University of Groningen

Experimental analysis and modelling of the behavioural interactions underlying the coordination of collective motion and the propagation of information in fish schools

Lecheval, Valentin Jacques Dominique

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2017

[Link to publication in University of Groningen/UMCG research database](#)

Chapter 1

General introduction

1.1 Collective motion in fish

Collective motion is ubiquitous in fish: it is assumed that 50% (i.e. approximately one fourth of all vertebrates species (IUCN, 2017)) of the 34,515 species of fish known nowadays (Eschmeyer et al., 2017) swim in groups at some point of their life (Shaw, 1978). Gregariousness in fish has even led to very large groups of thousands to millions of individuals (e.g. in herrings) yielding striking examples of collective motion such as bait balls (Figure 1.1).

The organisation of groups of fish is very diverse across species – and varies in time for some species (Tunstrøm et al., 2013). Groups are usually referred to as *shoals*, *swarms* or *schools*. All groups of fish that have aggregative tendencies can be termed as *shoals*. When the group members adopt the same orientation (i.e. they have a tendency to *polarise*) the group is called *a school*. In contrast to *schools*, groups that are loosely structured and whose members have random orientations although maintaining a significant degree of cohesion, are labelled *swarms* (Delcourt and Poncin, 2012, for a review).

In fish, it is commonly assumed that living in groups may improve the efficiency of individual motion (Hemelrijk et al., 2014), foraging (Pitcher et al., 1982) and, most of all, protection against predator threat (Krause and Ruxton, 2002). The latter is achieved thanks to several mechanisms, commonly termed as, among others, dilution of risk (Foster and Treherne, 1981), confusion effect (Ioannou et al., 2007), predator detection (Elgar, 1989) or attack-abatement effect (Turner and Pitcher, 1986). It has been found that predation threat increases the cohesion of fish shoals (Seghers, 1974; Herbert-Read et al., 2017). Still, it is unclear whether collective pat-
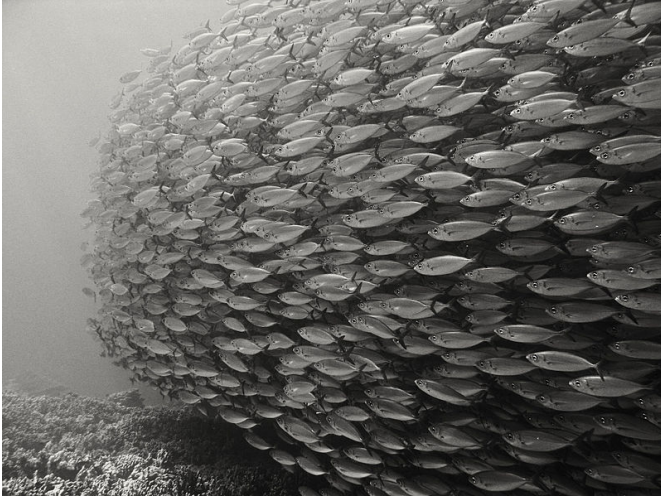
Figure 1.1: Edge of a *Caranx latus* bait ball. Work by Steve Dunleavy published on Flickr (under licence CC BY 2.0).

terns reported in fish are adaptive or not – that is if they actually increase survival of individuals when a group is attacked for instance (Parrish and Edelstein-Keshet, 1999). In particular, since there is a great diversity of collective patterns, it is possible that some of them are evolutionarily neutral, or even pathological, as the rotational formation (so called *milling*) of army ants (Delsuc, 2003) that is also found in fish (Tunstrøm et al., 2013). Therefore, it seems essential to distinguish biologically relevant features from non-adaptive epiphenomena as well as to describe the causal links between mechanisms at the individual-level and group patterns to improve the understanding of fish aggregations in nature (Parrish et al., 2002).

The multiplicity of the levels at which groups of fish (and of animals in general) can be described makes them complex systems. The relations and feedback loops of the genes, the brain, and the social behaviour are entangled across several scales in time, from organismal development to evolutionary time, and space, from DNA molecules to groups of millions of individuals (Robinson et al., 2008). The study of these challenging systems thus requires to carefully define the extent of the time and spatial scales examined.

It seems necessary to characterise and quantify the interactions between individuals underlying the collective behaviours to make causal links from the neural and cognitive basis of individual behaviours to the collective behaviours in which these neuronal and cognitive processes are involved (Weitz et al., 2012). This thesis aims to investigate the behavioural mech-

anisms that are involved in the control of the coordination of motion and in the propagation of information within groups of fish.

This thesis consists of two main parts. The first part investigates how schooling behaviour emerges from the interactions between individuals. The second part examines how information propagates in groups of fish in response to internal and external perturbations. In what follows I present the framework of my thesis and a short review of the propagation of information among animals.

1.2 Analysing collective motion in fish

There have been recent developments in experimental and modelling methods in the field of collective behaviour in fish. They are shortly reviewed below.

1.2.1 Modelling methods

It is not necessary, and it is even impossible in large groups, for each fish swimming in shoals to have a complete knowledge of the group properties (such as the average orientation of the group members). It is commonly assumed that collective behaviour in fish is not choreographed by leaders but results from self-organization processes. In these systems, the collective patterns emerge from the local interactions among individuals that only have access to partial information (Bonabeau et al., 1997; Camazine et al., 2001). Models of collective motion in fish therefore investigate how the collective behaviour in a school emerges from assumed local interactions.

Seminal work of the late twentieth century has emphasized theoretical and general (i.e. not restricted to a taxon) mechanisms (see Lopez et al., 2012, for a review). Studies have mainly suggested theoretical rules of interactions between individuals, involving attraction, alignment and repulsion for most of them, and shown that group properties emerged from these rules. As pointed out by several authors, different quantitative combinations of these three basic rules can lead to the same properties observed at the collective scale (Weitz et al., 2012; Lopez et al., 2012). If several initial hypotheses can be compatible with the same properties at the group level, it is thus difficult to shed light on the actual individual mechanisms involved in the coordination of groups for a given species by looking at the collective behaviour.

As claimed by Weitz et al. (2012) and Lopez et al. (2012), the methodological framework introduced by Gautrais et al. (2009, 2012) is relevant to

overcome the difficulty mentioned above. In these two studies, a bottom-up data-driven method of modelling has been introduced. Data-driven modelling implies that every step of the modelling process, i.e. all hypotheses required in the formulation of the model, are validated against data. Bottom-up stands for starting first with a model of motion of a single fish swimming spontaneously, which is validated against experimental data (Gautrais et al., 2009). Then, they used this model and added terms of interaction with a second fish and more (Gautrais et al., 2012). These two studies, by closely combining experimental data and modelling approaches at each step, found mathematical formulations for the stimulus-response functions governing decisions of fish in response to the position and orientation of its neighbours. The authors have found that a gradual weighting between alignment (dominant at short distances) and attraction (dominant at large distances) best accounted for their experimental data. They also reported that the parameters governing these two types of interactions depend on the average speed of fish, leading to an increase in group polarization with swimming speed, a direct consequence of the predominance of alignment at high speed. However, here, the interactions of a fish with the walls of the tank or with other fish were only assumed to take phenomenological functional forms fitting well the experimental data. In other words, the mathematical equations of the interactions were not truly extracted from the experimental data nor derived from a theoretical framework. Thus, a natural question which arises is whether the fair quantitative agreement of the model with experiments actually constitutes an implicit validation of the assumed forms of the interactions. This question is addressed in the first chapter of this manuscript.

Other authors have also tried to measure the interactions in groups of fish from their experimental trajectories but without testing whether their findings could be used in a model to predict group properties (Katz et al., 2011; Herbert-Read et al., 2011).

Recently, other models have included a reconstruction of the visual fields of fish (Strandburg-Peshkin et al., 2013; Rosenthal et al., 2015; Collignon et al., 2016). Although these approaches are promising, they may suffer from a lack of specific experimental validation of the model of the sensory networks.

1.2.2   Data Collection

For a long time, studies of collective motion in fish have suffered from a lack of experimental data. These last decades have seen important improvements in computing efficiency as well as in data storage and quality

of video recording. It is thus easier than before to obtain data of collective motion in animal groups and to run computer-intensive simulations of computational models. For instance, the reconstruction of the 3D positions of thousands (up to 2,600) of starlings (*Sturnus vulgaris*) has been done with a stereo-photography method (Ballerini et al., 2008), leading to trajectory reconstruction (Attanasi, Cavagna, Del Castello, Giardina, Grigera, Jelic, Melillo, Parisi, Pohl, Shen and Viale, 2014; Evangelista et al., 2017). This method has also been used with swarms of wild midges ranging in size between 100 and 600 individuals (Attanasi, Cavagna, Del Castello, Giardina, Melillo, Parisi, Pohl, Rossaro, Shen, Silvestri and Viale, 2014).

An important improvement in tracking has recently been achieved (Pérez-Escudero et al., 2014). Common multitracking systems calculate the most likely assignment of identities of individuals by taking into account the previous movements of the animals. These systems generally have problems when two or more individuals cross or touch because it can be difficult to find the correct identities after the point of overlap. The new algorithm suggested by Pérez-Escudero et al. (2014) works by extracting from the video a signature or fingerprint for each individual. These fingerprints are used to identify individuals in each frame, keeping the correct identities even after crossings or occlusions. In contrast to previous methods, this new feature makes the tracking of long videos (e.g. several hours) more efficient with respect to identity matching than before – even if issues of computational time still have to be addressed for large groups (when group size exceeds 20 individuals).

1.3 Propagation of information in animal groups

Several patterns of escape have been proposed as survival strategies when groups of fish are attacked by a predator (Pitcher and Wyche, 1983). Pitcher and Wyche (1983) report manoeuvres observed in schools of sand-eels (*Amodytes* sp.) in response to approaches of mackerel (*Scomber scombrus*). These patterns were called *avoid*, *herd*, *vacuole*, *hourglass*, *split - join* and *flash expansion* (see Figure 1.2). They have also been observed in other species such as herrings (*Clupea harengus*) (Pitcher et al., 1996; Nøttestad and Axelsen, 1999; Axelsen et al., 2001). All these patterns were reproduced by computer-simulations (Inada and Kawachi, 2002; Zheng et al., 2005; Lett et al., 2014). The difficulty in studying collective behaviour under predator threat is not only to explain which collective patterns minimize risks of individuals (assuming that the patterns are not all different outcomes of the same behaviour, as suggested by Axelsen et al. (2001) and
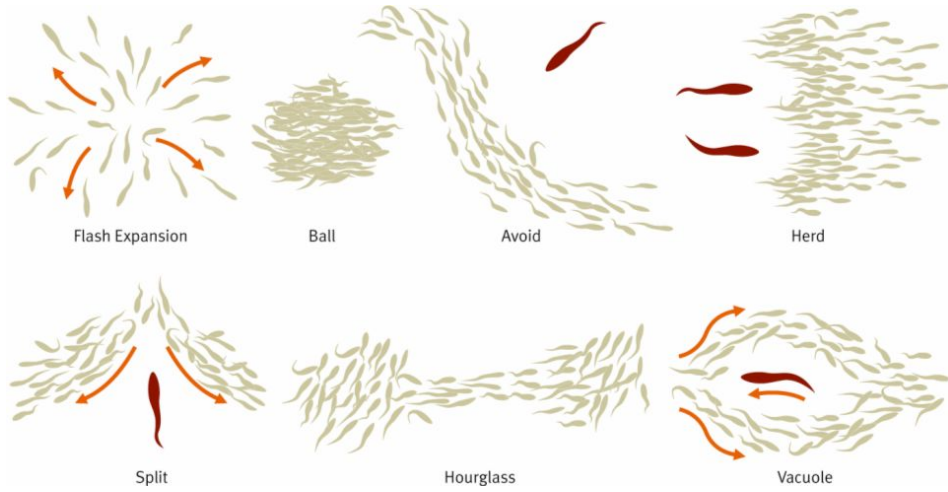
Figure 1.2: Collective responses of fish schools under predator threat (Pitcher and Parrish, 1993). Reproduced from Dugatkin (2013).

Inada and Kawachi (2002)) but also to understand how individuals make their choices according to the local information. This requires to investigate how information is propagated, i.e. which cues are shared, which are the individuals sharing information in a school and to describe how fish react to this information.

Results from laboratory experiments showed that, when a perturbation external to the group is applied (an artificial sound stimulus), schools of herring escape by being aligned with their neighbours and going away from the perturbation (Domenici and Batty, 1994). Two modes occur in the distribution of lags between the emission of the stimulus and the reaction of fish: a short lag for fish close to the stimulus and a long lag for fish distant from it. It was also found that the responses with a long latency were more accurate in responding away from the stimulus. The hypothesis of Domenici and Batty (1994) is that the short latency escapes are responses to the sound stimulus and that the long latency escapes are responses to startled neighbours. As for the latter, individuals can integrate the information from both the sound stimulus and startled neighbours and therefore increase the accuracy of their response by adding to the sensory information received by the sound stimulus the swimming direction of startled neighbours. It seems that, in this case, besides the direct emission of the stimulus, social information is also very important for individuals to make accurate decisions and react collectively. Several authors have investigated the individual-level mechanisms that underlie information transfer.

Besides differences in their results considering the relative importances of alignment, repulsion and attraction forces (which could be dependent on the species, the experimental set-ups or the methods of analysis used), all recent studies agree that the speed of individuals is a key element in the information flow of the undisturbed groups (Katz et al., 2011; Herbert-Read et al., 2011; Gautrais et al., 2012) as well as disturbed ones (Herbert-Read et al., 2015). The interactions between fish and thus the properties of the group change with the ecological context (e.g. feeding vs predator threat) (Schaerf et al., 2017). The information flow in a shoal can also be altered by the composition of the group which depends on parameters such as the age, the sex or the numbers of congeners (Hoare and Krause, 2003; Ward et al., 2017). For instance, in adult guppies, it has been found that novel foraging information spreads at a significantly faster rate through subgroups of females than subgroups of males (Reader and Laland, 2000).

When a flotilla of ocean skaters (*Halobates robustus*) is attacked, individuals increase velocities and rate of turning (Treherne and Foster, 1981). This results in a transition from a state where individuals are aligned and moving slowly to a state where individuals are moving rapidly and randomly. This transition of collective behaviour in reaction to predator threat is thought to have two consequences: confusion of the predator because of unpredictable (*protean*) behaviour and fast and synchronised dispersal of the flotilla. This transmission of predator avoidance within the group was faster than the speed of the approach of the predator. Treherne and Foster (1981) called this fast transfer of information the *Trafalgar effect*.

Social waves called shimmering waves also occur in other groups of animals such as the giant honeybees *Apis cerana*, *Apis florea* and *Apis dorsata*. Hundreds of giant honeybees at the surface of their nest (the *bee curtain*) flip their abdomens upward resulting in impressive waves. This behaviour has been linked to a behaviour of defence against attacks by wasps in the species *Apis dorsata* (Kastberger et al., 2008). Two different effects have been shown by Kastberger et al. (2008): repellence of wasps at a distance of at most 50 cm from the nest and confusion of wasps very close to the nest. The fast propagation of the wave within all layers of the bee curtain is achieved thanks to several mechanisms (Kastberger et al., 2014). Most of the shimmering-active bees were acting in a *bucket bridging*-like manner that is receiving information from a close neighbour at one side and transferring it to a close by neighbour at the other side. A small part (about 15%) of the shimmering-active bees elicits abdominal flipping before any bucket-bridging activity can be detected in their neighbourhood, contributing to a *saltatoric* propagation of the wave by creating a *daughter*

wave. The result of the saltatoric process is to speed up the propagation as well as to facilitate changes of direction. Waves can also occur without predator attack but this results in short waves only (Kastberger et al., 2008).

Waves in presence of predators can also be termed agitation waves when they involve a sudden change of direction from the group motion. Such waves have for instance been described in birds (Procaccini et al., 2011). As for fish, it has been investigated by monitoring anchovy school (*Engraulis ringens*) movements and their reactions to sea-lion (*Arctocephalus australis* and *Otaria byronia*) attacks in Peruvian waters (Gerlotto et al., 2006). The attacks of sea-lions result in waves of agitation expanding in concentric circles around the sea-lions. Gerlotto et al. (2006) show that the signal of these waves is not damped so that the same information (i.e. the direction of the predator) is transmitted through the entire school, resulting in a reorganized collective structure. Although these collective patterns have been reported independently in the field for several species (see for instance Radakov (1973) and Axelsen et al. (2001) who described a pattern called *density propagation* in herrings (*Clupea harengus*)), the behavioural mechanisms used by individuals in fish schools to propagate these signals are poorly understood. Velocity changes of individuals in response to stimuli (i.e. their speed and their direction) without centralised control are assumed to be essential to propagate escape waves (Herbert-Read et al., 2015).

The principles of the social waves described for flotilla of ocean skaters and giant honeybees as a collective pattern emerging from the local interactions between the agents of a system (that is as a self-organizing pattern) have been modelled in many different situations involving a wide range of living systems. In starling flocks, a model suggests that the agitation waves result from the successive changes of orientation of birds performing escape manoeuvres and not from density waves (Hemelrijk et al., 2015). In emperor penguin, a model has been used to describe the waves observed in penguins huddles occurring when penguins form dense clusters of thousands of individuals to protect themselves against cold temperatures and wind (Gerum et al., 2013). In this work, the model assumes very simple interactions between individuals: each individual has a preferred distance from its close neighbours that they are trying to maintain. When a perturbation occurs (e.g. a bird moving forward), it triggers a disordering of the group, each individual moving to recover its preferred distance from neighbours, in the same way drivers behave in traffic jams. This model was able to reproduce the collective properties of the waves observed in

the field, namely the propagation in all directions, suggesting a mechanism that could make huddles merging.

In many cases, a social wave occurs in a group when individuals exhibit a transition from a state **A** to a state **B** (e.g. the direction of motion of the group that changes during a collective U-turn). A simple and common example of such propagation of information is the Mexican wave, "La Ola", that can be seen, for instance, in many stadiums during sport events (Farkas et al., 2002, 2003). These two papers respectively address the propagation and the initiation of these waves by presenting a model combining local and global interactions unfortunately not derived from a fine-grained analysis of empirical data, i.e. not validating the model at each scale of description. In this example, individuals are modelled as transiting from an inactive state (e.g. people watching the game) to an active state (people standing up being involved in the wave). The model shows that triggering a Mexican wave requires a critical mass of initiators. Other biological examples of state transition leading to a social wave are the landing process in birds (Bhattacharya and Vicsek, 2010), the stop-and-go behaviour of sheep (Pillot et al., 2011; Toulet et al., 2015) or the striking synchronized flashing among fireflies such as *Pteroptyx cribellata* (Camazine et al., 2001, chap. 10, for a review).

1.4 Communication in fish schools

When communication and information transfer in fish groups are investigated, it is important to have some idea about what kind of information a fish perceives, for instance, information about the number and identity of the neighbouring fish that can actually interact with a focal fish. The use of social information enables individuals to coordinate their motion as well as to respond to threats without having to verify the presence of danger independently. What follows is a general picture of how environmental cues may be used by fish when they share information. It is likely to vary from one species to another and to depend on the ecological conditions (light exposure, turbidity, presence of obstacles, etcetera) (Hartman and Abrahams, 2000). The internal mechanisms in the fish brains involved in the interactions with congeners (namely the neuronal scale) are beyond the scope of this thesis.

Fish communicate through various signals related to different sensory systems which can be classified as follows, according to Helfman et al. (2009, chap. 6):

1. Mechanoreception

2. Chemoreception

3. Vision

4. Electroreception

5. Magnetic reception

Mechanoreception involves the lateral line and the inner ear. The lateral line permits the fish to detect disturbances in the water such as currents, prey, predators, congeners and obstacles. It is of main importance when considering predator–prey interactions and fish coordinating in a shoal (Partridge and Pitcher, 1980; Faucher et al., 2010; Polverino et al., 2013). The inner ear detects sound in water.

Fish, when inspecting for predators, also rely on chemical substances and visual cues either emitted by the environment (e.g. odour of the predator or visual detection of the predator), or shared (intentionally or not) by congeners (e.g. the chemical alarm substance diffusing from an injured fish or a fish escaping some undetected stimuli with a strong flight behaviour). For instance, although the three-spined stickleback has been classified as a *microsmatic* species that is as a species relying more on vision than on olfaction (Teichmann, 1954; Honkanen and Ekström, 1992), it seems that chemical cues are involved in several processes such as recognition of congeners and foraging (Ward, 2004; Webster et al., 2007). Unlike visual cues, chemical substances might be hard to manipulate for a predator and therefore may be more reliable information for prey (Brown, 2003). However, visual cues, as well as hydrodynamical signals perceived by the lateral line system, are likely to propagate much faster than chemical cues through a shoal (Hunter, 1969; Brown and Laland, 2003). Therefore, it is commonly suggested that the key systems actually used by fish to coordinate their motion are Mechanoreception and Vision.

1.5   Thesis overview

In this thesis, I have investigated the behavioural mechanisms underlying the coordination of motion and the propagation of information in schools of a gregarious fish, the rummy-nose tetra (*Hemigrammus rhodostomus*). This small freshwater fish (mean body-length of $\sim 3\,$cm) lives in the Lower Amazon River basin in Pará State (in Brazil) and Orinoco River basin in Venezuela (Reis et al., 2003) (Figure 1.3). The *Hemigrammus* taxon is assumed to be non-monophyletic (Marcos Mirande, 2009) and includes 51 species throughout South America (Carvalho et al., 2010). Little has
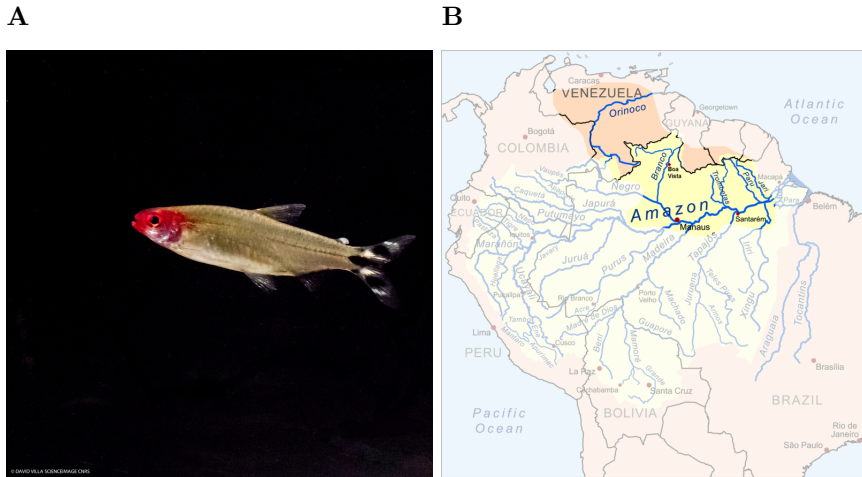
A

B

Figure 1.3: A). Photograph of a rummy-nose tetra (*Hemigrammus rhodostomus*) kept in our laboratory. Credits to David Villa ScienceImage/CBI/CNRS, Toulouse. B). Map of the distribution of the rummy-nose tetra (highlighted regions, that correspond to the Orinoco river basin and to the lower Amazon river basin). Adapted from a map made by the user Kmusser on Wikipedia and shared with a CC BY-SA 3.0 licence.

became known about this species since its discovery in 1924 (Ahl, 1924), especially regarding its ecology, despite its success for aquarists. This success in fishkeeping is likely to be the result of the coordination seen in the schools of *H. rhodostomus* (Figure 1.4). Only a few papers have studied the *Hemigrammus* taxon beyond taxonomy and phylogeny. It has been shown in *Hemigrammus bleheri* that the lateral line was essential to the shoaling behaviour (Faucher et al., 2010). How *H. bleheri* swims in pairs or in trios when facing a water flow has also been investigated (Ashraf et al., 2016). The choice of *H. rhodostomus* as a model species in our research is supported by (i) their schooling behaviour being obligate, (ii) the ease of buying them (from standard pet shops) and (iii) the ease of keeping them in our facilities.

This thesis will follow an approach based on a tight combination between experiments and modelling to connect individual and collective levels (Camazine et al., 2001; Sumpter et al., 2012; Weitz et al., 2012) that was already initiated by the team in Toulouse (Gautrais et al., 2012; Lopez, 2015). This methodology consists in, given a global pattern, to first focus on experimental observations at the individual level. The findings that, for instance, concern the interactions between animals, are incorporated into

Figure 1.4: A polarised school of swimming rummy-nose tetras. Credits to David Villa ScienceImage/CBI/CNRS, Toulouse.

data-driven models whose predictions are tested against experimental data at the collective level.

1.5.1 Part I: What are the individual-level interactions and behavioural rules that give rise to coordinated swimming

Part I (Chapters 2 and 3) is dedicated to the behavioural mechanisms that underlie the coordinated swimming in schools of *H. rhodostomus*.

In Chapter 2, we focus on the motion of a single individual and pairs of individuals swimming freely in a circular arena. Fish have been monitored while swimming in circular arenas of different radii. *Hemigrammus rhodostomus* has a burst-and-coast swimming behaviour. This swimming behaviour consists of cyclic bursts of swimming followed by a coast phase in which the body is kept motionless and straight. It is thought to provide hydrodynamic efficiency (Weihs, 1974; Videler and Weihs, 1982). The discretisation of the trajectories on the basis of this intermittent swimming mode drove the analysis of experimental data and the modelling. We developed a new method to measure and disentangle the interactions between a fish and the wall and between pairs of fish and tested these findings in a model. In particular, our findings strongly support the presence of an explicit alignment interaction.

Chapter 3 addresses specifically the question of the integration of information from multiple sources. This issue has rarely been explored in pre-

vious studies and current models usually assume reactions averaged over pairwise reactions computed with respect to each separate stimulus, possibly weighted, e.g., by the distance to the stimulus – at the notable exception of (Collignon et al., 2016). As for the latter, the authors develop an interesting hypothesis where fish react by sampling one turning angle from the sum of the probability density functions of turning angles measured in reaction to each stimulus. Unfortunately, their model does not test the hypothesis specifically and many assumptions (with possible confounding effects) are tested at the same time. We develop a method based on experimental data to test hypotheses regarding the integration of stimuli from multiple sources and we investigate a simple hypothesis in which fish react only to the strongest stimulus we assume they perceive. The method is tested with experimental data in a ring-shaped tank with non-social stimuli (the walls of the corridor) and social stimuli (in groups of 2 and 5 fish). We find that the hypothesis that fish would react only to the strongest stimulus is not sufficient to reproduce the global properties found in experiments with 5 fish, suggesting that fish integrate more information.

1.5.2 Part II: How does information propagate in groups of fish in response to perturbations?

Part II (Chapters 4 and 5) aims to analyse and characterise the propagation of information in schools of *Hemigrammus rhodostomus*, in reaction to *internal* and *external* perturbations. *Internal* and *external* perturbations here refer to whether the stimuli are respectively elicited by a group member or not (e.g. a green light).

In Chapter 4, we analyse and model the propagation of information in response to internal perturbations, i.e. spontaneous collective U-turns occurring in a ring-shaped tank. The global properties of the propagation are characterised from experimental data in group sizes ranging from 1 to 20 fish. We formulate a theory-driven local to global model to explain the main properties of the collective patterns observed. Our model is inspired by the Ising model first suggested in statistical physics to describe ferromagnetism – and one of the simplest statistical models to show a phase transition in 2D (Brush, 1967). The main interest of the model is to show that social conformity is a possible mechanism to explain both the dynamics observed during the collective U-turns and the effect of the group size on the frequency of the collective U-turns.

Chapter 4 is thus a benchmark of the spatio-temporal dynamics of the propagation of information in response to internal and spontaneous perturbations in *Hemigrammus rhodostomus*. In Chapter 5, we develop an

experimental method to induce controlled external perturbations in order to investigate the propagation of information in this context. In particular, we conduct a preliminary study showing that aversive conditioning can (i) be used in this species, (ii) trigger collective escape reactions and (iii) be transferred from the conditioning set-up to another experimental set-up. We characterise the aversive conditioning and discuss long-term habituation and forgetting. We discuss these preliminary results in the context of propagation of information in reaction to external stimuli (here, a green light that elicits an escape reaction in conditioned fish). Our findings suggest that the proportion of conditioned individuals in a group is critical to trigger collective escape reactions in response to external stimuli. Our experimental results open promising possibilities regarding the use of conditioning experiments to investigate collective behaviour in fish and the propagation of information within groups in response to perturbations mimicking predatory perturbations in particular.

1.5.3   Appendices

The experimental work conducted in this thesis has been used in two other collaborations summarised in the appendices of the manuscript. In Appendix A, a framework based on Information Theory is used to quantify the dynamics of information transfer in school of fish. This method measures informative and misinformative flows and their spatio-temporal properties during the collective U-turns that occur in the ring-shaped tank. In Appendix B, the identity and respective influences of the neighbours of a focal fish are analysed by studying the short-term directional correlations between their trajectories.