europe.

Zubizarreta, L., Stoddard, P. K., & Silva, A. (2015). Aggression levels affect social interaction in the non-breeding territorial aggression of the weakly electric fish, *Gymnotus omarorum*. *Ethology*, *121*, 8–16.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Frommen JG. Aggressive communication in aquatic environments. *Funct Ecol*. 2020;34:364–380. https://doi.org/10.1111/1365-2435.13482