Social Recognition and Social Attraction in Group-Living Fishes

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Social aggregation is a widespread and important phenomenon among fishes. Understanding the questions of why and how aggregations form and are subsequently maintained is a central goal for behavioral ecologists. Research in this field has shown that aggregations are typically structured, non-random associations. This indicates that fish are able to differentiate between potential group-mates and that this ability mediates their association preferences, and, ultimately, the composition of their groups. In this review, we examine the characteristics that influence the expression of social attraction among fishes, before going on to describe the recognition mechanisms that underpin social attraction. Finally, we highlight a number of outstanding questions in the field with a view to generating a more complete understanding of social aggregation in fishes.

Keywords: grouping, shoaling, schooling, familiarity, relatedness, fish

INTRODUCTION

Social attraction describes the tendency of animals to approach and interact with conspecifics and is a basic mechanism underlying the formation of groups. Fundamental to social attraction is the need for animals to recognize conspecifics on the basis of cues arising from those individuals, so-called 'social recognition.' Here we define social recognition as the identification of conspecifics to a resolution that allows animals to mediate the social interactions that occur between them. In this way, animals are able to tailor their responses to the individuals that they encounter according to recognized characteristics. Such characteristics (including sex, age, coloration, and behavior) have been shown to be determining factors in the emergence of various social structures like dominance hierarchies and territorial assemblages, among others. Recent developments in both experimental and theoretical work have provided much greater insight into both the underlying mechanisms and functional consequences of social recognition, prompting us to synthesize this information here.

In this review, we focus primarily on social recognition in the context of group-living, with a particular focus on shoaling. Fish provide a fascinating opportunity to study both the functional and mechanistic underpinnings of social recognition and group choice decisions. Not only are fish the most speciose vertebrate order, but they span almost the entire spectrum of social organization and life-histories, ranging from the vast oceanic aggregations of some pelagic species, to the small, coherent groups of territorial fish. Additionally, fish have been used extensively for the study of social behavior, meaning that there is a rich literature in relation to social recognition and its role in determining social attraction. It has been estimated that over half of known fish species shoal at some point during their existence. Some shoal only during vulnerable, early life stages, while others live in groups throughout life. Based on this estimate, there are in excess of ten thousand species of fishes for whom shoaling represents a fundamentally important strategy that provides them with wide-ranging benefits (summarized in Ward and Webster, 2016).

The specificity to which fish are able to discriminate varies considerably, both within and between species. Social aggregations of fish tend to be dominated by, or even made up exclusively of, a single species, which implies at least the ability to distinguish between their own and other species, and a tendency to be socially attracted to conspecifics. Beyond this, fish are capable of making fine-scale assessments of potential social partners according to diverse phenotypic criteria that, either in isolation or in combination, serve to shape their association patterns. Further, fish are known to bias their behavior in favor of kin and familiar individuals, requiring a more specific form of social recognition. As individuals spend more time in close association, and as the complexity of social interactions increase, there is the potential for ever greater specificity to discriminate between animals, including the ability to recognize individuals.

In this review, we describe and discuss the current knowledge of social recognition and its manifestation through social attraction in group-living fishes. We begin by outlining the characteristics that influence social attraction in fishes, before moving on to consider the underlying mechanisms and sensory bases of recognition. Finally, we propose potential future work that might be done to resolve ongoing questions within this field.

CHARACTERISTICS MEDIATING SOCIAL ATTRACTION

Social recognition encompasses a wide range of different specificities, from basic categorizations of animals all the way through to individual recognition. Generally, the specificity of recognition capabilities relates to the ecology of the animals and the complexity of their social environment. For species such as herring and sardines that live in large schools comprising thousands or even millions of fish, there is perhaps little value in the ability to make fine-scale discriminations between individuals. By contrast, species of fish, including some cichlids and damselfish, that spend extended periods of time interacting repeatedly with a small number of conspecifics may derive important benefits from the ability to discern individuals.

We can characterize the process of recognition as occurring in three sequential steps (Sherman et al., 1997). The initial stage involves the production of cues by an individual. Various terms have been used to refer to this individual, including 'signaler' and 'sender.' Since cues may derive involuntarily through physiological processes, rather than as intentional efforts at communication, we subsequently refer to the cue-producing individual as the 'sender.' The second stage involves the detection of cues by another individual, whom we refer to as the 'receiver.' During this stage, the receiver references the sender's cues against a series of criteria, often referred to as a recognition template (Mateo, 2004). The sophistication of the receiver's ability to recognize the sender's cues depends both on the quantity and quality of the information contained in those cues, and on the complexity of the receiver's recognition template. The third and final stage of the sequence occurs in the form of a behavioral response by the receiver toward the sender. When the receiver detects the cues of a sender for the first time or following a period of separation, it may alter its behavior, biasing its response positively, for instance, associating with the sender, or negatively, for example through aggression. As recognition is a continuing process, if the sender and receiver are already in proximity, the receiver may not adapt its behavior toward the sender unless it perceives novel cues.

Broadly, recognition entails a receiver detecting cues from a sender and allocating the sender to a pre-existing category. These so-called class-level distinctions can enable simple differentiation between conspecifics and heterospecifics or more complex discrimination between kin and non-kin, or between familiars and non-familiars. Indeed, more sophisticated recognition may be achieved sequentially. After a receiver first determines that the individual in question is a conspecific, they may subsequently determine that it is a relative. Further, recognition need not be binary (e.g., 'kin' or 'non-kin'). Instead, individuals may recognize graded levels of kinship (e.g., 'sib,' 'half sib,' 'parent' or 'offspring'). If senders are allocated to multiple recognition classes, it may be recognized by the receiver as both kin and familiar (Frommen et al., 2007b). In some species, the ability to make class-level distinctions may be augmented by the ability to recognize particular individuals. In this case, the receiver learns the sender's characteristics and links those to a specific and unique identity. Among the many different species of fish that have been studied in the context of social recognition, there are examples occurring from the most basic, class-level discrimination all the way through to specific individual recognition.

Species-Level Recognition

One of the most basic forms of recognition involves the ability to discriminate conspecifics from heterospecifics. In binary choice tests, which are often used to examine the association preferences of shoaling species, focal fish that are presented with a choice between a group of conspecifics and a group of heterospecifics tend to show a strong preference for conspecifics (Keenleyside, 1955; Hemmings, 1966; Kinoshita, 1972; Sisler and Sorensen, 2008). The functional benefits of associating preferentially with conspecifics are wide-ranging and include access to pertinent social information and enhancement of anti-predator benefits (Ward and Webster, 2016).

Long range detection and attraction toward conspecific cues plays a crucial role in the settlement of, among others, social coral reef fishes. The life histories of such species involve larval dispersal after hatching. Following a period of pelagic feeding on plankton, the developing fish navigate toward appropriate reef habitat and then identify and home in on the cues of resident conspecifics who have already settled there (Sweatman, 1983, 1988; Booth, 1992; Atema et al., 2002; Dixson and Jones, 2018). In addition to the benefits of social grouping, the presence of conspecifics is an indicator of habitat suitability (Lecchini and Nakamura, 2013).

Social attraction is not, however, the only force that acts to drive the formation and maintenance of shoals. In addition to this active preference, passive assortment may occur so that fish self-organize into conspecific groups on the basis of similarities in habitat preferences, swimming speeds and activity

synchrony. Indeed, passive assortment via these forces can also drive the formation of mixed-species groups that share these characteristics (Krause et al., 2005; Killen et al., 2017). Nonetheless, such groups are known to fragment along species lines when under threat of predation (Wolf, 1985). Moreover, mixed species groups can be less cohesive and less aligned than single species groups and social information may flow less readily between heterospecifics than between conspecifics in some mixed species shoals (Ward et al., 2018). It seems likely that an active preference for associating with conspecifics works alongside passive assortment in shoal formation, and that both are important in maintaining shoal coherence.

Within-Species Recognition

While shoaling fish are strongly socially attracted to conspecifics, they may not be equally attracted to all such. Some elements of social recognition are concerned with the identification of fixed traits, such as kinship, while others relate to other qualities that are not intrinsic to the individual expressing them and which may change over the lifetime of that individual. The ability to navigate the social environment effectively often demands that individual fish are attuned to a suite of co-occurring characteristics in group mates and which allow them to adopt the appropriate social response in light of these.

Aspects of appearance and behavior, and the interaction between them, mediate social attraction and association preferences across a range of characteristics. Below, we will discuss within-species recognition on the basis of various attributes, such as sex, size, relatedness and familiarity.

Sex

Sex can influence shoaling behavior in a range of different ways, including directly, by influencing sociability and the expression of shoaling preferences, and indirectly, due to sexual dimorphism and differences in habitat preference and activity synchrony between the sexes. Some species of shoaling fishes show strong patterns of sexual segregation in their social behavior. In guppies, the larger females show a pronounced tendency to shoal in same sex groups, potentially as a mechanism for reducing harassment by males (Griffiths and Magurran, 1998; Darden and Croft, 2008; Richards et al., 2010). By comparison, males show a much-reduced social tendency (Griffiths and Magurran, 1998). However, even among species that do not show pronounced sexual dimorphism, shoals may be segregated to some extent by sex. For instance, male and female minnows use different parts of their habitat even outside the breeding season, leading to assortment by sex (Griffiths et al., 2014). Different preferences may be expressed according to context. In sub-adult threespine sticklebacks, fish preferred to associate with the opposite sex under low predation threat, but changed the preference in favor of same sex fish when predation risk was greater (Rystrom et al., 2018). The shoaling preferences of individuals is also mediated by the sex of the choosing fish. For example, female zebrafish prefer larger shoals over a smaller alternative shoal (Ruhl and McRobert, 2005). By contrast, in the cichlid species, *Neolamprologus pulcher*, females prefer smaller shoals than males

(Reddon et al., 2011). These choices likely represent a trade-off between the greater anti-predator benefits provided by larger shoals against considerations of competition for reproductive success or the greater opportunities for advancement in rank offered by smaller groups. Finally, the composition of shoals can often relate to the availability of potential shoaling partners. For instance, in seasonally breeding species, such as threespine stickleback, mixed-sex shoals fragment as breeding territories are established by males, leading shoals to be comprised primarily of adult females at these times (Vickery et al., 1988; Fitzgerald et al., 1992).

Size and Body Length

Shoaling fish typically express a preference to associate with conspecifics of the same size and shape as themselves in both the laboratory and in the field (Krause et al., 1996a,b; Peuhkuri, 1997; Ward and Krause, 2001; Ward et al., 2017; Kelley and Evans, 2018), potentially on the basis of forming phenotypically matched groups that maximize the anti-predator advantages of shoaling through the confusion effect or through the costs of behavioral asynchrony between differently sized fish (Theodorakis, 1989; Aivaz and Ruckstuhl, 2011). In the specific case of smaller fish avoiding larger conspecifics, there are also potentially advantages to minimizing the costs of competition. Since fish of the same size and species tend to travel at the same speed, this active preference is again bolstered by passive assortment in the formation and maintenance of groups.

Patterning and Body Coloration

Among species where there are multiple color morphs, individuals often prefer to associate with conspecifics that share the same patterning and coloration as themselves (Engeszer et al., 2007; Ledesma and McRobert, 2008; Snekser et al., 2010). As well as fixed differences in color, fish are capable of expressing different color patterns according to the local light environment and background. In Western rainbowfish, *Melanotaenia australis*, individuals acclimated to a dark background showed a strong shoaling preference for individuals also expressing the same dark coloration as themselves (Rodgers et al., 2010). By doing this, fish simultaneously maximize the predator confusion effect and reduce their per capita risk through the oddity effect (Landeau and Terborgh, 1986; Krakauer, 1995). Interestingly, this may also explain why fish sometimes join conspecific shoals characterized by a high degree of phenotypic homogeneity regardless of their own phenotype (Cattelan and Griggio, 2018).

Health and Parasitism

Aside from size and color, fish also assess the health of potential shoaling partners. This may be on the basis of externally visible indicators of parasitism, such as the spots of dark pigmentation that indicate infestation by some trematodes (Krause and Godin, 1996), the outgrowths of microsporidians (Ward et al., 2005a), or the presence of other external parasites, such as *Gyrodactylus* spp. (Croft et al., 2011; Rahn et al., 2015). Furthermore, infection and ill health may be signaled by other outward characteristics, including changes in coloration and swimming behavior (Sumpter et al., 2008). It has been shown that fish

recognize these characteristics of unhealthy conspecifics and actively avoid them in shoaling contexts (Barber et al., 2000). However, the metabolic costs of mounting an immune response and the longer-term muscle wastage resulting from infection can decrease the activity levels of infected fish, positing a role for passive assortment in the exclusion of unhealthy fish from shoals (Ward et al., 2002b).

Nutrition, Competitive Ability and Dominance

Nutrition and foraging ability influence shoal choice decisions, both from the perspective of the choosing fish and in terms of the social attractiveness of potential shoaling partners. For instance, hungry and foraging fish are less likely to shoal in general (Hensor et al., 2003; Hoare et al., 2004; Schaerf et al., 2017) and exhibit different preferences for shoaling partners relative to their well-fed counterparts (Frommen et al., 2007a). Fish also show a preference for well-fed conspecifics over their leaner, hungrier counterparts, potentially as a means of either gaining access to information from successful foragers, or to reduce competition by associating with less motivated foragers (Krause et al., 1999; Sumpter et al., 2008). Similarly, minnows (*Phoxinus phoxinus*) are able to assess the competitive foraging ability of potential group mates in relation to their foraging behavior, even outside of a feeding context, preferring to associate with less competitive individuals and thereby reducing some of the competition costs of social living (Metcalfe and Thomson, 1995). Among species that form dominance hierarchies, resource gathering potential is determined to some degree by rank. For this reason, angelfish preferentially associate with subordinate conspecifics rather than dominants (Gomez-Laplaza, 2005) on the basis of previous interactions.

Behavioral Syndromes

There is now a substantial body of literature documenting the existence of behavioral syndromes or 'personality' in animals (Dall et al., 2004; Sih et al., 2004; Bell, 2006; Reale et al., 2007; Sih and Bell, 2008; Dingemanse et al., 2010). For instance, some individuals are consistently more sociable, displaying a greater tendency to shoal. Often, this enhanced sociability covaries with the tendency to be more shy and cautious and also less aggressive (Budaev, 1997; Ward et al., 2004b; Leblond and Reebs, 2006). Studies have found that these more sociable individuals coordinate their movements more closely with conspecifics, which is a key element of coherent shoaling (Jolles et al., 2015, 2017; Planas-Sitjà et al., 2018). Perhaps in line with this, Cote et al. (2012) reported that western mosquitofish prefer to join shoals comprising sociable conspecifics over those made up of less sociable individuals. However, a test on threespine stickleback reported a preference for shoals of bolder individuals, even though such individuals are usually less sociable (Harcourt et al., 2009). This might be explained by research on guppies, *Poecilia reticulata*, in which shoals of bold individuals and shoals of both bold and shy individuals performed a foraging task more efficiently than a shoal composed only of shy individuals (Dyer et al., 2009). Despite these important individual characteristics, the social environment can have a powerful mediating effect on the expression of individual behavior, resulting in the emergence of collective, group-level personality (Webster and Ward, 2011; Hamilton and Ligocki, 2012; Burns et al., 2017; Jolles et al., 2017).

Relatedness

The ability to recognize kin forms the basis for both inbreeding avoidance and the ability to behave nepotistically, that is, to bias behavior in favor of kin. Under laboratory conditions, there have been numerous studies documenting the ability of fish to recognize kin and subsequently to demonstrate an association preference for them (Behrmann-Godel et al., 2006; Griffiths and Ward, 2011; Makowicz et al., 2016). In threespine sticklebacks, the preference for kin is independent of prior social experience (Frommen et al., 2013). In some cases, this preference is mediated by sex. For instance, female rainbowfish (*Melanotaenia eachamensis*) show significant association preferences for same-sex siblings, but avoided their male siblings, suggesting that they are able to balance the benefits of kin association against the potential costs of inbreeding (Arnold, 2000). The benefits of associating with kin can range from faster growth rates to greater shoal cohesiveness and increased co-operation (Hain and Neff, 2009; Hesse and Thünken, 2014; Hesse et al., 2015; Thünken et al., 2015).

Although the ability to discriminate kin is widespread among fishes, there is relatively little evidence to suggest that relatedness plays a major role in structuring association patterns among the majority of social fish species in the wild. Nonetheless, where it does occur, the cooccurrence of close relatives within shoals is most often observed during early life stages. For instance, in coral reef fishes, which disperse following hatching to feed in the pelagic zone before returning to the reef to settle, close relatives at the same developmental phase may be seen cohabiting shortly after settling. Among humbug damselfish, within colony genetic relatedness is typically minimal, however related juveniles may be found at the same colony (Buston et al., 2009). Similarly, in the humbug's congener, the three-spot dascyllus (*Dascyllus trimaculatus*), pairs of siblings may be found in close association following their return to the reef, suggesting that they may have traveled together during their larval development over a period of around a month (Bernardi et al., 2012). There are parallels in this pattern of early life associations among kin in guppies, where juvenile siblings associated in shoals though only in high predation environments (Piyapong et al., 2011), and in juvenile black perch, *Embiotoca jacksoni*, which associated in sib groups at a young age and directed aggression toward unrelated juveniles from other broods (Sikkel and Fuller, 2010).

The pattern of kin association occurring primarily early in life among many species might be because the advantages of kin association are greatest during vulnerable early life stages and gradually decrease as the fish age and grow. Alternatively, it may be an epiphenomenon driven by the initial proximity of members of the same brood when they are first born, or hatch, and their synchronous dispersal from the nest. Evidence of relatedness playing a role in shaping social groups of adult fish is comparatively rare. Genetic analysis of relatedness among shoals of adult guppies showed no obvious kin-structuring (Russell et al., 2004). Similar results have been reported for minnows (Bernhardt et al., 2012), cod (Herbinger et al., 1997) and salmon in the Baltic

(Palm et al., 2008) and in groups of clownfish (Buston et al., 2007). Comparatively few studies have shown evidence for kin grouping among free-ranging adult fish, although Pouyaud et al. (1999) reported the existence of relatedness as a factor shaping the shoaling of the Tilapine cichlid, *Sarotherodon melanotheron*. In another cichlid, *Neolamprologus caudopunctatus*, females, but not males, appeared to disperse from their natal nest in sibling groups (van Dongen et al., 2014). Migratory charr, however, retain some degree of kin association beyond early life (Fraser et al., 2005).

Familiarity and Individual Recognition

Familiarity is another key factor that shapes the patterns of association between fishes. We define this broadly as the recognition of and preferential biasing of behavior toward conspecifics based on prior social experience. There are different mechanistic paths that lead to the apparent social recognition of familiar individuals: one that is based on the recognition of a general, group-specific label which does not require the receiver to identify specific individual identities, and another that is founded on so-called true individual recognition. The criteria for this latter, complex form of individual recognition is that the sender's cue, the receiver's template and its response to the sender should each be unique and specific to that individual sender (Tibbetts and Dale, 2007). Most studies of familiarity in fishes have been concerned primarily with the manifestation of familiarity in terms of an association preference and subsequently with examining the functional consequences of this, rather than examining the mechanistic basis of its development. This is partly to do with the fact that, ultimately, the expression of familiarity in relation to association preferences is at least superficially similar, regardless of the mechanism at play. We discuss the mechanisms later in this review, confining ourselves for now to examples of the expression of familiarity and the benefits associated with it.

Association preferences for familiar conspecifics have been reported across a diverse range of fishes, including sticklebacks (Barber and Ruxton, 2000), guppies (Magurran et al., 1994; Cattelan et al., 2018), minnows (Griffiths et al., 2007), shiners (Farmer et al., 2004), rainbowfish (Brown, 2002), cichlids (Jordan et al., 2010b; Lee-Jenkins and Godin, 2013), salmonids (Courtenay et al., 2001), sharks (Keller et al., 2017), damselfish (Jordan et al., 2010a), and others (reviewed in Ward and Hart, 2003; Griffiths and Ward, 2011). In some circumstances, fish may even prefer to associate with familiar heterospecifics over unfamiliar conspecifics, although the functional benefits of this are unclear (Ward et al., 2003).

Associating with familiars is known to deliver a broad range of benefits, including stabilizing interactions among groups members by reducing aggression (Hojesjo et al., 1998; Seppa et al., 2001; but see Doran et al., 2019) and decreasing competition (Utne-Palm and Hart, 2000). As groups stabilize, individual members can devote a greater proportion of their time to more advantageous activities, such as foraging and mating (Griffiths et al., 2004). In fact, associating with familiars can increase foraging efficiency (Ward and Hart, 2005), potentially through greater information transfer through social networks (Atton et al., 2014), and the facilitation of social learning (Swaney et al., 2001). In addition to this enhanced foraging efficiency, shoals composed of familiar individuals are more cohesive and ordered, which may maximize the anti-predator advantages of shoaling (Chivers et al., 1995; Davis et al., 2017). Overall, the extent of the benefits enjoyed through the preferential association with familiar individuals was indicated by a study on minnows in which fish chose to shoal with familiars in preference to a larger shoal of unfamiliar conspecifics (Barber and Wright, 2001).

In addition to this group-level familiarity, some fish are also capable of true individual recognition, although this is more likely to develop in species who live in relatively stable social environments, in which they repeatedly interact with the same individuals. For instance, clownfish (*Amphiprion bicinctus*) live alongside the same individuals for much of their lives and show an ability to recognize their partner fish (Fricke, 1973). In the territorial cichlid species *Astatotilapia burtoni*, males can recognize individual rival males and infer their competitive ability (Grosenick et al., 2007). While these species may have developed the ability to recognize specific individuals due to their social system, research has also highlighted how different contexts may influence the ability to recognize individuals. Under threat of predation, performing predator inspection alongside a co-operative individual may yield benefits (Mesterton-Gibbons and Dugatkin, 1992). In territorial contexts, remembering the outcome of previous interactions may reduce future levels of aggression with the same individuals [i.e., the 'dear enemy' effect, Jaeger, 1981 (on salamanders); Saeki et al., 2018], although this may result through time-place learning rather than necessarily being individual recognition. Given the higher memory costs associated with learned individual recognition, it may be adaptive to adjust the specificity of recognition based on the context. Fittingly, research has shown that in a shoaling context, three-spine stickleback did not invest in individual recognition (Ward et al., 2009), but in a predator context (Milinski et al., 1990) and in a territorial context (Waas and Colgan, 1994), sticklebacks could differentiate between specific individuals. We consider further examples in relation to the cues and mechanisms of individual recognition in a later section.

MECHANISMS OF SOCIAL RECOGNITION AND SOCIAL ATTRACTION IN FISHES

In the previous sections, we described the characteristics upon which fish base their association preferences. However, the process by which fish detect such characteristics and use these to discriminate involve a range of different mechanisms and sensory modalities. Recognition often occurs on the basis of a template, providing a means for individuals to reference the attributes and cues of others. In some instances, however, local attraction may be mediated, at least initially, by the detection of movement. For instance, as the optomotor response develops, fish are drawn toward the movement of moving conspecifics (Lemasson et al., 2018). The relatively greater attractiveness of more mobile individuals or shoals (Pritchard et al., 2001; Gomez-Laplaza, 2006) may be one factor that induces fish to approach bolder conspecifics, which tend to be more active than their shyer

counterparts. Nonetheless, the more specific categorization and identification of sympatric animals typically relies on a more formalized process of recognition.

Recognition Templates

To achieve recognition, animals must process the cues provided by another individual and compare them against a 'recognition template' (Mateo, 2004). Broadly, these recognition templates can be categorized as: context-based associative learning, phenotype matching, and learned characteristics (Bradbury and Vehrencamp, 1998). These templates provide a means of categorizing (and therefore recognizing) the various contextual, auditory, chemical or visual information gleaned from other individuals. In some instances, the recognition template may be genetically determined, meaning that the receiver has an innate ability to recognize and categorize the cue, or it can be acquired through learning. Generally, genetically determined templates use more fixed and stable cues, such as major histocompatibility complexes (or MHCs), whereas templates arising through learning or self-referencing may rely on more transient and flexible cues, such as those mediated by diet or environment. In the following sections, we discuss each type of recognition template in more depth and provide examples from research on a wide range of fish species.

Context-Based Associative Learning

Context-based associative learning is a basic mechanism by which animals can 'recognize' other individuals based on the spatial or temporal features in their immediate environment rather than based on any cue provided by an individual themselves. As a mechanism, it is likely to persist in instances where an observable environmental feature reliably correlates with identity. For instance, parent fish may 'recognize' fry or eggs within their burrow or nest as their own offspring. Given its simplicity, this mechanism can expose parents to the risk of brood parasitism (Sato, 1986; Polačik et al., 2019). However, using the same context-based mechanism, parent fish can infer from the number of cuckolders present at a spawning site the proportion of the brood they have sired, which subsequently increases or decreases the rate of filial cannibalism or parental investment (Gray et al., 2007). Again, this is a simplistic recognition template, which can increase the risk of accidentally consuming their own offspring. For these reasons, context-based associative learning may be restricted to specific situations (e.g., before offspring have hatched and become mobile) and often necessitate the integration of more complex recognition templates. For instance, the Lake Tanganyikan mouth-brooding cichlid, *Simochromis diagramma,* collects eggs into its mouth based on contextual cues (e.g., these eggs are in the vicinity of where I mated) but subsequently employ more complex methods of kin-recognition to expel the eggs of the parasitic cuckoo catfish, *Synodontis multipunctatus,* from the buccal cavity (Blažek et al., 2018).

Phenotype Matching

Unlike context-based recognition, phenotype matching potentially provides a more flexible recognition tool that can be employed in a range of contexts and generally provides a greater degree of specificity. Phenotype matching allows for recognition through the comparison of the phenotypic cues of an unfamiliar individual against a template. The template may be formed either innately (the receiver has a pre-determined ability to recognize cues), be self-referent (i.e., based on one's own phenotype: does this individual look, sound or smell like me?) (Dawkins, 1982; Holmes and Sherman, 1982; Mateo, 2004) or experience-based (often, though not always, through imprinting during an early, labile developmental stage).

Regardless of how the phenotype template is formed, these templates can either be fixed or flexible. Innate or imprinted templates tend to be fixed, whereas self-referencing can in some instances be fixed while in others allows flexibility. For instance, though self-referencing can often provide a flexible means of recognition through the use of a variable template that reflects the receiver's current, continually updating phenotype, when used in kin recognition, the receiver self-references against a recognition template based on its own genetic profile. Given that an individual's genotype will not change during its lifetime, a self-referent kin recognition template is effectively fixed.

Kin Recognition Through Phenotype Matching

In the context of kin recognition, phenotype matching relies on the use of cues that are more likely to be similar among related individuals than between distantly related or unrelated individuals. However, the formation of the kin recognition template often depends on the reproductive system of the species in question. For instance, many species that spend initial developmental periods in close proximity to kin (e.g., many nest-building species, mouthbrooders and livebearers) rely on imprinting during early life stages. Broadcast spawners, on the other hand, are less likely to encounter siblings during early life stages and may subsequently be more likely to rely on self-referencing. Research on Arctic charr, *Salvelinus alpinus,* which hatch alongside their siblings, revealed that individuals reared in isolation were not able to recognize unfamiliar kin whereas individuals reared in proximity to siblings could, indicating that the phenotype template is learned in this species (Winberg and Olsen, 1992). Similarly, zebrafish, *Danio rerio,* are capable of recognizing unfamiliar kin using chemical cues, although this ability does not develop in individuals deprived of kin odors on the 6th day post fertilization (Gerlach et al., 2008). This suggests that their kin phenotype template is learned and that this learning occurs specifically on the 6th day after fertilization. Interestingly, when researchers exposed zebrafish to heterospecific odors on this crucial 6th day, individuals did not develop a preference for heterospecific odors. Therefore, despite zebrafish relying on a learned phenotype template, there exists some innate predisposition or sensitivity to conspecific rather than heterospecific cues.

The failure to recognize kin without exposure to odors on the 6th day post-fertilization suggests that zebrafish are not able to phenotype match through self-referencing, although this may not always be the case in other species. For instance, research on African cichlid fish, *Pelvicachromis taeniatus,* found that reproductive males were able to discriminate between sisters and non-related females despite being isolated at the egg stage.

In this case, the ability of males to recognize kin must be based on an innate and self-derived olfactory template (Thünken et al., 2014). However, research on this same species found that juveniles, who are social (unlike reproductive-stage males), did not discriminate between the olfactory cues of shoals differing in relatedness when they had been raised in isolation from egg stage. Interestingly, they also found that cichlids raised in the presence of heterospecifics developed a preference for unfamiliar heterospecific chemical cues over unfamiliar conspecific cues (Hesse et al., 2012). This highlights the role of learning in kin recognition template and, in opposition to the work done on zebrafish, it suggests that there is no fixed predisposition for conspecific cues in this species. Furthermore, this work indicates that the mechanisms of phenotype matching may be dependent on life stage (e.g., social, juvenile stages vs. solitary, adult stages) or based on context (i.e., shoaling preferences vs. mate choice).

Different phenotype matching mechanisms may even be used by different individuals of the same species. Bluegill sunfish (*Lepomis macrochirus*) have a complex mating system in which males can either become a dominant breeder, meaning they court females and provide parental care, or they can become satellite males, meaning they adopt a sneaky mating strategy and provide no parental care (Gross and Charnov, 1980). As a result, offspring sired by parental males are more likely to be surrounded by kin than the offspring sired by sneaky males. Hain and Neff (2006) examined the effect of this asymmetry in nestmate relatedness on the recognition mechanisms adopted by different offspring. They found that when the offspring of parental males were given a choice between the chemical cues of unfamiliar kin and unfamiliar non-kin (i.e., the full siblings of the sneaky male offspring), they showed no association preference. However, when the offspring of sneaky males were presented with the same choice, they showed a clear association preference for the chemical cues of their siblings. Given that all offspring were reared together, this rules out the possibility that the offspring of sneaky males were using a learnt phenotype template. Instead, these results suggest that only the offspring of dominant males relied on a learnt phenotype template while sneaky male offspring used self-referencing to distinguish between kin and non-kin.

Cues Used in Kin Recognition Through Phenotype Matching

Although the examples above have demonstrated the use of chemical cues in kin recognition (as have many other studies, e.g., Quinn and Busack, 1985; Olsen, 1989; Brown et al., 1993; Olsen and Winberg, 1996; Mehlis et al., 2008), very few studies have identified which features of a chemical signature are used in kin recognition. However, research has focused on the specific chemical cues mediated by the major histocompatibility complex (MHC), which is a set of genes that control immunological recognition in vertebrates. MHC molecules function by binding to pathogen-derived peptides and displaying them on cell surfaces for the immune cells to inspect. Ultimately, these peptide and MHC complexes are shed from the surface of the cell and expelled in saliva and urine, contributing to the chemical signature of each individual (Milinski et al., 2005). Given the heritability of MHC genotypes, these MHC-mediated chemical cues are particularly useful when distinguishing between kin and non-kin given that related individuals are likely to have similar genotypes and therefore similar chemical signatures. In fact, some researchers have referred to the use of these chemical cues in kin recognition as genotype (rather than phenotype) matching, although the mechanisms are the same.

The use of MHC-chemical cues in kin recognition was demonstrated in an experiment by Olsen et al. (2002), in which juvenile Arctic charr (*Salvelinus alpinus*) preferred to swim in water containing cues from a sibling with the same MHC class II genotype as themselves compared to water of siblings with dissimilar MHC class II genotype. However, when presented with the cues of an MHC-similar non-sibling and an MHC-dissimilar sibling, focal individuals showed no preference. These results were mirrored in work conducted by Rajakaruna et al. (2006), in which juvenile Atlantic salmon (*Salmo salar*) and juvenile brook trout (*Salvelinus fontinalis*) failed to differentiate (or had no preference) between MHC-different kin and MHC-similar non-kin. These studies both indicate that while MHC class II genotypes play an important role in kin-recognition, there are likely other chemical cues, possibly derived from other components of the genotype, that aid in kin-recognition. This is bolstered by the fact that both juvenile Atlantic salmon and juvenile brook trout showed a preference for kin over non-kin when neither had similar MHC class II genotypes (Rajakaruna et al., 2006).

Interestingly, Olsen et al. (2002) also found that when Arctic charr were reared in isolation, they did not show any behavioral preferences based on MHC odors, suggesting that their recognition template is not innate or self-referent but learned. However, this may not be universally true across all fish species. Indeed, current research hints at the possibility of innate recognition through phenotype matching [e.g., cichlids (Thünken et al., 2014)], although no study to date has specifically demonstrated innate recognition through MHC-based genotype matching.

Despite the widespread use of chemical cues in kin recognition, there are also examples of fish requiring visual cues (Steck et al., 1999) or a combination of visual and chemical cues for kin recognition through phenotype matching (Van Havre and FitzGerald, 1988). For instance, Hinz et al. (2013) expanded on the work by Gerlach et al. (2008) to show that larval zebrafish required visual exposure to kin on the 5th day post fertilization in addition to chemical exposure to kin on the 6th day post fertilization to form a template for kin recognition through phenotype matching. When larvae were provided with only visual or chemical cues, or with only the cues of non-kin, they developed no preference for kin versus non-kin chemical cues. The presence of both chemical and visual cues appears to facilitate kin recognition in later life. Arnold (2000) found that Lake Eacham rainbowfish, *Melanotaenia eachamensis,* only formed weak kin recognition abilities when provided with chemical cues. However, strong kin recognition abilities were expressed more clearly when fish were provided with both chemical and visual cues (see also Le Vin et al., 2010). It is possible that by relying on a phenotype template shaped by both visual and chemical cues, individuals can increase the likelihood of imprinting on the

correct stimulus. More generally, it may be that the recognition template is most accurate in the presence of multimodal cues and that recognition is bolstered when these cues coincide (Ward and Mehner, 2010).

Species Recognition Through Phenotype Matching

Thus far, we have discussed phenotype matching in the context of kin recognition. However, ample evidence suggests that this mechanism can be used at a more basic level to discriminate between conspecifics and heterospecifics. The mechanisms underlying species recognition share much in common with those that promote kin recognition in that they both rely to a large extent on cues that are intrinsic to the animals. The preference of fish to associate with conspecifics in shoal choice decisions is well established and wide-ranging among social animals, however, the question of whether the template involved in species recognition is innate, fixed by imprinting or self-referent has received comparatively little attention. As with kin recognition, the formation of the template may depend to a degree on the reproductive strategy of the species and thus the probability that young fish develop in proximity to conspecifics. For instance, striped kribs (*Pelvicachromis taeniatus*) reared in the nest of a congeneric species, the common krib (*Pelvicachromis pulcher*) subsequently showed a preference for the odors of heterospecifics over conspecifics, suggesting that the young imprinted on the fish with which they were surrounded in early life rather than self-referencing (Hesse et al., 2012). In a similar way, a study by Warburton and Lees (1996) reported that guppies that had been reared among swordtails (*Xiphophorus helleri*) subsequently showed a preference for associating with those heterospecifics. In both of these cases, the development of the recognition template appears to have been formed by early life experiences rather than being either innate or self-referent. In a parallel example, Spence and Smith (2007) found that zebrafish preferred to shoal with the color morph with which they were raised rather than individuals displaying the same color morph as themselves. With the exception of zebrafish, which scatter their eggs and provide no parental care, little research has examined the development of kin or species recognition templates in broadcast spawning fish, representing a clear priority for future research.

The studies discussed above have exemplified the way in which many species, often those that are reliably surrounded by kin during early developmental stages, use imprinting to form fixed recognition templates. However, the potential exists for mistakes to occur through imprinting, which may have severe fitness costs. For instance, Stephenson and Reynolds (2016) found that juvenile guppies exposed to conspecifics infected with the parasite, *Gyrodactylus turnbulli*, subsequently showed an association preference for those conspecifics carrying the parasite, which is likely to put them at risk of infection. Generally, however, the ramifications of incorrect species recognition in the context of shoaling are not this extreme. On the other hand, species-recognition in the context of mating is more likely to have severe consequences when individuals cannot correctly differentiate between viable mates (i.e., conspecifics) from non-viable mates (i.e., heterospecifics), especially in environments where closely related species overlap. Accordingly, Magurran

and Ramnarine (2004) found that male guppies (*Poecilia reticulata*) from isolated populations were unable to discern between conspecific females and heterospecific females (*Poecilia picta*). However, males from sites where the two species live sympatrically could recognize conspecifics from heterospecifics. This suggests both the ability for species recognition mechanisms to adapt and evolve over time as well as the use of phenotype matching in the discrimination of different species.

Cues Used in Species Recognition Through Phenotype Matching

The sensory cues used in species recognition potentially varies across different fishes, however chemical cues are likely to play a major role (Levesque et al., 2011). The use of chemical cues allows a high degree of specificity. In a study using six closely-related cyprinid species, Sisler and Sorensen (2008) reported that common carp, *Cyprinus carpio*, and goldfish, *Carassius auratus*, were clearly able to distinguish conspecifics from heterospecifics. Further, the ability to detect conspecifics is lost in fish whose olfactory sense has been ablated (Sorensen and Baker, 2015). Ward et al. (2002a) demonstrated that chub, *Leuciscus cephalus,* prioritize chemical cues over visual cues to shoal with conspecifics rather than heterospecifics (European minnows, *Phoxinus phoxinus*) when the cues were presented in juxtaposition. In fact, when presented with two mixed species shoals, chub spent increasingly more time with shoals as the percentage of conspecifics increased. Given that European minnows outcompete same-sized chub in mix-species shoals, phenotype matching may be an important mechanism used by chub to enhance their foraging success by shoaling preferentially with conspecifics. Among social reef fishes, chemical cues are also used to distinguish conspecifics (Sweatman, 1988; Doving et al., 2006) and may be important in determining the patterns of aggression between heterospecific competitors (e.g., Bay et al., 2001). Coppock et al. (2016) found that among four different species of damselfish, three showed a preference for conspecific chemical cues while all four actively avoided heterospecifics cues. In this case, conspecific associations may be generated by both attractive and repulsive forces.

In addition to chemical cues, species-level recognition can be achieved using a visual, auditory or even electrical cues. For instance, weakly electric fish have species-specific electrical organ discharges, providing an electrical template for species recognition (Kramer and Kuhn, 1994). In coral reef fish, UV markings on the face and body have been found to promote species recognition (Siebeck et al., 2010). In many African cichlids, females prefer the coloration patterns of conspecific males over heterospecific males (Seehausen et al., 2008). This visual phenotype template has been proposed as a mechanism behind the sympatric speciation of these fishes, although there is evidence that species-specific acoustic calls may further aid in species recognition and sexual isolation (Amorim et al., 2004, 2008).

Flexibility in Phenotype Matching

Thus far, we have discussed phenotype matching as a recognition template mediating long-term species-level and kin-level

preferences. However, phenotype matching can also provide a more flexible template used in short-term and shifting preferences. This is due to the fact that phenotype matching can provide a means of recognition using variable cues. One way in which flexibility can be achieved is by updating association preferences on the basis of recent experience. Juvenile angelfish, for example, adapt their preference in favor of associating with the color or pattern morph of the individuals that they most recently interacted with Gómez-Laplaza (2009) and a similar flexibility may underlie temporal shifts in preference for individuals with a matching color morph in rainbowfish (*Melanotaenia australis*) (Rodgers et al., 2010). In this case, the color expressed by the fish changes as a function of their environment, hence flexibility is required to enable individuals to adopt a shoaling preference according to their current phenotype. Though it seems likely that visual cues play a major role in this, it is possible that the preference may be augmented by chemical cues. For instance, although Ward and Krause (2001) found that body length matching in fish could be achieved through visual cues alone, Ward and Currie (2013) found that it could also be achieved through chemical cues alone. In these cases, fish appear to be self-referencing on the basis of continually updated cues in order to assort with same-sized individuals, which may provide important anti-predator benefits. However, the question of how a fish knows how large it is (or what color it is) and thus how to match its size (or color) with conspecifics purely on the basis of visual cues remains unknown.

The mix of chemicals contributing to a fish's chemical signature represent a continually changing representation of both intrinsic factors, such as their physiological state, and extrinsic factors, such as the animal's environment or diet (Henneken et al., 2017; Nikonov et al., 2017). These cues are known to affect association preferences with fish preferring to shoal with individuals that smell most like themselves, which clearly implicates self-referent phenotype matching as the mechanism. In particular, fish show an association preference for conspecifics that have eaten the same diet as themselves (Olsen et al., 2003; Ward et al., 2004a, 2005b). In addition to this, fine-scale differences in water chemistry among habitats also mediate shoaling preference, with fish favoring conspecifics that have occupied a similar habitat over those from a different habitat. The adaptability of this mechanism was examined by Ward et al. (2007), who reported that free-ranging sticklebacks transplanted between habitats gradually adopted a preference for individuals from their new habitat. The specific time frame involved in the shift in this preference appears to be in the order of 1–2 h (Webster et al., 2007). Although the precise nature of the chemical cues involved is not yet known, a study by Bryant and Atema (1987) reported that a change in the diet of yellow bullhead catfish, *Ameiurus natalis*, precipitated a change in urine-borne amino acids and, most importantly, a change in response toward those individuals by conspecifics. Diet quality may also influence association decisions and potentially provides a means of distinguishing between individuals on the basis of their foraging ability and determining which have valuable social information. In particular, the proportion of protein in the diet mediates association preferences, with individuals preferring

to associate with conspecifics who had recently consumed a high protein diet (Ward et al., 2011). Again, the dietary cues are most likely expressed through amino acids in the urine (Kleinhappel et al., 2016).

Recognition typically involves the discrimination of multiple traits sequentially or even simultaneously. The ability to assess a third party on the basis of a suite of traits can lead to straightforward decisions when preferred traits are interlinked. For instance, kin recognition is obviously aligned with species recognition, however, in other cases, the co-occurrence of conflicting cues can give insight to the basis of association preferences. For example, in a study involving two stickleback species, the threespine stickleback (*Gasterosteus aculeatus*) and the ninespine stickleback (*Pungitius pungitius*), threespine sticklebacks associated with heterospecifics that had been fed the same diet as themselves in preference to conspecifics that had been fed with a different diet (Kleinhappel et al., 2016). Similarly, Ward et al. (2003) found that the preference of chub for conspecific shoals disappeared when they had to choose between unfamiliar conspecifics and familiar heterospecifics. In both cases, fish are capable of species recognition, yet chose to associate with heterospecifics based on the presence of different, perhaps more pertinent, cues (e.g., diet and familiarity). Ultimately, these studies demonstrate the many levels of recognition that can be achieved through phenotype matching and the subsequent complexity involved in making association decisions.

Learned Individual Characteristics – Familiarity and Individual Recognition

True individual recognition involves the ability of a receiver to associate a unique and distinct set of a attributes with the individual identity of the sender, and then to express a distinct pattern of behavior toward the sender (Beecher, 1989; Gheusi et al., 1994; Gherardi et al., 2012) see also Steiger and Mueller (2008). Consequently, this is most likely to be seen in stable groups, where individuals interact frequently and repeatedly over time. Further, it is a cognitively demanding process and it may be that at least some of the documented cases of familiarity, wherein fish bias their behavior in favor of individuals with whom they have prior social experience, may involve a more general recognition mechanism, focused on some group or population-specific cue. For individual recognition to evolve, selection must act not only upon the receiver, to be able to perceive and recognize cues from the sender, but also upon the sender itself, to produce salient and easily detected, recognizable and individually specific cues. This will likely only happen where these is a mutual net benefit to the sender in being recognized by the receiver (Tibbetts and Dale, 2007). These may be related to mediation of aggressive or agonistic encounters between members of stable groups or between nearby territory holders, for example. Where these conditions are not met, as may be the case in many ephemeral, fission-fusion shoals, there might be no pressure favoring adaptations for individual recognition, from either a sender or a receiver perspective. Instead, class-level recognition of the types discussed above may be sufficient for fish to make adaptive social decisions.

Nevertheless, there is evidence that some fish are capable of recognizing non-related individuals independently of context on the basis of prior social experience and learning. This ability is likely associated with cognitive constraints that limit the number of individuals whose identities may be learned (Fischer et al., 2014). Griffiths and Magurran (1997b) inferred individual recognition among guppies that lived in small, isolated pools during the dry season. They showed that guppies preferred to shoal with fish taken from their own 'home' pool, but only when the population of fish within that pool was lower than 40 or so. This preference was absent when the population of the pool was greater than this, and Griffiths and Magurran (1997b) suggest that this might reflect an upper limit on the number of separate identities that guppies can learn. If the recognition here were based on a class-level template of some sort, they argued, then the guppies should have displayed a preference for others from their own pool irrespective of the population size. Ward et al. (2009) used a different approach to tackle this question, determining that guppies were capable of learned individual recognition. First, they established that guppies preferred to shoal with unfamiliar groups that had experienced the same diet and environmental condition as themselves, which suggests an ability to recognize certain familiar group-level characteristics, via phenotype matching. Second, they established that guppies could differentiate between two shoals that had been maintained in the same tank as themselves (hence with the same diet and environmental cues), but that they preferred the group with whom they had directly interacted (rather than the ones who had been separated by an opaque barrier). Given that the guppies in this experiment were not closely related, it is unlikely that this preference was the result of kin recognition. Furthermore, given that both individuals had the same environmental and diet chemical signatures, it is unlikely that phenotype matching was the recognition template generating this preference. Instead, their results suggest an ability to recognize individual chemical cues based on experience with specific individuals.

A study by Griffiths and Magurran (1997a), demonstrated that this individual recognition template in guppies developed over a period of 12 days after repeated interactions with the same individuals. In discus fish, individuals were able to recognize fish with whom they had been housed for 3 months based on specific facial color patterns (Satoh et al., 2016). These studies help demonstrate that individual recognition is often the result of long learning periods. However, fish are also capable of more rapid learning. For instance, Dugatkin and Michael (1991) found that guppies could discriminate between two individuals and show a consistent preference for the individual that was more cooperative during a predator inspection trial (i.e., the one that swam closer to the predator). This preference was consistent whether focal individuals were made to choose between the pair directly after the predator trial or 4 h after the predator trial.

Various cues can be used to form an individual recognition template. In weakly electric African mormyrid fish, signature electric organ discharges (EODs) can be used to achieve individual recognition (Paintner and Kramer, 2003). In a study by Hanika and Kramer (2005), territorial males of *Marcusenius macrolepidotus* increased aggression when presented with longer

duration EODs. However, this aggression dropped off when the playback EOD was from a familiar rival. This provides support for the 'dear enemy' effect and suggests that these weakly electric fish can use EODs as a template for learned individual recognition. In further support of the 'dear enemy' effect, Kohda et al. (2015) found that male cichlids, *Neolamprologus pulcher*, reduced aggression when presented with models that had the same facial color patterns as a familiar rival. In addition to the dear enemy effect, this study also demonstrates the use of visual cues in forming individual recognition templates and points to the importance of facial features in individual recognition more broadly (Leopold and Rhodes, 2010; Wang and Takeuchi, 2017; Hotta et al., 2017). Given the greater cognitive demands of individual recognition, it is likely to develop in socially stable species or in specific contexts characterized by repeated interactions with the same individuals. In fact, the ability of sticklebacks to recall familiars decayed over the course of 1–2 weeks when individuals were no longer interacting (Utne-Palm and Hart, 2000).

OUTSTANDING QUESTIONS

How Do Shoal Preferences in the Lab Shape Social Organization Patterns in Nature?

Social preferences based on recognition and active choice have been investigated experimentally using a number of approaches. Perhaps the commonest is the choice test, in which a test subject is presented with two or more stimulus fish or groups of fish and allowed to interact with both. The amount of time that it spends with one relative to the other is taken as a measure of shoaling preference, with a significant bias toward one stimulus group over the other(s) implying recognition of some trait particular to that stimulus group (e.g., Wright and Krause, 2006). Variations on this approach have been used in many of the examples discussed below. A less commonly used method of assessing social preference is one based upon self-organization. Here, a number of fish are placed together into an arena and allowed to separate into groups. Various statistical approaches can then be employed to allow the investigator to determine whether these groups are random subsamples of the larger pool of fish or whether they assorted by some factor. Different versions of this approach were used by Barber and Ruxton (2000) and Atton et al. (2014) to explore the effects of familiarity upon fish shoal composition. The shoal choice test can be criticized for presenting the test subjects an unnatural stimulus; it is unlikely that fish in the wild will ever be presented with a simultaneous choice between two perfectly different stimulus shoals, such as a shoal of large versus a shoal of small conspecifics. This is probably true much of the time, though not always. Guppies living in pools separated by shallow rapids travel in small groups that regularly meet and exchange members; in one study, Croft et al. (2003) describe encounters between shoals as occurring every 14 s on average. In a field study of golden shiners (*Notemigonus crysoleucas*), shoals met on average every minute

or so (Krause et al., 2000). Hence, fishes living in high densities in small bodies of clear water might have many opportunities for near simultaneous observation and assessment of shoals, lending this assay a degree of ecological validity, at least under some circumstances. One clear advantage of choice test experiments over other assays is that, if designed rigorously, it can allow for recognition to be explicitly tested for. With further elaborations, this approach can also be used to explore the mechanisms of recognition, for example by blocking certain sensory channels or by systematically varying or manipulating sender cues. Even if we allow the criticism that simultaneous choices are unlikely to occur in nature under many conditions, the choice test still represents a powerful approach for demonstrating recognition and social preferences. Further, it allows us to examine how fish might weigh the relative importance of multiple different criteria in respect of potential shoaling partners, for instance whether they prioritize size, sex, color or other characteristics, and how they integrate these factors in making a decision of which shoal to join. Data from choice tests can be used *a priori* to derive hypotheses about shoal composition when studied under more natural conditions, or *post hoc*, to probe already-observed shoaling patterns.

Other Factors Affecting Shoal Composition

In some cases, fish shoal composition might not solely be shaped by active choices by group members. For example, the decision of an individual to join a group might reflect a lack of alternative choices, and predators may play a role in 'pruning' groups by targeting certain phenotypes. In addition, abiotic factors may also play a role. Some of the ideas discussed here are speculative but may warrant further investigation. The take home message here is that shoal structure can emerge without active choice (or in the absence of options to choose between) and researchers should be careful in assuming that the composition of fish shoals reflects decisions based upon recognition by the fish.

Many species of fish prefer to shoal with conspecifics and with groupmates of a similar body size. Such preferences may be adaptive, since predators may disproportionally target odd individuals, and costs to appearing different to the rest of the group will therefore be high. Where individuals are able to choose, we might expect them to select shoals of the same species or phenotype to their own. Shoals frequently split and reform, however, and individual fish can stray or become separated from their group. While being odd may be costly, being alone might be even more so, since many of the anti-predator asocial foraging benefits of grouping should accrue even to odd individuals. Under such conditions, it might pay a lone fish to join any group it encounters, even if it differs from the majority of fish within the group. This might explain why mixed-species groups are often numerically dominated by a majority species, with the other species occurring as minorities (Krause et al., 2000; Pavlov and Kasumyan, 2000). It would be interesting to quantify whether the predation and associated risks of lone fish are lower compared to similar fish that are odd members of mixed species or phenotypically mixed shoals. We predict that this will often be the case. We also predict that mixed species shoals will be less common, or at least more short-lived when the densities of all of the member species or phenotypes are greater, since this will afford more opportunities to encounter and shoal with matched groupmates.

Related to the oddity effects discussed above, in theory, targeting of odd individuals by predators might have the overall effect of reducing diversity and promoting greater within-shoal homogeneity. In this way, a shoal that initially contains a range of phenotypes might become more similar over time, as less common phenotypes are removed, without the need for active shoal choice or self-organization by the members of the shoal. It is unclear how important this process is in nature, and it is not clear whether such a pruning process could keep pace with changes in shoal composition as groups encounter one another and exchange individuals. A testable hypothesis here is that the actions of predators and the threat of predation should contribute to greater homogeneity in shoal composition in habitats with abundant predators.

Finally, assortment by body size might arise as a function of swimming energetics. If smaller-bodied fish have to expend more energy to keep a given pace than larger ones do, then shoals may be come segregated by size when moving and perhaps may even split. This effect may be exacerbated when fish are swimming against a current or holding station in moving water. This effect has already been described within shoals, where larger individuals tended to be in frontmost positions in the traveling shoals (Deblois and Rose, 1996; Reebs, 2001; Ward et al., 2017). This would lead to the prediction that groups of fish in faster-flowing water, and faster moving groups, would be more closely assorted by body length.

Assessing Social Recognition Mechanisms in Naturalistic Settings

Building on our previous point, assays of social attraction and recognition in the laboratory often involve the presentation of consistent stimulus cues with a high signal to noise ratio. For instance, studies using chemical cues are often undertaken using high concentrations of those cues and in the absence of other, potentially relevant cues that might be encountered by free-ranging fish. As a first step, such studies offer a reasonable means of determining whether fish are able to detect such cues and how they respond to them. However, determining how these cues influence the behavior of fish in the wild demands that greater ecological relevance is built into future experiments. One possible approach to this is to conduct experiments using water from the natural environment, including a mix of different chemical cues, and thus providing a more representative signal to noise ratio against which to measure social recognition and social attraction.

Broadening Our Understanding of the Mechanisms of Social Recognition

While considerable work has been done to elucidate the factors that shape the association decisions of group-living fishes, research into the mechanistic bases of this lags behind. The chief exception to this is in the context of kin recognition, which has been well studied. However, even in this case, work remains to be

done to characterize the key attributes of the cues used. Many questions remain in regard to understanding the type and the ontogeny of templates used by fish to recognize conspecifics and to distinguish between conspecifics. Similarly, more work needs to be done to identify the sensory modalities used to differentiate between conspecifics and the salient characteristics of the cues that are used. An obvious example is how fish recognize and avoid diseased conspecifics, which has been resolved in other taxa [e.g., amphibians (Kiesecker et al., 1999), mammals (Kavaliers et al., 2005), and crustaceans (Behringer et al., 2006)].

SUMMARY AND CONCLUSION

Social recognition forms the basis of social organization. In the context of group-living in fishes, it permits individuals to distinguish between potential grouping partners and mediates differences in social attraction among them, ultimately structuring and shaping patterns of association among individuals. A combination of a basic social attraction toward conspecifics and more passive processes such as activity synchrony and co-ordination of swimming speeds are likely sufficient to explain the large, structured aggregations of pelagic fishes. Nonetheless, the groups formed by many other species are often reliant on more complex forms of recognition and, in turn, permit the development of more intricate patterns of association

and social behaviors. Examples of these include groups that are structured by relatedness or familiarity, encompassing individual recognition, and which persist over extended periods of time. Our understanding of the mechanisms of social recognition, including the recognition template used by receivers and the characteristics of the cues expressed by senders, requires further research, not least in order that we might be able to predict how social fishes will adapt to future environmental challenges. Approaches that combine both detailed insights of patterns of social organization in free-ranging fishes with an understanding of the underlying mechanisms of social recognition and social attraction offer the best means to advance this field of research.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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